Mary Lee Abshire Jensvold, Ph.D.
Editor

Chimpanzee Behaviour

Recent Understandings from Captivity and the Forest

ANIMAL SCIENCE, ISSUES AND RESEARCH

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MARY LEE ABSHIRE JENSVOLD
EDITOR

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PREFACE

The chapters in this edited volume discuss recent findings and views on chimpanzee behaviour. With dwindling numbers in the forests of Africa and burgeoning numbers in captivity, chimpanzees, as a species, are in a critical place in time. Free living communities of chimpanzees live with cultures and ways of doing that are unknown to humans, but essential to the lives of each community member. These cultures and those who live in them are disappearing at an alarming rate. Meanwhile, in North America and Europe chimpanzee research has ended, leaving hundreds of chimpanzees waiting for sanctuary placement. Zoos continue to bring new chimpanzees into captivity. A diaspora, captive chimpanzees have no possibility in life except captivity with its contrived communities and broken cultures. We can use what we have learned from chimpanzees to improve their care.

The Chimpanzee & Human Communication Institute (CHCI) at Central Washington University was the home of Washoe and her family of signing chimpanzees from 1980 - 2013. A sanctuary for chimpanzees, this institute was a leader in humane noninvasive behavioral studies, compassionate and chimpanzee centred care, and a training ground for young primatologists. This book brings together some of what transpired in those walls. Most of the chapters are authored by students of CHCI, myself included.

Chapter authors Cleve Hicks (Chapter 1) and Crickette Sanz (Chapter 2), now with field sites of their own, received graduate training while caring daily for this group of chimpanzees. The lessons they learned there are reflected in their chapters through observational research and insight into the significance of the behaviors they observed in the forest. Gestures were a fundamental aspect of the communication research at CHCI. Catherine Hobaiter (Chapter 3) expands on concepts, themes, and future direction in studies of gesture from the forest.

Sign language studies in Allen and Beatrice Gardner's cross-fostering laboratory at University of Reno Nevada were rooted in ethology and experimental psychology. This approach was the foundation of Roger and Deborah Fouts' approach at CHCI and earlier work at the Institute for Primate Studies at University of Oklahoma. These unique projects allowed a view like no other into chimpanzee perception and experience. From these projects were archival products of the chimpanzees' days, including artwork and records of sign language output. Alexandra Casti and Jessica Martinson (Chapter 4) used artwork for thesis research while at CHCI. Chapter 5 compares patterns of signing from CHCI to recent patterns at Fauna Foundation. Signing chimpanzees can tell us what they are thinking. This leads us to deeper questions of ethics and how we care for chimpanzees. Chapter 6 suggests ways to care for chimpanzees that are informed by the decades of care for Washoe and her family, and by those who care for them.

Friends of Washoe, a non-profit organization has a mission to support Washoe and her family; to study communication and ways to improve captive conditions for all apes; and to promote peaceful coexistence between human and non-human animals through education and awareness. This book would not have been possible without support from Friends of Washoe. Central Washington University provided support, as well as Fauna Foundation in Carignan, Quebec. Carolyn Yates provided copy-editing services. Finally, but most importantly, my deepest gratitude lays with chimpanzees, for letting me and others watch. Hopefully what we learn we can use to improve conditions for you in the forest and in captivity.

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Chapter 1

HANDLING AND CONSUMPTION OF VERTEBRATE PREY BY CHIMPANZEES (*PAN TROGLODYTES SCHWEINFURTHII*) IN THE NORTHERN DEMOCRATIC REPUBLIC OF THE CONGO

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ABSTRACT

We present direct and indirect evidence for predation on vertebrates by Eastern chimpanzees (*Pan troglodytes schweinfurthii*) at two sites in the northern Democratic Republic of the Congo: Bili-Uéré and Ituri, which are part of one of the largest and most interconnected chimpanzee populations in Africa. In this chapter, we provide the first data on chimpanzee prey preferences in the region, which at Bili-Uéré includes direct evidence for consumption of a leopard (*Panthera pardus*) and indirect evidence for consumption of a tree pangolin (*Phataginus tricuspis*) and two tortoise species of the genus *Kinixys*. In the Ituri Forest, we describe a direct observation of chimpanzees guarding and probably consuming the carcass of an okapi (*Okapia johnstoni),* likely pirated from a leopard, as well as indirect evidence of tortoise consumption. Further east in an Ituri forest fragment, we recorded an adult female chimpanzee carrying the carcass of a galago, probably *Galagoides thomasi,* although we did not confirm consumption. Altogether, these observations give us a portrait of a chimpanzee population with an unusual selection of vertebrate prey.

Keywords: Northern Democratic Republic of Congo, Eastern chimpanzees (*Pan troglodytes schweinfurthii*), faunivory on tetrapods

INTRODUCTION

Free-living chimpanzees (*Pan troglodytes*) have been observed to hunt for vertebrate prey across their range in Africa (reviews in Wrangham & Riss, 1990; Stanford, 1998; Uehara, 1997). Red colobus monkeys (*Piliocolobus* spp.) are chimpanzees' preferred prey wherever these two primate species occur together across Africa (Boesch, Uehara, & Ihobe, 2002; Stanford, 1998; Watts & Mitani, 2002). Nevertheless, chimpanzee prey preferences appear to vary somewhat between sites; for instance, galagos appear in the diet at Fongoli, Senegal (Pruetz & Bertolani, 2007) and giant forest squirrels and hyraxes are eaten at Mahale, Tanzania (Kawanaka, 1982). Researchers found clear differences in prey species preferences between neighbouring communities in Budongo, Uganda (Hobaiter, Samuni, Mullins, Akankwasa, & Zuberbühler, 2017), and some populations even prefer different age classes of the same prey species (Boesch & Boesch-Achermann, 2000). Some of this variation may be explained by differences in prey availability (e.g., red colobus are absent at Budongo and thus not hunted; Newton-Fisher et al., 2002) or in forest structure (Boesch & Boesch-Achermann, 2000), but considering the extraordinary variety of traditions found in chimpanzees across Africa (Whiten et al., 2001), there is likely a cultural component to prey selection as well (Hobaiter et al., 2017).

In this chapter, we present evidence for several cases of inferred or observed consumption of vertebrates by chimpanzees living in the forests of northern Democratic Republic of Congo (DRC). We also describe one case of a chimpanzee handling a dead galago. Previously, consumption of noninsect meat by chimpanzees has not been reported from this area. As red colobus are absent from forests north of the Uele River (Hicks, 2010), it is important to know which, if any, of the potential vertebrate prey species there chimpanzees might consume instead.

Of particular interest in the current chapter are two observed cases involving chimpanzees and leopards (*Panthera pardus*), one at Bili-Gangu and one at Ituri. Across Africa, chimpanzees have a complex relationship with leopards; in some cases they fall prey to them (Taï Forest, Côte d'Ivoire: Boesch & Boesch-Achermann, 2000; Mahale: Nakazawa, Hanamura, Inoue, Nakatsukasa, & Nakamura, 2013), but they have also been seen to direct aggression towards these big cats (Taï Forest: Boesch, 1991), in one case using a branch to repeatedly jab at a leopard hiding in a hole (Boesch, 2009). Similar encounters have also been described at Gombe, Tanzania (Goodall, 1986). In one dramatic episode at Mahale, a group of 33 chimpanzees were observed attacking an adult leopard and a cub inside of their den, finally snatching and killing, but not eating, the cub (Hiraiwa-Hasegawa et al., 1986). In Beni, DRC, Kortlandt (1967) observed and photographed free-living chimpanzees mobbing and throwing sticks at a stuffed leopard in a semiexperimental setting. Our observations at Bili and Ituri add even more complexity to this contentious relationship between carnivore and predatory primate.

METHODS

Study Sites

Bili-Uéré

Northern DRC is home to a large and continuous population of Eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Hicks et al., 2014). The first author, T. Hicks (TH), conducted the Bili Chimpanzee Research Project, an in-depth study of chimpanzee material culture in the Bili-Uéré region (Figure 1), between 2004 and 2016 (Hicks, Kühl, et al., 2019; see Hicks, 2010, for a detailed description of the study region). TH and team made over 100 contacts with the apes, as well as a number of direct observations (Hicks, 2010; Hicks, Roessingh, & Menken, 2012). They systematically recorded all items of food, plant or animal, directly observed to be eaten by chimpanzees, as well as feeding remains (Hicks, 2010), in the context of following the chimpanzees and recording their behaviour. Whenever the team observed evidence of meat-eating, they also recorded GPS waypoints, the age and sex of the chimpanzees involved if known, and the duration of the incident. The team photographed and collected remains of any animal carcasses thought to have been eaten by chimpanzees and identified them using *The Kingdon Field Guide to African Mammals* (Kingdon & Largen, 1997). C. Stanford of the University of Southern California and D. Lawson of Collections, Education, and Conservation, Zoo Atlanta, identified the tortoise species potentially pounded open by the chimpanzees. The team also inspected fresh chimpanzee dung samples for signs of animal remains (for details, see Hicks, 2010; Hicks, Kühl et al., 2019).

In addition, as TH and team walked along recces and transects at different study sites both to the north and south of the Uele River, they recorded the presence of nonhuman primates, other mid- to large-sized mammals, and, more opportunistically, small mammals and tortoises. For more details of the individual study regions, and the survey methodology, including kilometres walked, see Hicks (2010) and Hicks (2014). Over an 8-month period from 2012 to 2013, K. Dierks of the PanAfrican project set out 23 camera traps across a 7 x 3 km grid system in the Gangu Forest to record the passage of terrestrial animals (Hicks, 2014), providing more detail on species presence and abundance in this region.

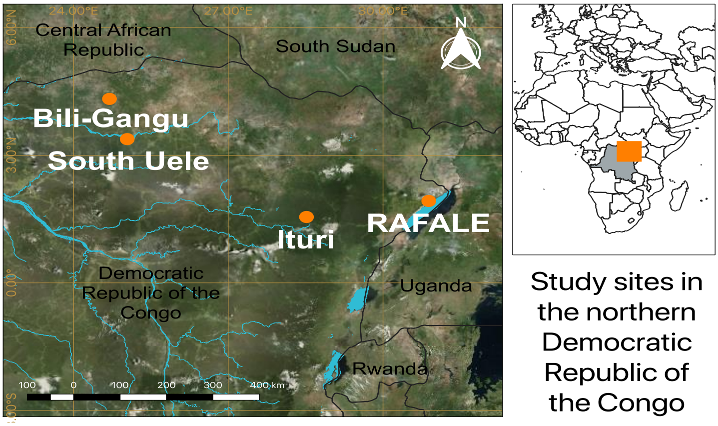


Figure 1. Map of the Democratic Republic of Congo (DRC) with and the North and South Uele regions, the Ituri Forest (at the Afarama Research Camp) and the Relict Altitude Forests of the Albert Lake Escarpment (RAFALE) forest fragments highlighted. Grey represents savanna-associated habitat.

As described in detail below, in September 2006 Ligada Faustin (LF), the Bili Chimpanzee Research Project's most experienced local Zande assistant, observed a case of a chimpanzee consuming a leopard carcass. LF had worked for the project for several years prior to TH's involvement. He received extensive training in basic data collection from TH during the 2004-2005 field season, including how to use a GPS, collect dung and hair samples from chimpanzee nests, use a camera to record behaviors, and accurately record data in a notebook in French. LF frequently led teams to contact chimpanzees and recorded data using a camera, notebook, GPS, and watch.

Ituri Forest

The Ituri Forest, located in northeastern DRC between 0 and 3 degrees north latitude and 27 and 30 degrees east longitude (Figure 1), is also inhabited by Eastern chimpanzees. John Hart (JH) conducted research on the ecology of the Bambuti foragers there between 1973 and 1976 (Hart, 1979). He and Terese Hart then conducted research on the fauna and flora in Ituri between 1980 and 1983 (Hart & Hart, 1989; Hart, 1995). Between 1985 and 2007, they regularly conducted wildlife surveys for the Wildlife Conservation Society from their bases in forest camps such as Afarama (Hart et al., 2008). They were aided in their data collection by Bambuti and other local Congolese. They also accompanied Bambuti foragers on hunting and gathering expeditions in the context of studies of the Mbuti hunting economy (Hart & Hart, 1986). These surveys allowed the Harts to make reserve-wide assessments of large mammals and human impact. Part of this work involved surveying for chimpanzee nests (Grossman, Hart, & Dino, 2006; WCS, 2008). Although the Harts did not conduct systematic surveys for chimpanzee artifacts nor did they analyze dung samples for dietary content, they did note any interesting predation events they happened to observe.

RAFALE (Ituri Fragments)

In 2015, Anne Landisoit (AL) identified an isolated population of Eastern chimpanzees in high-altitude forest fragments along the Relict Altitude Forests of the Albert Lake Escarpment (Figure 1; for more details about the study region, see Laudisoit et al., 2016; Huyghe, 2017; Scholier, 2017). RAFALE consists of 16 fragments, covering a total of approximately 65 km², scattered over the steep slopes of the Lendu plateau (800 m to 2000 m asl) and along the Albert Lake Escarpment (SW: 1°35.2’N, 30°36.27’E, to NE: 2°01.49’N, 30°54.01’E). The landscape is dominated by secondary riverine forests clustered around rapidly flowing rivers that form a discontinuous mosaic interspersed with subsistence agricultural land (e.g., maize, cassava, beans, and sorghum). Between March 2016 and June 2017, AL carried out four exploratory expeditions in three fragments (gross combined surface area: 18.15 km²) to document the flora and fauna via recce surveys, linear transects, camera trap inventories, and live observations. Chimpanzee density was estimated at 3.8 ind./km² within the fragments, with nest sites generally found at high, steep locations (Huyghe, 2017).

In 2017, AL and team analyzed 46 fresh and dry dung samples from recce walks and transects in the three RAFALE forest fragments, including at chimpanzee nest sites. They placed the dung in individual plastic bags and washed it over a fine mesh tray with clear water (McGrew, Marchant, & Phillips, 2009; Tutin & Fernandez, 1993), drying and storing seeds and other nonvegetable material for later identification. AL also filmed interviews with villagers who recounted their observations of chimpanzees and other wildlife, and filmed chimpanzee behaviours whenever possible with handheld cameras or cameras traps. Between March 2016 and June 2017, she collected approximately six hours of camera trap footage from 48 cameras that covered an area of 18 km^2.

RESULTS

Bili-Uéré, Northern DRC

Fecal Analyses

TH's team conducted dung washes on 46 chimpanzee dung samples from 33 localities, including nest groups, at Bili-Gangu during the 2004-2005 field season. None contained the remains of noninsect animal prey. The same was the case for the 21 dung samples washed by the PanAfrican team at Bili in 2012 (see Hicks, Kühl et al., 2019).

Presence/Absence of Potential Vertebrate Prey

We documented potential vertebrate prey occurring at the study sites (see table 1). For site waypoints and more details about each, see Hicks (2010; 2014); for the Ituri fragments, see Scholier (2017). Failure to document a particular species does not necessarily mean it was not present, just that we found no evidence for it. In some cases, however, such as the lack of red colobus and okapi at all sites north of the Uele River, we are unlikely to have missed a species if it were present.

Table 1. Confirmed Presence of Potential Chimpanzee Vertebrate Prey at Different Survey Areas

Site	Lp	Ok	Yb	Bd	By	Od	Rr	Lp	Tp	**Rc**	**Rt**	**Cg**	**Gc**	**Bb**	**Am**	**Gm**	**Dm**	**Db**	**Pn**	**Pm**	**Bm**	**Gd**[a]	**Gt**[a]	To
N Uele region																								
CampLouis	x		x	x	x	x	x		x		x	x	x	x	x	x		x		x		x	x	
Gangu	x		x	x	x	x	x		x		x	x	x	x	x	x		x	x					x
Bili S	x		x	x	x		x				x	x	x	x	x	x		x						
Zapay			x	x	x		x				x	x	x	x				x		x				
Gbangadi	x		x	x	x	x	x				x	x	x	x	x	x								
Bambillo	x		x	x	x	x	x				x	x	x		x	x		x						x
Dume	x		x	x	x	x	x				x	x	x	x	x			x						x
S Uele region																								
Lebo	x			x			x				x			x	x		x	x						
Lingo				x			x			x	x	x	x		x	x								
Zongia	x	x	x	x	x		x			x	x	x	x	x	x	x		x	x					x
Leguga		x		x	x	x	x				x	x	x	x	x	x		x	x					x
AkumaYo			x	x	x		x			x	x	x			x	x	x	x	x					
MbangeW		x		x	x			x		x	x		x	x	x	x			x					x
MbangeE	x	x			x		x		x	x	x	x	x	x	x	x		x	x					x
Bambesa	x			x	x		x				x	x		x	x	x		x						x
Buta											x						x							
Site	Lp	Ok	Yb	Bd	By	Od	Rr	Lp	Tp	**Rc**	**Rt**	**Cg**	**Gc**	**Bb**	**Am**	**Gm**	**Dm**	**Db**	**Pn**	**Pm**	**Bm**	**Gd**[a]	**Gt**[a]	To
Ngume	x	x	x	x	x				x	x	x	x		x	x	x								x

Ituri region																								
Afarama[b]	x	x	x	x	x	x	x	x	x	x	x		x[d]	x	x	x	x	x			x			x
RAFALE	*[c]					x		x	x	x	x	x	x	x		x					x		x	

Note. Species (sympatric primates appear in bold): Lp = Leopard (*Panthera pardus*), Ok = Okapi (*Okapia johnstoni*), Yb = Yellow-backed duiker (*Cephalophus silvicultor*), Bd = Blue duiker (*C. monticola*), By = Bay duiker (*C. dorsalis*), Od = other duiker (*Cephalophus* spp.), Rr = Red river hog (*Potamochoerus porcus*), Lt = Long-tailed pangolin (*Phataginus tetradactyla*), Tp = Tree pangolin (*P. tricuspis*), **Rc** = Red colobus (*Piliocolobus oustaleti*), **Rt** = Red-tailed guenon (*Cercopithecus ascanius*), **Cg** = Crowned guenon (*C. pogonias*), **Gc** = Guereza colobus (*Colobus guereza*), **Bb** = Olive baboon (*Papio anubis*), **Am** = Agile mangabey (*Cercocebus agilis*), **Gm** = Grey-cheeked mangabey (*Lophocebus albigena*), **Dm** = Dent’s monkey (*C. denti*), **Db** = Debrazza’s monkey (*C. neglectus*), **Pn** = Putty-nosed monkey (*C. nictitans*), **Pm** = Patas monkey (*Erythrocebus patas*), **Bm** = Blue monkey (*C. mitis*), **Gd** = Prince Demidoff’s galago (*Galago demidovii*), **Gt** = Thomas’s dwarf galago (*Galagoides thomasi*), To = tortoises of the genus *Kinixys*. Sources: North Uele and South Uele regions: T. Hicks (2010), Hicks (2014), Hicks (2019); tortoises and smaller duikers: Hicks (2019). (Days at site looking for primates: Camp Louis: 284, Gangu: 190, Bili South: 43, Zapay: 8, Gbangadi: 6, Bambillo: 9, Dume: 15, Lebo: 24, Lingo: 9, Zongia: 8, Leguga: 14, Akuma-Yoko: 10, Mbange West: 9, Mbange East: 15, Bambesa: 13, Buta: 3, Ngume: 8). Ituri Forest, Afarama: primates: Thomas (1991); tortoises: Hart (2019); okapi: Hart & Hart (1989); other fauna: Hart et al. (2008); pangolins: Makana, Madidi, & Bikumbu (2006), Arioti (1985). The Harts spent years at this site. RAFALE (Ituri fragments): A. Laudisoit (2019; all from camera traps or live observation); Scholier (2017). Note that this table is not comprehensive and includes mostly small- to mid-sized mammals known to be eaten by chimpanzees here or elsewhere, as well as tortoises of the genus *Kinixys*. The lack of an x in a cell does not mean the species is absent, just that we found no evidence for its occurrence. Chimpanzees were present at all of the sites. Nonprimate savanna species such as warthogs and bushbucks (both present at Bili) are not included here as we have little evidence of the chimpanzees visiting the savannas. Larger species omitted here such as giant forest hogs and forest buffalo are present north and south of the Uele (Hicks, 2010) and also at Ituri (Hart et al. 2008). For North and South Uele kilometres walked per survey and time in each forest, see Hicks (2010; 2014). [a]In 2005, TH filmed a group of three Thomas’s dwarf galagos in gallery forest in the Camp Louis site (N 4º21’72,” E 24º56’72”) (identified by Simon Bearder, personal communication, 10 December 2013). In 2001, T. Butynski recorded the vocalizations of Prince Demidoff’s galagos at Camp Louis (T. Butynski, personal communication, 2 January 2014), which Bearder also identified. [b]Also present here are L'Hoest's monkey (*Cercopithecus l’hoesti*) and Hamlyn's monkey (*C. hamlyni*), omitted from this table in the interests of space. [c]RAFALE: Leopards are reported from the Dzoo Forest (N 1°55’37,” E 30°53’21”) but have become rare, with the last sighting by locals in 2015. [d]Angola colobus (*Colobus angolensis*) are present in the Dzoo forest as well.

Tree Pangolin (*Phataginus Tricuspis*)

Availability of Tree Pangolins in Northern DRC

We documented the presence of tree pangolins at several sites in northern DRC (table 1). The abundance of this cryptic, nocturnal species is difficult to estimate in the forests of Bili. We saw none on the transects, although we found the tracks of the more conspicuous giant pangolin (*Smutsia gigantea)* four times, and we also found the skeleton of one in 2012. We saw tree pangolins as bushmeat on several occasions in the town of Bili, usually in smoked form.

Evidence for Consumption of a Tree Pangolin, Gangu Forest (North Uele), 2005

On 30 June 2005, TH and team were nearing the end of our third 55-km transect through the remote and pristine Gangu Forest (Hicks, 2010). The chimpanzees in this area, 40 km from the nearest road or village, showed naïve behaviour toward humans (Hicks et al., 2012). Through the night and into the day, we had been listening to a large group of the apes pant-hooting and tree-drumming nearby. Drawn forward by more tree drums, screams, and pant-hoots from approximately 50 m south, we (TH, LF, and tracker Mbolibie) left the transect to make contact at 14:18 hours, soon encountering a chimpanzee footprint and fresh dung and feeding remains at a *Parinari excelsa* tree. We continued to move towards the intermittently vocalizing chimpanzees. At 15:44 hours, in the midst of a volley of pant hoots from many different individuals, we heard a large chimpanzee running on the ground, barking, screaming, and apparently attacking a shrieking individual. We advanced towards these sounds and on the ground in dense forest (4°16.46’N, 24°37.61’E) we encountered the freshly-killed carcass of a tree pangolin (*Phataginus tricuspis*) (Figure 2a). Screams and chasing sounds continued 25 m south, and I (TH) followed these retreating sounds 150 m southwest, making visual contact with four chimpanzees (an adult male, an adult female, and two juveniles) engaged in tool-assisted predation on *Dorylus kohli* ants, i.e., ant-dipping. Following the contact (described in detail in Hicks, 2011; Hicks, Kühl, et al., 2019), we returned to examine the dead pangolin. Thirty-seven cm southeast of the carcass was a fresh 17.5 x 13 cm chimpanzee footprint (Figure 2b), indicating that the chimpanzees we had heard earlier at that spot were likely responsible for the damage to the carcass. A few metres from the pangolin was an abandoned anthill that appeared to be hand-excavated minutes earlier by the chimpanzees. The head, limbs, intestines, and inner body wall of the pangolin had all been consumed, leaving only the scaly carapace (73 x 13 cm) and tail (41.5 x 8 cm at base) relatively intact. The inner body wall had been scraped with teeth, and a small piece of meat had been chewed off the tip of the tail. A leopard would likely have consumed the entire pangolin carcass, scales and all, consistent with the pangolin scales we often found in leopard and hyena dung. We saved the pangolin carcass and smoked it back at camp. Its remains bore a striking resemblance to the carcass of a pangolin consumed by chimpanzees in the forest of Bossou, Guinea (Sugiyama & Koman, 1987).

On 14 January 2007, also in the Gangu Forest, we found another tree pangolin that had been partially consumed in a nearly identical way. The age of the specimen, however, made it impossible to determine whether or not chimpanzees had been responsible.

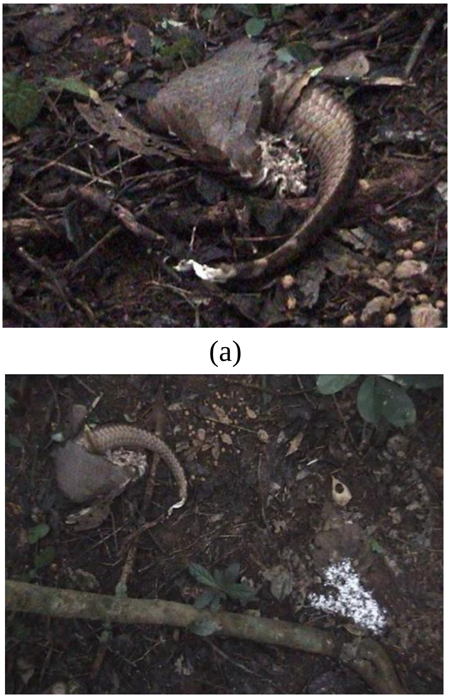
Tortoises (Genus *Kinixys*)

Tortoise Availability in Northern DRC

Although they are found at a number of sites in northern DRC (table 1), tortoises do not appear to be particularly common in the region. During the 2004-2005 field season at Bili-Gangu, TH found only two on the 160 km of transect walked, and none during the 2006-2007 season. They likewise appeared to be rare in forests south of the Uele River.

First Evidence for Consumption of a Tortoise, Bili (North Uele), 2005

On the morning of 27 March 2005, TH and team were moving along a transect through dense, rocky forest on a hillside emerging from a stream valley. At 10:45, tracker Garavura spotted a smashed tortoise shell lying on the transect at 4°22.071’N, 24°45.716’E. The shell had been split in half, leaving only one of the halves at the site, and was surrounded by scales which had been detached from the shell. The shell appeared to have been fractured by an impact against a hard object, leaving a square-shaped gap on the surface. One rotting leg with meat still attached and a hip bone remained inside the shell (Figure 3). From the putrefied condition of the leg, the carcass appeared to date from between one and two weeks past. Half a metre north, a cracked scale from the shell lay on the surface of a rock, and beside the rock was tortoise dung, apparently flung from the tortoise when it was slammed against the rock. C. Stanford and D. Lawson would later identify the tortoise from photographs of its shell as a Bell’s hinge-back tortoise *(Kinixys belliana).*



(a)

(b)

Figure 2. (a) The remains of a tree pangolin (*Phataginus tricuspis*) apparently consumed by a chimpanzee. (b) The researchers found a chimpanzee footprint 37 cm southeast of the freshly-consumed pangolin (powdered for the photograph to make it stand out).

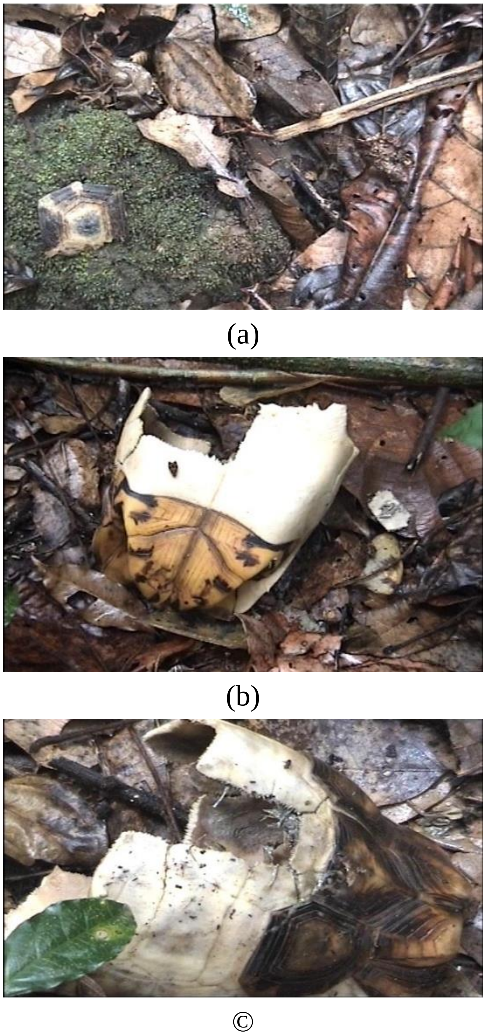


Figure 3. Three images of the smashed Bell’s hinge-back tortoise (*Kinixys belliana*) found at Bili. (a) Scale on a rock next to the shell, with tortoise faeces and innards beside the rock. (b) The shell as originally found. (c) Here, we had flipped the shell over and photographed its top.

Thirty-five metres northeast of the pound site was an old chimpanzee tree nest, and two days later we would find fresh chimpanzee dung 300 m west. In addition, nine days earlier and 200 m northwest, local assistant Makassi Constant had made contact with at least six chimpanzees. Clearly the apes visited this area frequently. Given the proclivity of northern DRC chimpanzees for pounding open other food sources such as termite mounds, fruits, and apparently giant snails (Hicks, Kühl, et al., 2019), the likely culprit in this case was a chimpanzee as well.

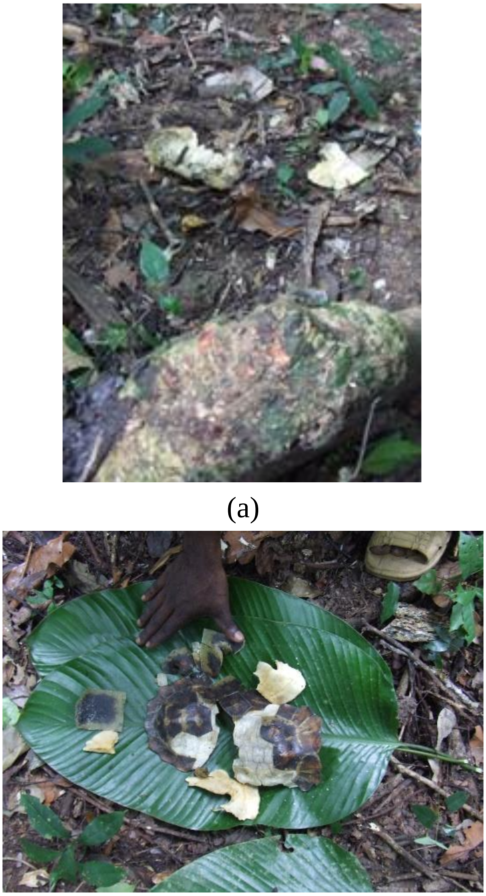
During TH’s first months at Bili, prior to the incident described above, several local project assistants claimed that the chimpanzees frequently smashed tortoises against rocks and ate them. When the survey team traveled to the village of Lebo over 100 km south, TH asked the locals which animals were eaten by the chimpanzees. Several responded with the word *kobá* (tortoise in Lingala), and mimicked how the chimpanzees would smash the animals against rocks. Villagers in other remote settlements described, unprompted, the same behavior, although a variant described from south of the Uele River involved chimpanzees rubbing the bottom of the tortoises’ shells to force them to emerge, at which point the chimpanzees would eat them.

Evidence for Consumption of a Second Tortoise, Leguga (South Uele), 2008

On 25 March 2008, TH recorded a second tortoise (*Kinixys erosa*) pound site in the forest of Leguga, south of the Uele River, at 3°22.872’N, 25°02.585’E. Unlike the case at Bili, this site was linked to multiple items of fresh chimpanzee evidence.

On 24 March, in the village of Leguga, we were alerted to a tortoise pound site by a villager, Alphonse, who had assisted us in our chimpanzee surveys two weeks before. Three days earlier, having heard chimpanzee pant-hoots at 3:00 and 6:00 hours, he had walked towards the sounds and observed chimpanzee signs from the forest trail. He followed the tracks to a pounded tortoise, which at that time still contained some meat.

On the morning of 25 March, Alphonse and two other locals led us down the trail to the site. Approximately 800 m east of the main village road, and 25 m from the trail, I (TH) observed the tortoise, which indeed had been pounded open upon the buttress of a tree (Figure 4). The site was found near an agricultural clearing, which we were told the chimpanzees sometimes visited, allegedly to eat pineapples. We were approximately 1 km west of a group of chimpanzee tree nests and artifacts that Alphonse had shown us two weeks before. The men accompanying us told us that earlier that morning they had heard chimpanzees pant-hooting nearby to the west.



(a)

(b)

Figure 4. (a) The smashed *Kinixys erosa* shell found in the Leguga Forest. Notice the bruising on the buttress of the tree. (b) Here we have gathered the shell fragments onto a leaf.

The pounded tortoise was several days old. There was no flesh left in the tortoise shell, and millipedes were crawling around inside. The carapace, originally 22 x 12 cm, was split in two, and had been pounded against the 51-cm-high buttress of an *ekoya* tree 42 cm north. The tree buttress was scarred with bruises across a 6 x 4.5 cm area; within this space were six separate smaller strike marks. A piece of bone which had splintered off and been flung from the shell lay 7 cm away. Between the tree buttress and the breast bone of the tortoise lay numerous fragmented scales, and beneath the shell lay another shattered scale.

Seventeen metres from the smashed turtle was a flimsy 5.5-m-high day nest, also a few days old. At the same site, we found two stick probes thrust into what appeared to be insect mounds and apparent digging marks made by the chimpanzees in the dirt.

Leopard (*Panthera Pardus*)

Leopard Availability at Bili

Leopards appeared to be common in both the Camp Louis and Gangu Forests, frequently visiting the research camps in both of these regions (Hicks, 2010). TH encountered their tracks six times on 160 km of transects walked in 2005, and their tracks, kills, and dung 12 times on 821 km of recces and transects (Hicks, 2014) in 2012. In Gangu in 2005, TH and team encountered an adult leopard on the transect stalking a group of red river hogs (Hicks, 2011), and in 2012 found a red river hog carcass stashed by a leopard in a tree (Hicks, 2016). During the 2012-2013 field season, camera traps in the Gangu Forest captured 46 clips of leopards (0.02 per camera day) (Hicks, 2014).

Consumption of a Leopard Carcass by a Chimpanzee, Bili 2006

On 8 September 2006, LF led a team to the Gangu Forest to construct a new research camp (Camp Gangu: 4°19.34’N, 24°41.53’E). This particular forest had been chosen due to its high density of chimpanzees (Hicks et al., 2014) and their reported lack of fear toward humans (Hicks et al., 2012). While LF and his assistants constructed a satellite camp on a hilltop over the Langba Stream, he recorded the following series of observations in his notebook (translated from the French by TH, with comments by TH added in italics):

> 17 September 2006 – We spent the sixth work day constructing shelters for the new camp. At 5:00 hours, we heard chimpanzees vocalizing (*crient*) to the southeast, toward the Langba River. Since we had arrived here to construct the houses at 8:00 hours, the chimpanzees had continued to vocalize very loudly less than 300 m away. We continued to work. The chimpanzee vocalizations (*criés*) continued all day.
>
> 18 September 2006 – The seventh work day we spent tying the roofs on the houses. At 5:00 hours, the chimpanzees vocalized in two groups, one to the north and one to the south. Upon our arrival at the new camp at 10:00 hours, the vocalizations started again, just as had happened the day before. I asked the cutters, why have the chimpanzees been vocalizing for two days straight, from the same direction? I left three workers to continue the camp work and took Kangonyesi and Garavura toward the source of the sounds. When we arrived, we found a chimpanzee on the ground 10 m from us, eating something white. *LF says that the chimpanzee was a medium-sized individual and had its back to the observers, and they watched it feed for about 5 minutes. The site was in dense forest on a hilltop above a river, in an area visited frequently by chimpanzees (4°19.52'N, 24°41.44'E).* We could not see well what the chimpanzee was eating. I asked Kangonyesi to cough once, and when he did, the chimpanzee moved off by climbing up a vine into the trees. Arriving at the site, we found a leopard apparently killed by the chimpanzee. The haunches and the two back legs had been eaten by the ape. We examined it well and searched the leopard's body, and saw that it had two wounds on the neck and one on the side of the shoulder blade. I took a sample of the leopard (its paw). *LF cut off the front paw just above the wrist and brought it back to Bili.* It was killed by the chimpanzee itself. The time is 10:49 am. *The two back legs were mostly missing, confirmed LF. He thought that the bite marks on the neck and shoulder had been made by a chimpanzee, as there was much tearing where the meat had been ripped from the presumed fatal wounds, consistent with chimpanzee bites and not the puncture wounds of big cats. The leopard's neck appeared to have been broken. When TH revisited the site with LF 3*

> *weeks later, no remains of the leopard were found, although there was a disturbed patch of soil where the leopard had lain. Fresh cut marks from a machete were present on the tree, which LF said he made at the time of the observation to mark the spot. LF described how he had seen a pool of urine a few metres from the carcass, and he speculated that that was where the leopard had been killed (and lost control of its bladder). He acknowledged that he could not be sure whether or not the leopard had been killed by chimpanzees, but thought it likely. The leopard was not a cub, but was not a particularly large individual in LF's estimation.*

LF returned to Bili on 28 September 2007 and presented the leopard paw to TH. It was still in good condition and was only just beginning to give off an odor. The spotted paw, which we later preserved in alcohol, measured 10 cm from the dew claw to the third claw (Figure 5).

Local Reports of the Chimpanzee-Leopard Relationship in Bili-Gangu

Ever since the early days of the Bili Chimpanzee Project, locals have told stories about the Bili apes killing lions, leading to the origin of the Bili apes' lion-killer reputation in the international press (e.g., Young, 2004; "From Myth to Reality," 2007; Young & Barnett, 2006; and rebuttal of the latter by Hicks, 2006). All of the project trackers, local Zande from the region, insisted that leopards never hunt chimpanzees, even juveniles, because the chimpanzees are too large and powerful. TH dissected five leopard scats found near Camp Louis, and found no remains of chimpanzees, only of duikers. We can conclude little, however, from such a small sample size. Two of the project's Zande trackers claimed to have seen, decades before, chimpanzees eating leopards in nearby forests. Olivier Esokeli of Bili says that when he was hunting in the forest with his father as a boy, he saw six adult chimpanzees pin down and kill a leopard. Benoit Imasanga describes how he once heard chimpanzees making a noisy commotion near his camp and, following the sounds into a gallery forest, found the mangled carcass of a leopard surrounded by numerous chimpanzee prints.

(a) (b)

Figure 5. (a and b) Ligada Faustin in the town of Bili with the leopard (*Panthera pardus*) paw described in the text.

Ituri Forest, Northeastern DRC

Evidence for Tortoise Predation

Over the course of three decades of field work in the Ituri Forest, JH and team observed indirect evidence of chimpanzees handling and consuming hinge-backed tortoises (*Kinyxis erosa*). They found approximately ten tortoises that appeared to have been smashed or pried open, at some of the sites associated with stick tools, which led JH and local foragers to attribute the kills to chimpanzees. One of the five tortoises seen personally by JH had been pried open with a stick, which was found projecting from inside the shell (Figure 6 shows that shell in storage). Some of the other tortoises had apparently also been smashed or pried open with sticks. In most cases it looked as if the chimpanzees had, after prying open the shells, eaten the tortoise flesh and organs, and in one case bite marks appeared to be visible on the shell. JH observed no evidence that any of the tortoises had been smashed against a substrate.

Figure 6. A hinge-backed tortoise (*Kinixys erosa*) pried open by chimpanzees in the Ituri Forest, eastern DRC (photograph by JH).

Pirated Okapi Killed by a Leopard

In the Ituri Forest in 1989, JH encountered chimpanzees that appeared to be consuming an okapi (*Okapia johnstoni*) carcass, thought to have been pirated from a leopard. This is one of the first documented accounts of the consumption of a large mammal by chimpanzees. The observation is of relevance to the theory of human evolution which posits that several million years ago our hominin ancestors increasingly began to pirate mammalian carcasses from large carnivores (Shipman, 1986), a behavior proposed to have contributed to our differentiation from other great apes.

In the late afternoon, JH was travelling through dense underbrush in mixed forest with project radio tracker Nobirabo, about an hour’s walk south of Afarama Camp (1˚33 N, 28˚31 E). They were searching for the now-stationary radio collar of a subadult okapi they had last tracked moving through this part of the forest, prior to its suddenly having ceased all movement about 24 hours earlier. They assumed the okapi was dead. As they moved towards the source of the transmission, without warning they encountered two large adult male chimpanzees about 3 m away, crouched over the fresh carcass of the focal okapi. The chimpanzees were startled by the arrival of the researchers and stood up on their hind legs to get a better look. Their hair stood up on end and they screamed, displayed slightly, and fled into the undergrowth. JH and Nobirabo investigated the okapi carcass and observed it to be scarred by recently-made leopard claw marks. They also noted that the animal's belly had been partially devoured, consistent with how they had seen leopards eat their prey before. In addition, they noted that the young okapi's still soft-sutured skull had been freshly split open, apparently by biting, exposing the brain material. At Ituri, where JH and team had earlier observed many ungulate carcasses predated by leopards, they had never seen the big cats feed on a braincase in this manner, and thus they judged that this had probably been done moments before by the chimpanzees. The following day, when they returned to the same site to look for the okapi carcass, they saw that it had been dragged approximately 5 m into thicker vegetation, and had been further disarticulated and consumed.

RAFALE (Ituri Fragments), Northeastern DRC

AL and team surveyed 18.2 km² of steep slope forest fragments (12 km of recces and 6.6 km of systematic transects) and documented the presence of chimpanzees (Laudisoit et al., 2016; Huyghe, 2017; Scholier, 2017). Out of 46 chimpanzee dung samples analyzed, six contained what appeared to be hairs; four of these were found in dung samples the day after the galago handling event described below, approximately 12 m from that site. Given that these latter dung samples were approximately one day old, the hairs most likely did not from the galago observed being handled by the chimpanzees. At the time of writing, the unidentified hairs are being analyzed via DNA barcoding.

Handling of a Galago Carcass

On 9 May 2017, between 8:20 and 10:20 hours, AL and team observed a group of at least 17 chimpanzees approximately 65 m northeast on a mountain slope, at 1°55.38’N, 30°53.08’E. At 10:15 hours, following a series of noisy screams, an adult female with an infant clinging to her belly appeared in a subgroup of five chimpanzees (three adult males, one adult female, and one younger female) carrying a fresh galago carcass in her mouth (Figure 7; see video at https://youtu.be/uJO4338IBLQ). This was most likely a dwarf galago (*Galagoides thomasi*), the only galago species which has been recorded on camera trap footage in this area (S. Bearder, personal communication, 10 December 2013). The adult female chimpanzee climbed onto a fallen tree on which two adult males were resting. Both males approached her and peered at the small prey in her mouth. As she sat down, she removed the galago from her mouth with her right hand and held it in front of the faces of the adult males. A young female climbed onto the trunk, sat down beside the group, and the adult female presented the galago to her as well. For the following two minutes, the adult female was obscured behind a large dead branch. When she emerged, she had left her infant on the ground and the galago remained obscured. Six more group members gathered around her (two adult females, three young individuals, and one infant male). At 10:18 hours, as the other chimpanzees slowly moved away from her, the adult female turned so that AL could again clearly view the galago, now held in her right foot. At 10:19 hours, she placed it back into her mouth, holding it tightly between her lips, then transferred it several times between her hand and her mouth. She departed downhill at 10:23 hours. Seven minutes later she was recorded on a camera trap walking downhill, still carrying the lifeless galago in her mouth. We do not know whether or not she later consumed the prey.

(a)

(b)

Figure 7. (a) A fresh galago carcass held in the mouth of an adult female chimpanzee, seated in the centre of the photo behind two youngsters. (b) An adult male chimpanzee peers at the galago carcass held before his face by the adult female. Screenshots by Caroline Thirion, from a video by AL; www.carolinethirion.com/mbudha-source-chimpanzees/).

Reports by Local People of Other Types of Faunivory, Bili-Uéré and RAFALE

Bili-Uéré

Most local assistants of the Bili Chimpanzee Project claim that the chimpanzees do not prey on monkeys, only leopards and duikers. We gathered several reports from residents of Bili and also at Ngume south of the Uele River (see Hicks, 2010) of chimpanzees eating duikers. Bili resident and project worker Makassi Constant, however, told TH that black and white colobus monkeys are the apes' mortal enemies, and that the two species often do battle in the trees. He claimed to have witnessed, years before, a black and white colobus kill a small chimpanzee in the canopy by biting its throat. Other than these stories, to date no evidence has been found of predation by chimpanzees on monkeys in northern DRC, which is surprising given the widespread presence of monkeys in chimpanzee diets across Africa.

At Bili, the trackers and other villagers frequently claimed that the Bili chimpanzees use their hands to dig aestivating fish from small streambeds during the dry season. The Azande frequently dam small streams and dig for fish, and the local assistants claim that when dam-fishing in the Gangu Forest they frequently find chimpanzee knuckle prints, dig marks, and fish remains around muddy holes in riverbeds. Unfortunately, we were unable to spend much time in the forest during the months in which the behaviour is supposed to occur (February to April) and were unable to confirm it.

RAFALE

Local farmer and hunter Bedidjo worked as AL's guide in 2017. He claims that in 2015, when hunting in the Rogo Forest approximately 3 km southwest of the galago incident described above, he saw three chimpanzees eating a blue monkey (*Cercopithecus mitis* cfr *stuhlmanni*) that had been caught in his snare and thus can be considered scavenged.

DISCUSSION AND CONCLUSION

Although our data are limited, the observations presented in this chapter suggest that chimpanzees of northern and northeastern DRC may have an unusual profile in terms of vertebrate prey, having apparently consumed a tree pangolin, an okapi, a leopard, and tortoises, and at RAFALE an individual was seen carrying a dead galago possibly for subsequent consumption. Although we failed to find any remains of vertebrate prey in our dung washes at Bili or at RAFALE, this is not surprising given our small sample size (see Moore et al., 2017). The chimpanzees of the Taï Forest in Ivory Coast are famous for their elaborate monkey-hunting behaviour, and yet for the first few years of the study, negligible vertebrate remains were found in fecal analyses (Boesch & Boesch, 1989). It took years before the first monkey hunt was directly observed at Taï.

Chimpanzees were observed eating a pangolin at Bossou, Guinea (Sugiyama, 1981), and in the Ndoki Forest, Republic of Congo, researchers found the remains of what was probably a pangolin in a dung sample (Kuroda, Suzuki, & Nishihara, 1996). Hicks (2010) presented possible evidence gathered by other researchers of pounded tortoises in the Maiko Forest, eastern DRC, although this cannot be considered conclusive.

So far, no evidence of monkey hunting has been found in Bili-Uéré or Ituri. Throughout their range in Africa, wherever chimpanzees and red colobus (*Piliocolobus* spp.) are sympatric, the apes hunt the monkeys, preferring them to all other prey (Boesch et al., 2002). We found no red colobus at Bili or any of the other forests surveyed north of the Uele River (Hicks, 2010), but they were present in most of the forests surveyed south of the Uele, as well as at Ituri. Clearly it would be premature to claim that monkeys do not make up a part of the chimpanzee diet in northern DRC. To date the only primate prey observed to be handled (cf. Hirata, Yamakoshi, Fujita, Ohashi, & Matsuzawa, 2001; Cibot, Sabiiti, & McLennan, 2017), if not consumed, by the chimpanzees of northern DRC is the galago described in this chapter. Chimpanzees prey on galagos in Fongoli with the use of tools (Pruetz & Bertolani, 2007, Pruetz et al., 2015) and, rarely, without tools at Gombe (O'Malley, 2010) and Ngogo, Uganda (Watts & Mitani, 2015), but predation on nocturnal strepsirhines is otherwise unusual behaviour for the species (McGrew, 1992).

Although chimpanzees at a number of sites have been observed behaving aggressively toward leopards, our observation of the consumption of a leopard at Bili-Gangu is the first observation, to our knowledge, of a free-living chimpanzee feeding on a big cat. We do not know how the Ituri Forest chimpanzees came to be in possession of the okapi leopard-kill, i.e., whether they stole it from a stash in a tree, found it on the ground, or perhaps even chased the leopard away from it. What is clear, though, is that within 24 hours of a leopard killing the okapi, two adult male chimpanzees had commandeered the carcass and appeared to be feeding on its brain.

Chimpanzees only rarely scavenge or pirate kills made by baboons or (possibly) leopards (e.g., Hasegawa, Hiraiwa, Nishida, & Takasaki, 1983; Goodall, 1986; Muller, Mpongo, Stanford, & Boehm, 1995; Watts, 2008). They are generally not known to scavenge the remains of larger mammals, which makes our report of the possibly scavenged or pirated okapi carcass at Ituri particularly notable. Cibot et al. (2017) described two cases of chimpanzees handling small dead animals without consuming them in Bulindi, Uganda; however, it was unclear if the chimpanzees had found the carcasses already dead or had killed the animals themselves.

Even after decades of study at several long-term field sites, chimpanzees continue to hold surprises. Although predation on tortoises, galagos, and pangolins is not unprecedented, the consumption of a leopard has not been seen before in this species. At Bili-Gangu, it is impossible to know whether the chimpanzee scavenged or killed the leopard, although LF's interpretation favours the latter. Even more questions are raised by our observation of Ituri chimpanzees in possession of an okapi clearly killed by a leopard. Until now, possible evidence of chimpanzees pirating carcasses from leopards has been only circumstantial (Hasegawa et al., 1983), and the apes usually ignore the carcasses of larger mammals (see Watts, 2008, for a review). Such an observation undermines a proposed key difference between chimpanzees and our early bipedal ancestors: the idea that chimpanzees fail to take advantage of carnivore kills as a potential food source, which has been proposed as an important dietary shift in hominins (Shipman, 1986; Moore et al., 2017). Although in general chimpanzees target smaller mammals such as duikers and monkeys, their presence at the carcass of this juvenile okapi raises the possibility that at least some populations may include larger prey in their diets, possibly pirated from carnivores.

In northern DRC, chimpanzees frequently sleep in ground nests (Hicks, 2010; Hicks, Kühl, et al., 2019), which could potentially make them more vulnerable to leopards and other carnivores. The chimpanzees of northern DRC may have in some sense turned the tables on leopards, which are, in other chimpanzee populations, known predators. This may explain why in this population, the apes appear to be unafraid of nesting on the ground (Hicks, 2010). For the moment, though, these intriguing observations raise more questions than they provide answers. Further studies of this large and widespread population are required in order to understand how they fit into our developing understanding of chimpanzee behavioural variation.

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For more information on the RAFALE landscape, see https://www.friscris.be/files/1018164/PosterRAFALE_Laudisoit.pdf. (https://www.friscris.be/nl/publications/rafale-project-relict--refuge-altitude-forests-of-the-albert-lake-escarpment-ituri-drcongo(75ef9965-0453-4d8c-b3be-37fd756f51c9).html.

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Chapter 2

NICHE CONSTRUCTION AND DEVELOPMENTAL BIAS IN CHIMPANZEES AND GORILLAS

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ABSTRACT

Examining the environment as a background condition for the vast degree of behavioural diversity observed within the clade of African apes has proven insufficient in explaining some of the most interesting and salient differences among our closest living relatives. In this review, we apply the framework of the Extended Evolutionary Synthesis to examine the relationship between great apes and their environments. We cite examples of wild chimpanzees and gorillas modifying their environments in ways that systematically influence selection pressures acting on current populations and their descendants. We also compare potential developmental biases within populations to determine if some kinds of variation may be more common than others and could therefore play a role in driving evolutionary change. Our aim is not only to broaden the consideration of niche construction to include great apes, but also to identify the "ecological legacies" that these species may bequest to future generations that facilitate scaffolding of complex skills.

Keywords: great ape, ecology, culture, learning, social inheritance

INTRODUCTION

Understanding the immense variation across hominids in sociality and in technological skills has proven a formidable challenge for biological anthropologists. Research into both of these topics traditionally proceeds by considering the environment as a background condition for the vast degree of behavioural diversity observed within the clade of African apes. However, this approach has proven insufficient in explaining some of the most interesting and salient differences among our closest living relatives. In this study, we invoke the framework of the Extended Evolutionary Synthesis (EES) to examine the relationship between great apes and their environments and also the potential role of developmental bias. More specifically, we review field observations of sympatric chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*) in the Goualougo Triangle of northern Republic of Congo to identify how these apes change their social and physical environments in ways that may systematically influence selection pressures acting on current populations and their descendants. We hypothesize that complex technical behaviours (such as tool-assisted foraging) modify the environment and generate "ecological legacies" that could help novice tool users to acquire technological skills. This may be a factor contributing to the maintenance of complex tool use of chimpanzees in this region over generations. We further hypothesize that both chimpanzees and gorillas dynamically adjust their social behaviour and patterns of association to functionally influence their social environment and that of conspecifics.

Extended Evolutionary Synthesis: A Broader View of Evolutionary Processes

The EES highlights extragenetic influences that may contribute to inheritance (Gilbert, Opitz, & Raff, 1996; Pigliucci & Müller, 2010; Laland et al., 2014, 2015). While retaining fundamental tenets of evolutionary theory, the EES emphasizes the role of organismal agency and reciprocal pathways of causation in evolutionary changes. It provides a framework that includes not only the evolutionary processes that directly affect gene frequencies, but also those that bias the outcome of natural selection, as appears in Figure 1 (Laland et al., 2015).

Niche construction and developmental bias are two forces proposed to shape the direction and rate of evolution. "Niche construction" can be defined as the "process whereby the metabolism, activities and choices of organisms modify or stabilize environmental states, and thereby affect selection acting on themselves and other species" (Laland et al., 2015). Rather than taking the environment as the background condition that generates one-way selective pressure on organisms, the EES emphasizes how organisms make nonrandom modifications to environmental states and thus generate the very selective pressures to which they are subject (Odling-Smee, Laland, & Feldman 2003). Over multiple generations, these processes can facilitate long-term stability of environmental conditions and enhance the complementarity of organisms and their environments

(Laland, 2015; Laland et al., 2015). "Developmental bias" includes processes that "systematically channel the generation of phenotypic variants along certain pathways, and thereby bias the direction and rate of evolution by, in part, determining the variants that are subject to selection"

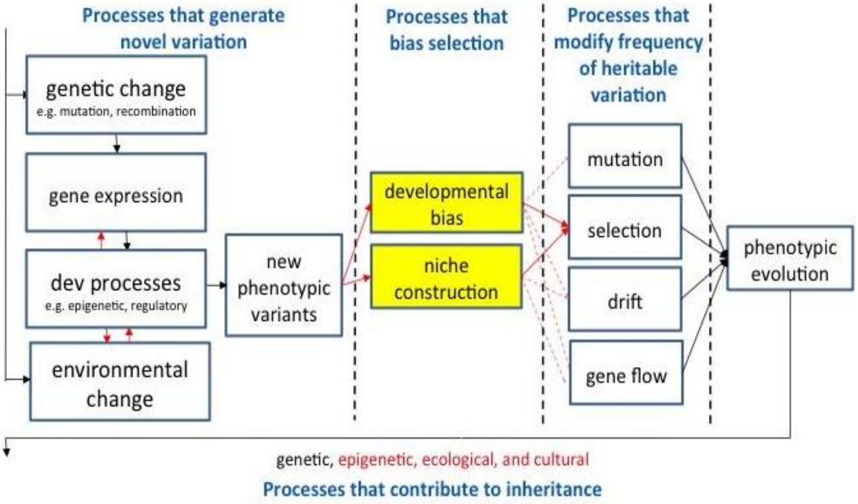

Figure 1. The structure of the EES. Adapted from "The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions" by K. N. Laland, T. Uller, M. W. Feldman, K. Sterelny, G. B. Muller, A. Moczek, E. Jablonka, and J. Odling-Smee, (2015), *Proceedings of the Royal Society B*, 282 (1813), 20151019 p. 8. Copyright 2015 by Royal Society Publishing. Open access. Retrieved from https://royalsocietypublishing.org/doi/full/10.1098/rspb.2015.1019.

(Laland, 2015). These processes may involve the interaction of numerous biological, social, and environmental forces that effectively bias the expression and retention of specific phenotypes. Many of the best-known examples emphasize the role of developmental bias as a constraint on how different aspects of physical development can proceed (Maynard-Smith et al., 1985), or on what variants of body form are likely to evolve (Arthur, 2011). However, developmental bias may be essential in the generation of adaptive variants, and may even be pervasive across taxa (Laland, 2015; Uller et al., 2018). Further, developmental bias could play an important role not only for morphological features (e.g., the number of limbs), but also for the acquisition of learned behaviours (Laland et al., 2015). A fundamental component of this process is "ecological inheritance." This refers to the way environmental changes can accumulate, comprising a nongenetic legacy that is passed to, and can shape, the actions and development of descendant organisms as well as other species (Odling-Smee et al., 2003; Erwin, 2008).

Extended from ecological niche theory (Odling-Smee, Laland, & Felding, 1996; Laland, Olding-Smee, & Felding, 2000), the "social niche" is the set of social conditions required for species-typical social organization and structure as shaped by interactions and/or associations with conspecifics across multiple, overlapping social networks (Flack et al., 2006; Bergmüller & Taborsky, 2010). Therefore, "social niche construction" is the process by which individuals, dyads of individuals, or collective units "influence the composition and dynamics of their social environment" (Saltz et al., 2016). Social niche construction has the potential to positively affect the niche constructor(s) and their offspring's abilities to adapt under various social pressures (Lipatov, Brown, & Feldman, 2011; Saltz et al., 2016). The flexible expression of social behaviour in response to local social or environmental pressures could confer numerous evolutionary advantages. For example, dynamic maintenance of social relationships could facilitate or improve transmission of information, access to social and ecological resources (e.g., coalition partners, consortships, food, sleeping sites), and the ability to navigate power structures (e.g., dominance hierarchies) (Flack 2012; Malone, Fuentes, & White, 2012).

Ecological Inheritance

Nest Construction

Each evening, great apes construct sleeping platforms. The proposed functions of these nests include decreasing the risk of predation, reducing exposure to disease, increasing thermoregulation, and improving sleep quality (Baldwin et al., 1981; Fruth & Hohmann, 1996; McGrew, 2004; Fruth, Tagg, & Stewart, 2018). Ape nests may be detectable for only a few days to several years, depending on nest construction type, materials used, and rainfall. These nests have lasting impacts on the environment and possibly the ecology of future generations of apes as they comprise identifiable traces of ape presence and can facilitate the germination of ape foods. The specific vegetative structures (wooden basins created by interwoven twigs and branches, or leafy beds fashioned from herb stalks) of ape nests are highly salient in the environment and indicate ape residency and possibly even density in an area. Further, there is evidence that ground nest construction by gorillas facilitates the growth of seeds that are deposited in the nests within gorilla faecal deposits. Habitat choice can affect seedling development rates, which were found to be two to ten times higher within nests in open canopy forest versus other conditions (Haurez et al., 2015). Choices of habitat for nesting and foraging may also systematically channel the generation of phenotypic variants along certain pathways. Through nest building, apes can alter their environments in ways that influence evolutionary processes (Figure 2).

Figure 2. Nest construction as an organism-induced change in the environment.

Tool Sites

All studied chimpanzee populations exhibit some form of tool-using behaviour (McGrew, 1992; Shumaker, Walkup, & Beck, 2011). However, there is variation in the size and complexity of their tool-using repertoires (Sanz & Morgan, 2007; Sanz & Morgan, 2010). Some chimpanzee communities rarely exhibit few tool behaviours, whereas others show diverse tool repertoires. In additional to ecological variables, social learning is proposed to influence the immense intraspecific variation observed among chimpanzees in tool-assisted foraging (e.g., McGrew, Tutin, & Baldwin, 1979; Whiten et al., 2001). Some of the physical impacts of tool use on the environment are detectable to subsequent visitors to the tool site. These environmental changes and tool traces could facilitate social learning through local enhancement and stimulus enhancement. Selection of particular types of plant materials for tool making, transport of these tool materials to a tool-using site, and leaving these tools inserted in the soil could also promote the increased availability of suitable tool materials for future tool users. In sum, we suggest that tool-use sites may include a variety of organism-induced changes in the environment (see Figure 3).

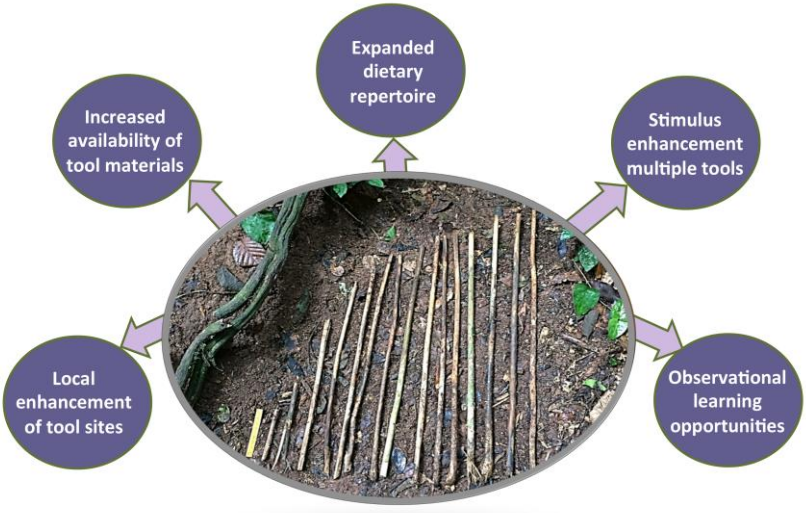

Figure 3. Tool-use sites as an organism-induced change in the environment.

Tool locations may be revisited over years by generations of chimpanzees, as has been shown at nut-cracking sites in West Africa with archeological evidence dating back to 4,000 years (Mercader et al., 2007). Tool behaviours differ in the types of locations targeted and types of tools used, which means that tasks differ in their potential ecological legacies. While tools made from perishable materials (herbs, twigs, branches) are not amenable to long-term preservation, these materials and their changes in the environment are detectable and may provide important information to subsequent tool users over several days to months (depending upon the tool material and target location). Chimpanzees in Central Africa have some of the most diverse and complex tool-using behaviours documented among the animal kingdom (Sanz & Morgan, 2007). Our observations indicate that niche construction and developmental bias may facilitate such diverse and complex tool behaviors.

Social Niche Construction

Chimpanzees

Chimpanzee social organization is generally characterized by male philopatry, female emigration, minimal spatial-temporal cohesion across a larger community (which in total may be comprised of 20 to over 140 individuals; McGrew et al., 2004; Watts & Mitani, 2001), and fission-fusion social dynamics, which involves flexible formation of smaller foraging parties of variable membership (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004). However, community social structure and party composition vary in relation to social and ecological variables (reviewed by Malone et al., 2012). Proponents of traditional socioecological models have attempted to identify rules for species-wide responses to ecological factors or competitive regimes, with varying degrees of success (van Schaik & van Hooff, 1983; c.f., Strier, 1994; Thierry, 2008). In contrast, a social niche construction framework considers how group members may preferentially select with whom and where to spend their time, and how this flexibility could facilitate adaptive responses to immediate environmental (e.g., food resource distribution) and social pressures (e.g., dominance instability, mating opportunities).

Flexibility in constructing one's social niche likely enables individuals to maximize opportunities (i.e., for socializing, feeding, or mating) not only across variable settings, but also over the lifespan. For example, female chimpanzees immigrating to a new community often remain in the peripheral edges of the community range, occupy low dominance status, and persist in low-quality core areas. Developing affiliative relationships with more established residents is critical to integrating into a new community. Relative to the gradual socialization process in one's natal group during development, immigrant females must abruptly establish and maintain social relationships with potentially long-lasting consequences. For example, an immigrant female's reproductive success might partially depend on her ability to outcompete resident females to establish high-quality core areas and mating opportunities (Thompson et al., 2007). Forming social relationships with males also could be necessary to secure support in such conflicts with resident females (Kahlenberg, Thompson, & Wrangham, 2008). Formation of high-quality relationships with individuals of both sexes could also provide immigrant females, and their offspring in future years, with not only access to food resources and mating opportunities, but also information about the social customs specific to that group. Furthermore, a chimpanzee's social skills may reflect the social dynamics and opportunities that she was exposed to during ontogeny, largely via her mother's social niche. These considerations highlight an intergenerational component of social niche construction both in the development of social skills and in the construction of one's own social niche.

The termite-gathering context provides an example of one setting in which chimpanzees may moderate the frequency, duration, and context in which they associate with particular conspecifics (e.g., Aureli et al., 2008). Social tolerance in close proximity has been hypothesized to aid in facilitating the transfer of information among conspecifics (Coussi-Korbel & Fragaszy, 1995; van Schaik et al., 2003), thereby sustaining complex tool-using behaviours in a population (van Schaik & Pradhan, 2003; Sanz & Morgan, 2013). Selective association among conspecifics who share highly tolerant relationships could enable foraging in close proximity on this high-quality resource (Fraser, Schino, & Aureli, 2008; Massen & Koski, 2014) and also facilitate the overlap in space and time that is necessary for social transmission of complex foraging skills. This may promote the horizontal transmission of information among peers, such as from immigrant subadults who can introduce new tool variants into a community (O'Malley et al., 2012). In addition, maternal choices of social associates in tool contexts could shape the social environment in which immature chimpanzees learn to use tools. Chimpanzees plan their tool use (Byrne, Sanz, & Morgan, 2013) and thus they could similarly be capable of planning with whom they use tools.

Gorillas

Variation in the social organization of gorillas is influenced by predation pressure, food availability, reproductive opportunities, and other socioecological variables (Doran & McNeilage, 1998; Harcourt & Stewart, 2007). Understanding the characteristics of social systems such as group stability, structure, and composition can aid in clarifying the roles that these factors play in the social niche construction of gorillas. Group stability influences an individual's ability to make accurate predictions about outcomes of inter- and intragroup social interactions (Sascher, Durschlag, & Hirzel, 1998). Instability in a social system leads to pressures at both the individual and group level, which may have broader implications for sociality, health, and fitness.

Flexibility in constructing one's social niche likely enables individuals to maximize opportunities across variable settings and over the lifespan. Young adult male western lowland gorillas who emigrate have been found to remain in the vicinity of male kin, forming "neighbourhoods" where related males live close together. This creates a network of independent groups in which an individual may encounter a dispersed relative in another group during an intergroup encounter (Bradley et al., 2004; Forcina et al., 2019). Such extended male networks may aid younger males by providing opportunities to identify and attract reproducing females from other groups. As the potential competitors might be kin or a familiar individual, it has been suggested that associating within these neighbourhoods may serve to decrease aggression during intergroup encounters (Bradley et al., 2004). Additionally, these extended male networks may provide support against peripheral silverbacks or solitary males who attempt to encroach on resources.

Intergroup encounters provide a window into how social niche construction can impact group dynamics in gorillas, with broader implications for individual fitness and population viability. Variability within and between gorilla populations is expected to influence the relative roles of resource and mate defense during encounters between groups of conspecifics and, consequently, the nature of intergroup encounters (Sicotte, 1993; Tutin, 1996; Bermejo, 2004; Bradley et al., 2004; Doran-Sheehy et al., 2004). Behaviours exhibited by individuals before and during intergroup encounters are expected to vary depending on group composition, familiarity of peripheral individuals, and age and size of the dominant silverback (Harcourt, 1978; Yamagiwa, 1987, Sicotte, 1993). Male gorillas typically engage in more frequent and intense aggressive interactions than females (Cavigelli & Caruso, 2015). Conversely, silverback males also may influence the composition and dynamics of their social environment by opting to not engage in encounters with peripheral males or family groups by avoiding other groups altogether. This could serve to reduce the likelihood of female transfer between groups and also the risk of infanticide.

Western lowland gorillas also may alter the rate, duration, and setting in which they encounter conspecifics through choices in foraging location and ranging. Western lowland gorillas are predominately folivorous, but they preferentially and opportunistically feed on fruits when available even if this requires additional travel to these ephemeral resources. Longer daily path lengths elevate the likelihood of interactions with conspecifics, thus potentially providing knowledge about peripheral individuals and increasing the likelihood of information transfer during interactions. We propose that gorillas are capable of altering their social niche in ways that may bias the direction and rate of evolution.

Interaction of Niche Construction and Developmental Bias

Recent studies on ape nest building, tool sites, and habitat use prompt reconsideration of the relationship between apes, their environments, and the forces that generate behavioural variation. In this study, we review and synthesize our observations of African apes systematically changing their physical and social environments in ways that influence evolutionary processes. We examine these processes among Central chimpanzees and western lowland gorillas, which reside in sympatry throughout much of the Congo Basin. These species show a relatively high degree of dietary overlap and have been observed to co-feed on several food resources (Morgan & Sanz, 2006; Walsh et al., 2007). Their nesting behaviors also overlap, which has historically been an obstacle for efforts to precisely monitor these species through indirect traces. Odling-Smee et al. (2003) suggest that failure to detect character displacement in closely related sympatric species provides an opportunity to investigate whether there is evidence for organism-driven modification of the selective environment. The complex tool use exhibited by chimpanzees who are sympatric with gorillas, for example, could be a form of niche construction that facilitates access to high-quality food, expands the dietary repertoire, and reduces feeding competition. Here, we review the means by which chimpanzees and gorillas may modify their environments in flexible, dynamic ways to construct their ecological and social niches. We also consider how social niche construction may influence an individual's development in the social realm, and then use this information to address long-standing debates about the evolutionary forces involved in the emergence and maintenance of ape material culture.

METHODS

This research was conducted in the Nouabalé-Ndoki National Park (2°05'-3°03'N, 16°51'-16°56' E), Republic of Congo. The Goualougo Triangle study area is part of the Sangha River Tri-National Protected Area

Complex, which comprises 7,000 km^2 of contiguous forest spanning national parks and reserves across Republic of Congo, Cameroon, and Central African Republic. The Goualougo Triangle encompasses 380 km^2 of lowland forest with altitudes between 330 m and 600 m. The climate can be described as transitional between the Congo-equatorial and subequatorial climatic zones.

Direct observations of chimpanzees and gorillas in the Goualougo Triangle have been ongoing since February 1999. The main study group of chimpanzees is the Moto community, which at the time of this study consisted of 71 individuals, including 12 adult males and 24 adult females. Since 2013, a group of gorillas within the Moto chimpanzee community range has been habituated to researcher presence. The Loya gorilla group consisted of a dominant silverback, two females, a blackback, a juvenile male, and two infants during the time of this study. During daily follows of chimpanzee parties and the focal gorilla group, observers recorded location, forest type, group composition, activity patterns, feeding observations, and interactions between species.

Remote video recording devices with passive infrared sensors were used to determine chimpanzee and gorilla visitation at 12 fruiting trees over 46 months and 32 tool sites over 60 months. Detection of movement by the sensor caused the camera to record for 2-minute intervals until triggers ceased (Sanz, Morgan, & Gulick, 2004). Video footage was archived and converted to MPEG format for review, after which we coded videos using INTERACT software (Mangold, 2015). The footage was screened for time that large mammals were present.

We surveyed all ape nests encountered along systematically spaced line transects across the study area. We recorded nests of all ages during the first passage of all transects, but only fresh and recent nests were subsequently monitored for nest decay and used for survival rate analyses during subsequent passages (Morgan et al., 2016). We recorded the age class of the nest (fresh, recent, old, very old) during each passage following Tutin and Fernandez (1984). We designated each nest as built by chimpanzee or gorilla based on the presence of faeces, shed hair, odour, or other signs. We classified any nest without associated evidence of which ape species built it as great ape, and later attributed each to either gorillas or chimpanzees using a logistic regression model based on a set of explanatory variables associated with known gorilla and chimpanzee nests detected in this study (Sanz et al., 2007; Stokes et al., 2010).

RESULTS

Ecological Inheritance

Habitat Choice

Gorillas and chimpanzees overlap in several types of habitats, including mixed-species forest, monodominant *Gilbertiodendron* forest, and swamp forest (Morgan et al., 2006). Each species shows preferences in using some types of habitats to a higher degree than the habitat's overall representation across their range (Morgan et al., 2006). Within these habitats, they consume many of the same foods (67% overlap in food species consumed), but differ in the importance of specific foods in their diets. This can be directly observed in their biased visitation to food resources. As shown in Figure 4, we observed that gorillas frequented particular fruiting tree species more often than chimpanzees.

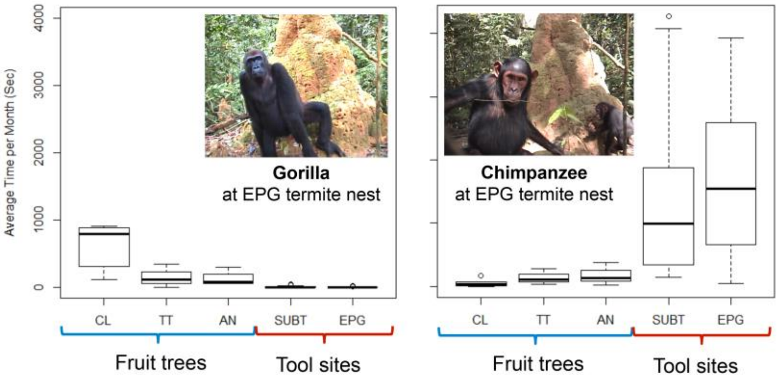

Figure 4. Habitat choice as developmental bias between chimpanzees and gorillas. Fruit trees included are CL = *Gambeya lacourtiana*, TT = *Tetrapleura tetraptera*, and AN = *Anonidium mannii*. Insect resources are SUBT = subterranean termite nests and EPG = epigeal termite nests.

Similarly, we rarely observed gorillas at *Macrotermes* nests, which chimpanzees frequented. Spending time at tool-using locations increases exposure to tools and tool users, which may directly and indirectly bias the interest of other individuals toward those localities and objects.

Nesting Behaviour

We surveyed a total of 4,703 gorilla nests and 7,764 chimpanzee nests during transect surveys across the study area (Morgan et al. 2006, 2016, 2018). Survival analysis was conducted on a subset of 1,035 fresh and recent nests and yielded a mean longevity of 146.4 days (Morgan et al., 2018). Most gorilla nests were constructed on the ground (60.7%), whereas chimpanzee nests were nearly all arboreal (99.8%). Gorillas constructed nearly half of their nests from terrestrial herbaceous vegetation (47.7%), and 92% of these nests were associated with gorilla faeces. In a study of gorilla feeding ecology, we reported that 79.9% of gorilla faeces (n = 631) contained remains of at least one fruit item (Morgan & Sanz, 2006). The average number of fruits per fecal sample was 1.63 ± 1.42, with up to eight species of fruit documented in a single faecal specimen. Other studies have shown that seeds deposited within gorilla nests have a higher chance of germinating, which would promote the growth of foods consumed by gorillas in particular habitats and areas of their home range (Petre et al., 2013; Haurez, Brostaux et al., 2015, Haurez, Dainou et al., 2015).

Tool Sites

Within the Goualougo Triangle chimpanzee population, termite fishing takes place at earthen nests of *Macrotermes* spp. (Sanz et al., 2004). Chimpanzees manufacture probes from particular species of herbs by removing a stalk from a stand of herb stems and then removing the large leaf at the end of the stem. The tip of the herb stem is then pulled through the chimpanzee's teeth to create a brush tip, which has been shown to increase this type of tool's efficiency in gathering termites (Sanz, Call, & Morgan, 2009). In surveying such tool-use sites, we recovered an average of 3.0 fishing probes (685 sites, range = 1, 30) at epigeal (above-ground) termite nests. Subterranean termite nests were associated with a similar number of fishing probes, but also included 4.1 puncturing sticks on average (94 sites, range = 1, 32). Puncturing sticks serve a different function than do fishing probes; they are inserted into the nest to create an access tunnel for the fishing probe. The chimpanzees' fishing and puncturing tools increase the saliency of these sites within the forest, as the tools are detached and modified, and represent a homogeneous assemblage of materials.

Both fishing probes and puncturing sticks accumulate with site visitations, as chimpanzees bring new probes (observed in 81% of tool using bouts) when they arrive to gather termites. They were observed reusing probes at the site in 10% of tool-using bouts and manufacturing fishing probes at the site in 9% of occasions. In contrast to the herbaceous fishing probes, which decay within days, wooden puncturing tools are durable and can be effective for months after manufacture. As such, it is common for chimpanzees to reuse puncturing tools deposited by other individuals during previous visits, and we documented reuse in 39% of bouts. Transport of new puncturing tools was observed in 57% of bouts, and tool manufacture at the nest in 4% of bouts. Chimpanzees sometimes left puncturing tools inserted in the termite nest matrix, which resulted in the growth of a sapling of the tool material plant species at the tool site.

We also identified and recovered tool assemblages from sites where chimpanzees had used saplings to perforate ant nests and herb wands to gather the insects. The use of a tool set to harvest army ants had not previously been documented in wild chimpanzees, but was indicated by tool assemblages at ant nests and then confirmed by direct observations (Sanz, Schoning, & Morgan, 2010). We found tool sets to perforate and dip for ants at 36% of tool sites (3.7 ant gathering tools per site, n = 284 sites, range = 1, 18 tools).

While the tool repertoire of the Goualougo Triangle chimpanzee population comprises more than 20 different types of tools, not all of these leave detectable traces (Meulman et al., 2012). We thus suggest that tool use in arboreal settings may not provide as many avenues for either immediate (such as stimulus enhancement) or long-term social facilitation through ecological legacies as is the case with terrestrial tool use.

Consistent with this prediction, we recovered relatively small tool assemblages from bee hives where chimpanzees had used wooden clubs to access honey (2.1 tools recovered, 14 sites, range = 1, 5).

Social Niches

Chimpanzees

We have previously documented variation in average foraging party size among Goualougo Triangle chimpanzees. Across contexts, average party size was 4.47 ± 1.47 individuals. Parties in the termite-gathering context are intermediately sized (2.23 ± 1.57) relative to the larger parties observed for chimpanzees feeding on fruit, leaves, or flowers and the smaller parties observed in the context of feeding on meat, bark, or pith (Sanz & Morgan, 2013). This flexibility in social grouping may reflect the differing priorities and opportunities across settings. For example, in the termite-gathering setting, mother-offspring parties and parties that contain at least some immatures (e.g., multiple mother-infant dyads) are more commonly observed than mixed-sex parties (Sanz & Morgan, 2013). Smaller parties that comprise close social associates could be more amenable to foraging in close proximity. In addition, it could also allow for safe exploratory behavior by immature chimpanzees, while maximizing opportunity for vertical and oblique transmission of technical skills between mothers or other skilled adults to immature chimpanzees. Nonetheless, we also routinely observed that even among adult and subadult peers, individuals in the termite-gathering setting often use tools in close proximity to other individuals and observe each other’s tool use, providing opportunities for horizontal transmission.

The termite-gathering setting is instructive for understanding how social niche construction may influence individual feeding ecology and degree of technical specialization. For example, in remote video footage, we have observed that there may be differences in how often or for how long particular individuals visit specific termite-gathering localities. For females, such preferences could influence the termite-gathering behaviour of their offspring as adults, generating characteristic patterns of mother-infant similarity (Laland et al., 2015). Anecdotally, we also observed that particular means of facilitation could be socially inherited. An orphaned subadult female, when younger, was the frequent recipient of tool transfers from her mother; these tool transfers function as a form of teaching (Musgrave et al., 2016). A younger male chimpanzee who was also orphaned, as an infant, began to extensively associate with this orphan female and routinely gathered termites with her. We have since documented tool transfers from this orphan female to the younger orphan male, including observations of multiple transfers of newly manufactured fishing probes in the same visit. Therefore an individual's social niche may impact tool-using behaviour as well as the modes of intergenerational transmission of these learned behaviours.

Gorillas

Gorillas tend to have a stable social system, yet the composition of gorilla groups differs between species. Maximum group size in mountain gorillas (*Gorilla beringei*) has been observed to exceed 20 individuals, while western lowland gorilla groups are typically observed in groups smaller than 20 individuals (Yamagiwa, Kahewa, & Basabose, 2003). Gorillas reside in one of three group structures: a family group consisting of one or more silverbacks, females, and their offspring; a bachelor group where there are multiple nonbreeding males; or a solitary silverback who has either left his natal group or departed a bachelor group. Mountain gorilla groups often include multiple silverbacks, with one of the males being dominant over the other silverbacks (Robbins, 1999). Western lowland gorillas live in groups with one silverback who is solely responsible for protecting resources. This dominant male may experience increased pressure (and thus increased stress), even though younger subordinate males may participate in mate and resource guarding (Bradley et al., 2004). Dominance and longer tenure lengths are correlated with reproductive success for males. However, the costs associated with sex and social position for single versus multimale groups remain to be assessed.

In gorillas, both males and females disperse upon reaching sexual maturity. Silverback males show less tolerance toward adolescent males as they mature and will expel younger individuals before they reach silverback status (between 10 and 15 years). Mountain gorilla males approaching silverback status are more likely to remain in their natal group and assist in group protection efforts, whereas western lowland gorillas almost always disperse from the natal group but may remain in its vicinity. Variability in male coalitions suggests that gorillas may have species-specific adaptations with regard to social organization, but the specific selective pressures and adaptive advantages remain to be determined.

DISCUSSION

The EES framework provides a way to understand how extragenetic inheritance may facilitate information transfer across multiple generations. This study aimed to summarize and synthesize our observations of chimpanzees and gorillas in the Goualougo Triangle, so as to determine the extent to which these apes may bias the selection pressures they face through various forms of ecological and social niche construction. In the ecological realm, we cite evidence of habitat choice, which may channel the generation of phenotypic variants along certain pathways. Nest construction and tool-use sites provide evidence of niche construction among apes, resulting in nonrandom modifications to the environment in advantageous ways (e.g., growth of tools or germination of preferred foods). Furthermore, flexibly adaptive social niches may have intergenerational effects and be associated with specific types of advantageous interactions in certain settings (e.g., tolerance in termite gathering, tolerant interactions between gorilla groups). In addition to broadening consideration of niche construction to include specific examples from great apes, we have also highlighted the "ecological legacies" that these species may bequest to future generations and their potential adaptive significance.

Ecological Inheritance and Task Complexity

Ecological legacies have the potential to facilitate scaffolding of skill acquisition and task complexity. Within the tool kit of the chimpanzees in the Goualougo Triangle, there may be a positive relationship between complexity of a task and the amount of information that learners inherit via the environment (see Figure 5). By inventorying the tools at different types of tool sites, we have found that there are differences in the nonrandom modifications of environmental states associated with different tool tasks that may vary in how much they facilitate ecological inheritance. For example, gathering of subterranean termites requires different types of tools, the most specific tool materials, and particular tool-using techniques.

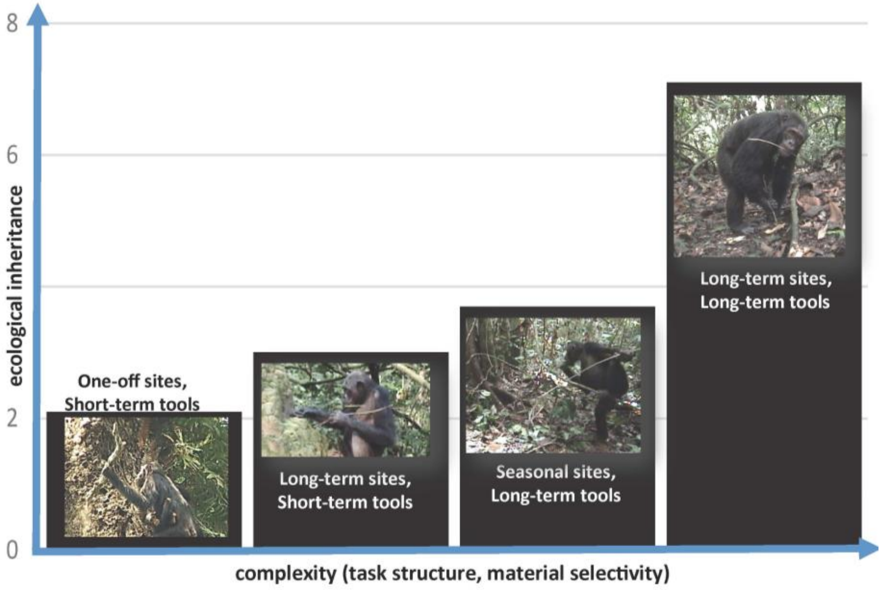

Figure 5. Relationship between ecological inheritance and tool complexity. The vertical axis indicates average number of tools recovered in tool sites. One-off sites with short-term tools are represented by honey gathering. Long-term sites with short-term tools are represented by gathering of insects at epigeal termite nests. Seasonal sites, with long-term tools include ant gathering behaviour observed within the Goualougo Triangle, Republic of Congo. Long-term sites with long-term tools are represented by gathering of insects at subterranean termite nests.

Chimpanzees revisit subterranean tool sites where changes in the nest substrate, accumulation of tools, and possible intersection with conspecifics may facilitate the maintenance of these particular foraging skills. Intergroup encounters among gorillas may also facilitate opportunities to maintain knowledge or transfer skills among individuals, with the degree of tolerance related to the type of information gained or exchanged between individuals (Forcina et al., 2019).

Variation in Ecological Inheritance

Despite adequate ecological opportunities for niche construction, habitat choice and social structure may intervene to amplify or reduce the likelihood of expression of tool behaviors across a landscape. Ecological inheritances were influenced by proximate factors such as the longevity of the tool site and perishability of the materials. Further, target resources (e.g., insect prey, honey, or water) differ in whether they can be repeatedly exploited and in the rate at which previously deposited tools are encountered. In addition to the goal-directed nature of the tool use itself, this variation highlights the non-random nature of the landscape modifications that chimpanzees impose through enactment of their tool traditions. An emerging field of research focuses on the “archeology of the perishable,” which examines not only the form and material of stone tools, but also the rich diversity of tools made from perishable materials and environmental traces of gathering materials on the landscape (Pascual-Garrido, 2018).

A key insight of the EES, and one of its principal emphases in contrast to the traditional evolutionary approach revolves around the important role of the organism in directing modifications of the physical or social environment and the impact these modifications can have in canalizing the development of future generations. One of the most important components of chimpanzee tool sites as constructed environments is the accumulation of tools, particularly at subterranean termite mounds. In the subterranean termite nest setting, the robust wooden puncturing tools used by chimpanzees to create puncturing tunnels are the frequent targets of infant attention. So, too, are the brush-tipped fishing probes used to gather termites, which illustrates that the use of these objects as tools likely influences their perception by young tool users. Herbaceous material is often present in proximity to tool sites, but manufactured tools differ from these raw materials in that they have been selected by conspecifics and are often modified from their original form (e.g., as an attached herb stalk) (Fragaszy et al., 2013). Brush-tipped fishing probes are emblematic of how such raw material is transformed. While a number of species with suitable flexibility and diameter exist in the environment and can be used successfully to gather termites, we have found that chimpanzee infants rarely attempt to acquire other materials such as twigs or vines to fish for termites (Musgrave et al., forthcoming). Instead, they receive tools from conspecifics, or they use discarded fishing probes near the termite mounds. Depending on the age of the tool, these herb tools occasionally still exhibit a brush tip. The choices of past tool makers with respect to raw material selection and tool modifications thus scaffold the learning of novice learners. Younger generations of tool users go on to select the same species and to follow the same manufacturing template for these brush-tipped probes, as the prior generation.

Subterranean termite nests also illustrate how conspecifics' past tool-using actions scaffold novices' activities. Puncturing subterranean nests is a physically challenging task, the difficulty of which precludes infants and juveniles from capably puncturing new access tunnels. However, these youngsters nonetheless have the opportunity to explore, fish from, and practice puncturing at the tool sites created by others. We often have observed young chimpanzees inserting puncturing sticks into the tunnels created by older chimpanzees. As youngsters grow, they progress to using puncturing tools with greater aptitude in partially created tunnels or reopening old tunnels that have become partially filled in. Access to the tools and tool sites of competent tool users is thus the foundation for skill development in these settings when youngsters neither manufacture their own tools nor have the skill or strength to access the underground termite nest chambers independently. In addition to shaping the general skill development of young chimpanzees, this may also lead to parent-offspring similarity (Laland et al., 2015), as young chimpanzees are routinely exposed particularly to the technical variants or preferences of their mothers and their mothers' associates.

Undoubtedly, specific, tool-assisted foraging skills could have immediate fitness benefits, and here we have discussed niche construction and developmental bias as they may manifest in one specific tool context. For chimpanzees (and potentially many other species) more broadly, however, developmental bias likely supports flexible and powerful learning abilities that enable novices to acquire a range of skills, the exact nature of which is biased in part by the constructed niche in which they develop (Flynn et al., 2013; Fragaszy et al., 2013). Indeed, chimpanzees' flexibility and aptitude for learning a wide range of behaviours, rather than rigidly adhering to any particular foraging variant, intersects with ecological variation to produce the diverse foraging behaviours documented in different populations.

The intergenerational persistence of tool behaviours can lead to long-term environmental modifications, which in turn, could increase the accessibility of this information to novice learners. Further, by providing additional information than might otherwise be available via individual exploration or observation of others, ecological inheritance could accelerate learning and acquisition in ways that increase the likelihood that cumulative cultural variants will emerge, be maintained, and potentially be expanded upon (Fragaszy et al., 2013). A rich portfolio of behavioural variants could be a necessary precondition for the accelerating development of human cumulative cultural abilities, i.e., selection for enhanced social learning capacities is more likely if there are a substantial array of beneficial behaviours that can be learned, offsetting the associated costs of increased brain size, maternal investment, and extended life histories (Henrich, 2017). Thus, understanding how niche construction and developmental bias intersect to scaffold learning in our closest living relatives offers unique insights into the emergence of cultural behaviour in the hominin lineage.

Insights and Future Directions

The framework of the EES and social niche construction in particular are well suited for examining the flexibility observed within great ape social systems. Social niche construction theory is parsimonious with many models of hominin brain, language, and sociocognitive expansion (Fuentes, 2018). Further, it is ideal for evolutionary modeling because it considers processes whereby emergent and self-reinforcing aspects of social systems can feedback to improve the constructor's fitness. Our consideration of social niche construction suggests a number of research directions that will aid in addressing long-standing questions about the evolution of social systems in hominids. For example, understanding the underlying mechanisms, or hierarchically structured simple rules, that entice individuals or groups to favour one (or more) flexible response(s) over others is an enduring pursuit within evolutionary biology (Aureli et al., 2008). Research on social niche construction in captive settings may provide useful comparative evidence for this endeavour, given captivity represents an independent suite of social and environment pressures through which individuals and groups persist. This may be of particular interest for chimpanzees, given the wide variety in observed social systems of captive chimpanzees (e.g., Cronin et al., 2014; Funkhouser et al., 2018) and the intriguing differences in social structure observed across contexts (e.g., Kanngiesser et al., 2011; Clark, 2011). Similarly, social niche construction may be useful in attempts to understand variation in the suitability and persistence of captive gorilla groups of certain compositions (e.g., Maestripieri, Ross, & Megna, 2002; Gartland et al., 2018).

Standardized approaches to identifying and comparing social niches have the potential to advance studies in comparative cognition on a number of topics, including understanding differences in hierarchical structure (across individuals, dyads, and groups); classifying relationships or individual's social roles; deciphering between relationships of certain types; and inferring evolutionary advantages of those relationships. More specifically, this approach could also aid in answering questions about the divergence of chimpanzee and bonobo social systems (Furuichi et al., 2015; Gruber & Clay, 2016). To operationalize models of social niches and their construction during ontogeny, we suggest that multidimensional social network analyses could be useful to simultaneously examine the effects of individuals, dyads, polyadic motifs, or ecological contexts on the network whole (Barrett, Henzi, & Lesseau, 2012; Flack, 2012; de Domenico et al., 2015; Smith-Aguilar et al., 2018).

Social niche construction may also provide important insights for understanding how populations face anthropogenic disturbance and conservation crises. Social niches are not expected to be uniformly affected by all individuals; rather, certain individuals are expected to have disproportionate effects on the social niches to which they belong (i.e., keystone individuals; Modlmeier et al., 2014). Investigating the flexibility with which social niches are reconstructed following the deterioration or removal of keystone individuals may assist conservationists in predicting and protecting the rate, flow, and direction of recuperative efforts (Morgan et al., 2006; Cameron et al., 2016). Simulations of social niche deterioration, fragmentation, and the suppression of cultural variation could further demonstrate the effects of human disturbance, logging, disease epidemics, or selective removals (e.g., poaching) on critically endangered primate populations (Junker et al., 2012; Morgan et al., 2018; Kühl et al., 2019).

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Chapter 3

CHIMPANZEE GESTURAL COMMUNICATION: SIGNALING AND MEANING FROM THE CHIMPANZEE PERSPECTIVE

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ABSTRACT

Signal meanings in animal communication have generally been identified as the information exchanged between individuals. Nonhuman primate signals have been shown to encode a rich range of information, such as nuanced context or signaler identity. In human language, meaning has been treated differently. Humans focus not just on the information encoded in the signal or on its effect on the receiver, but on what the signaler intended to communicate. With increasing evidence that chimpanzees share the human capacity for intentional goal-directed communication, we can begin to ask: What do chimpanzee signals mean?

To answer, we have two significant challenges to address. First, given that intended meaning is an internal mental state, what are the

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external, measurable features of a communicative event that we can use to decode chimpanzee meaning? Second, how do we parse a stream of signaling into individual signals that represent relevant units from a chimpanzee's perspective? I review our current understanding of chimpanzee gestural communication, the repertoires of signals available to them, and the different types of information they express in their use. To date, categorizations of chimpanzee behaviour have been subjective, which has resulted in substantial variation between studies. I suggest that increasingly large datasets from wild populations allow us to use chimpanzee behaviour as an objective means by which to describe repertoire and meaning in ape gesture, and that this approach better enables us to describe the communicative and cognitive capacities present in chimpanzees.

Keywords: gesture, *Pan*, communication, intention

INTRODUCTION

"What does it mean?" is the most obvious question to ask when considering any signal or system of communication, and yet it is one of the most challenging to answer. Even with a member of our own species with whom we share a language and cultural context, miscommunications occur.

One reason for these miscommunications is that the signals used in human language do not share a one-to-one association with the signalers' meanings. Words (in spoken language) and signs (in signed language) provide recipients with observable and measurable acoustic and visual information (Barutchu, Crewther, Kiely, Murphy, & Crewther, 2008; Mcgurk & Macdonald, 1976), but different signalers may use identical signals for different reasons. Homonyms are one such example; two speakers may use "bark" with the same visual-acoustic signal, but one intends for you to understand that she is talking about her apple tree and another intends for you to understand that she is talking about her dog. A further source of possible miscommunication is that even where both the visual-acoustic signal and the lexical-semantic meaning are the same, two speakers can use them to convey something very different. Grice (1991), in his exploration of speaker intent, uses the example of a job reference: the phrase “the candidate has excellent handwriting” is usually a compliment, but if your referee can find nothing else to say about you, it is quite the opposite.

Given the challenges in decoding signaler meaning in our own species, where does this leave us as comparative ethologists interested in exploring the communication of other species – including our closest relatives, the other great apes? While the problem may seem insurmountable at first, the challenges of exploring meaning in other species’ communication may not be too dissimilar to the ones we face, and resolve, in our own.

SIGNAL TYPES AND INTENTIONAL COMMUNICATION

Animal signals encode information within a wide range of modalities including visual, acoustic, tactile, olfactory, even taste, and all apes – including humans – employ large repertoires of these signals in day-to-day communication. But what, if anything, discriminates language-like communication from other types of signals?

The colour, taste, and feel of a berry encodes information about whether or not it is ripe to eat. Similarly, the colourful secondary sexual characteristics present in many primates – from Vervet monkeys’ blue testicles to females of many species’ bright pink oestrus swellings – encode information about sexual maturity and reproductive status. In both cases these signals are broadcast: they are on display whether or not a suitable recipient (or indeed any recipient) is present. Distinguishing such signals from language-like communication seems straightforward – they are involuntary fixed signals that are broadcast irrespective of any change in the signaler’s mental state, goal, or knowledge.

Other animal signals are harder to distinguish. Early research exploring communication in nonhuman primates focused on their vocalizations. In their seminal field studies, Cheney and Seyfarth (1992) established that monkey alarm calls functioned in a referential manner: other group members responded appropriately (e.g., by diving into thick foliage when an eagle alarm is given), as if the calls indicated the type of threat present. There is substantial scope for nuance in the type of information communicated, with alarm calls and call sequences encoding not just the type of predator but the urgency and proximity of the threat (Arnold & Zuberbühler, 2008; Cäsar, Zuberbühler, Young, & Byrne, 2013; Fichtel & Hammerschmidt, 2002; Murphy, Lea, & Zuberbühler, 2013). Careful field experiments have shown that, rather than responding only to the acoustic properties of an alarm call, Diana monkey recipients appear to generate a mental representation of the specific predator threat and respond to future information based on their current knowledge (Zuberbühler, 2000). As in many species' signals (Coppinger et al., 2017), we find audience effects in primate vocal communication. Here, signal production varies with the presence of specific types of individuals (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013; Slocombe & Zuberbühler, 2007). Nevertheless, to date there is very little evidence to suggest that the signaler intends for her audience to understand the information that she produces (Rendall, Owren, & Ryan, 2009; Seyfarth & Cheney, 2003).

On first glance this is hard to reconcile: the signals contain information that elicits an appropriate behavioural response in the recipient, one that often benefits the signaler, and their production varies with the audience's presence and type. How do these signals differ from language-like communication? They are certainly closely linked to it; however, the presence of an audience effect is not sufficient to demonstrate that the signaler intends to communicate to the recipient. Instead, these signals, while rich and nuanced, appear to often be an extension of the fixed reflexive signals described above. The likelihood of calling, or the call volume or length, may vary, but the signaler will produce the call even when alone (Coppinger et al., 2017), and variation in signal production can be explained as a function of variation in signaler arousal, given the presence and type of different audiences. When a chimpanzee increases her rate of food calling because an ally or higher-ranking individual appears to be near (Schel, Machanda, et al., 2013), she could be doing so after having formed an intention to tell them about the food, but she could also be more aroused or excited by the presence of a friend or high-rank individual, and that increase in arousal could lead her to call for longer or more loudly. While a richer cognitive interpretation remains possible, the simpler, more parsimonious explanation – that the signaler does not consider the recipient's mental state – remains more likely (Cheney & Seyfarth, 1996).

Even as language users, humans continue to produce many nonlinguistic, often involuntary, signals. Some of these are susceptible to audience effects – for instance, we smile more when someone is smiling at us (Provine, 1992; Wild, Erb, Eyb, Bartels, & Grodd, 2003) and laugh more when others are with us (Devereux & Ginsburg, 2001). I am very likely to yelp when I grab a too-hot pan from the stove. I will yelp whether or not there is someone else in the room, but I may yelp more loudly if you are about to grab the other side of it. Those yelps are quite different from my choosing to tell you with language that the pan is hot, which I would be less likely to do if you were in the room and had seen me yelp, and more likely to do if you walked in a moment later and were unaware of the danger.

What discriminates language is not the type of signal or its modality; it is in how we use it, for example in choosing whether or not to communicate to a specific recipient in order to achieve a particular goal, and doing so depending on what we know about them and the information they already have. Rather than fixed information that is encoded in the physical form of the signal, the relationship between spoken or signed words and their meaning is a function of the signaler's intention. To date, there is very little evidence of this type of intentional use of signals in nonhuman animals (Rendall et al., 2009; Seyfarth & Cheney, 2003).

The exploration of intentional communication in nonhuman species was inspired by the study of language development in young children. Bates, Camaioni, and Volerrra (1975) describe the distinction between illocutory acts, in which an infant deployed a conventionalized signal toward a socially recognized goal, and perlocutory acts, in which a signal may have an effect on the recipient, but without any evidence that the signaler intended it. As with other primates, we have no way to interrogate a 1-year-old child to find out her meaning or desired goal; instead we must infer whether these are present from cues in her observable behaviour. She might check whether or not her audience can see (or hear) her signal, and if not either move to another location or select a different signal. If her signal is intended to achieve an outcome, she should pause after signaling to see whether or not it was achieved, and if not persist or elaborate with additional signals. Take another human example: I walk into a busy pub and see that you are already ordering with the bartender. I would like you to get me a beer, but there is no point in waving to you because you are facing the wrong way. I have to call your name or move closer and tap you on the shoulder. Despite the fact that many others in the pub could see me wave, I have a specific audience in mind: you. I adjust my signaling or signaling location depending on your ability to perceive it. Once you can perceive my signals, I can now ask you for a beer – but I do not do so with an endless string of "beer-please-beer-please-beer-please" (despite the fact that the stimulus of my desire for a beer is a continuous state at this point). Instead I ask once and check to see if your behaviour indicates that you have understood me. If not then I will ask again, and if my original "beer please" signal is not doing the trick then I might change signals or add new ones, perhaps pointing to the bar tap. Crucially, despite that fact that my desire will not be satisfied until I start to drink the beer, once your behaviour indicates that you understand me, I stop signaling. All of these behavioural cues indicate that my communication is intentional: it is directed at a specific audience, with a specific goal in mind. We see these same behavioural cues in the gestural communication of great apes. They select an appropriate signal modality for their audience or move into an appropriate signaling location and wait for a response after signaling (Genty, Breuer, Hobaiter, & Byrne, 2009; Hobaiter & Byrne, 2011b; Liebal, Call, & Tomasello, 2004; Liebal, Call, Tomasello, & Pika, 2004; Tanner & Byrne, 1996; Tomasello, George, Kruger, & Farrar, 1985). Where signals fail, they persist (Hobaiter & Byrne, 2011a; Leavens, Russell, & Hopkins, 2005; Liebal, Call, & Tomasello, 2004; McCarthy, Jensvold, & Fouts, 2013) and elaborate (Cartmill & Byrne, 2007; Leavens, Russell, & Hopkins, 2005).

Around the same time that Bates was exploring intentional communication in young human infants, Plooij (1978) was describing the gestural communication of wild infant chimpanzees in Gombe Stream National Park. He found that the same gesture might be used toward several goals, and several gestures might share the same goal. He described this lack of a one-to-one association between signal and outcome as "openness, which is one of the most characteristic design features of human language" (p. 127).

While the gestural communication of great apes had been noted in early field studies of chimpanzees and gorillas (Goodall, 1986; Schaller, 1963), it was work with apes living in captive settings that first systematically explored their gesturing (Bard, 1992; Cartmill & Byrne, 2007; Leavens, Hopkins, & Bard, 1996; Pika, Liebal, & Tomasello, 2003, 2005; Tanner & Byrne, 1996; Tomasello et al., 1985; Tomasello, Gust, & Frost, 1989). At the time, decades of work suggested that primate vocal signals were typically fixed, with no evidence for open or intentional use, so it generated substantial excitement when researchers found abundant evidence for the apparently intentional use of gestures by chimpanzees (Leavens, Russell, & Hopkins, 2005; Tomasello et al., 1985, 1989) and other apes (Bard, 1992; Pika et al., 2003, 2005; Tanner & Byrne, 1996). Today, our view of vocal signals is more nuanced (Crockford, Wittig, & Zuberbühler, 2017). The criteria used to establish intentionality typically rely on detecting visual attention – not a necessary feature of intentional acoustic signals, including audible gestures (Hobaiter & Byrne, 2011b). We now have evidence of the intentional use of a type of alarm call in chimpanzees (Crockford, Wittig, & Zuberbühler, 2015; Crockford et al., 2017; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013), and of an apparently referential signal in a fish (Vail, Manica, & Bshary, 2013). With improving methods we may able to detect intentional communication more widely, particularly where there is strong selection for flexible communication to a specific audience, such as in some alarm or food signals. However, to date, the only two known systems of communication in which a large repertoire of signals is used in an intentional manner in everyday communication are human languages and great ape gestures.

Gestural signals form a central part of great ape communication. Adapted to typically dense forest habitats with relatively short lines of sight, the initial impression of an ape’s social world is overwhelmingly vocal. Chimpanzees in the Budongo Forest in Uganda are exposed to over five times more vocal signals than gestural ones but produce both vocal and gestural signals at around the same frequency (Hobaiter, Byrne, & Zuberbühler, 2017). As well as the evolutionarily urgent signals linked to danger, food, or sex, great apes employ gestures to navigate their everyday social needs such as grooming, travel, and play (Douglas & Moscovice, 2015; Fröhlich, Müller, Zeiträg, Wittig, & Pika, 2017; Fröhlich, Wittig, & Pika, 2016b; Genty et al., 2009; Graham, Furuichi, & Byrne, 2017; Graham, Hobaiter, Ounsley, Furuichi, & Byrne, 2018; Hobaiter et al., 2017; Hobaiter & Byrne, 2011ab, 2012, 2014, 2017; Pika & Mitani, 2006; Roberts, Vick, & Buchanan-Smith, 2012). They have large repertoires of gestures at their disposal to achieve these goals, with 80 to 100 signals, the majority of which appear to be species, or even family, typical (Byrne et al., 2017; Genty et al., 2009; Graham et al., 2017; Hobaiter & Byrne, 2011b). These repertoires could be significantly larger, with over a thousand gestural actions possible given the different combinations of movement and limb available to all apes (Hobaiter & Byrne, 2017). Given this potential repertoire, the overlap between species is impressive: around 70% across apes, and around 90% within *Pan*. Recent research included young children on the cusp of language production and found almost 90% overlap between their gestures and those of chimpanzees (Kersken, Gómez, Liszkowski, Soldati, & Hobaiter, 2018).

Great apes combine their gestures into sequences, even exchanging them back and forth (Genty & Byrne, 2010; Hobaiter & Byrne, 2011a; Liebal, Call, & Tomasello, 2004; McCarthy et al., 2013). Typically used from around one year of age (Bard et al., 2014; Schneider, Call, & Liebal, 2012), silent visual and contact-based gestures appear to emerge first (Schneider et al., 2012), with audible gestures later, likely reflecting the young apes’ increasing independence from their mothers (Fröhlich et al., 2016b; Plooij, 1978).

WHAT DOES IT ALL MEAN?

Given the evidence that great ape signalers use gestures intentionally to achieve a particular goal, we can do more than describe the information that is available to the recipient if they are able to decode it. We can explore what the signaler means to say in the language-like sense (Grice, 1957, p. 19). However, doing so is not straightforward. The lack of a fixed one-to-one relationship between intended meaning and observable behaviour makes the interpretation of meaning a challenge in even our own species. Combine that with additional errors due to miscommunication or misunderstanding and the picture starts to become very messy indeed. The first approach to resolving this problem was to describe gestures by the context in which they occurred; for example, as a play, feeding, or travel gesture (e.g., Pika et al., 2003, 2005; Plooij, 1978; Tomasello et al., 1985). In doing so we can employ observable behaviour to describe a gesture's use. However, imagine a situation in which the chimpanzee signaler's meaning is "go away!" She could use this gesture when playing, when feeding, or when traveling. In using the behavioural context to define a gesture's meaning, the gesture appears to be highly flexible, whereas the signaler's intention is quite specific. An alternative approach employed the recipient's response to explore meaning (e.g., Roberts et al., 2012) – asking what happens after a signaler produces the gesture? But a response to a gesture may include another gesture, a misunderstanding, or even a refusal. Instead, as in the busy bar above, the key to understanding a signaler's meaning may be in exploring what stops the signaler from continuing to gesture. Once your behaviour indicates that you know I want a beer, I stop signaling for one. My desire for beer has not (yet) been satisfied when I stop signaling: my signals are not a fixed response to a particular internal stimulus. A chimpanzee signaler's goal is to use their gestures to change the behaviour, or possibly even the understanding (Cartmill & Byrne, 2007) of their recipient (Cartmill & Byrne, 2010; Genty et al., 2009; Graham et al., 2018; Hobaiter & Byrne, 2014).

It remains possible that for any one case of gesturing signalers simply give up having failed to achieve their goal, or they may be persuaded to accept a different outcome by the recipient. But if specific types of gesture have consistent lexical-semantic meanings, in a similar way that particular words or signs have meanings in human language, then we should see a pattern emerging across multiple cases of the gesture's use. In fact, not only do gestures have specific meanings, but these meanings also appear to be consistent across signalers (Hobaiter & Byrne, 2014) and, in the very closely related chimpanzee and bonobo, are also largely shared across species (Graham et al., 2018). Using this method to describe signaler meaning, gestures retained their openness or flexibility, with some gestures employed toward more than one goal and some goals achieved by multiple gestures. In captive settings, the majority of gestural communication is recorded in play (e.g., Bard, 1992; Genty et al., 2009; Tomasello et al., 1985). In wild populations, play remains an important context for gesture use; however, wild chimpanzees employ their gestures to achieve a wide range of goals, with at least 19 meanings described to date, including two "negations" (stop that, move away; Hobaiter & Byrne, 2014). One problem with this method is that, by definition, the meanings described represent a limited set of imperative requests. Neither a declarative (e.g., "what a lovely fig tree") nor an imperative that does not require a change in behaviour (e.g., "stay there") could be described using this method, and there are likely additional meanings or categories of meaning that remain to be described. However, in the largest studies to date, researchers found that it was possible to ascribe a meaning to the majority of gesture types explored (Graham et al., 2018; Hobaiter & Byrne, 2014), so it seems likely that the majority of chimpanzee and bonobo gestural communication is deployed to achieve particular imperative requests. Interestingly, the redundancy within the gestural repertoire was not evenly distributed; some goals that reflect more nuanced social negotiations (e.g., for affiliation, negations) were associated with more gestures than those that reflected relatively simple requests (e.g., for grooming; Hobaiter & Byrne, 2014). As was found with long-term study of the primate vocal alarm calls, there may be additional greater nuance in gestural requests than is captured by our current descriptions of chimpanzee and bonobo goals (Arnold & Zuberbühler, 2008; Cäsar et al., 2013; Fichtel & Hammerschmidt, 2002;

Murphy et al., 2013). A chimpanzee signaler may want to be able to say “stop that” in one way to his alpha male and in another way to his little brother. While, to date, the majority of studies have explored different aspects of ape signaling in isolation (e.g., either gesture or vocalization), this approach does not reflect the real world of great ape communication. Just as we continue to gesture while speaking, even when talking on the phone (Bavelas, Gerwing, Sutton, & Prevost, 2008), great ape communication is an integrated combination of gestures, vocalizations, facial expressions, and many other signals (such as piloerection, indicating arousal). Providing a richer description of the meanings in great ape communication will require a more holistic approach that integrates signal types into the full socioecological environment in which communication occurs (Cheney & Seyfarth, 2018; Genty, Clay, Hobaiter, & Zuberbühler, 2014; Hobaiter et al., 2017; Pollick, Jeneson, & de Waal, 2008; Waller, Liebal, Burrows, & Slocombe, 2013; Wilke et al., 2017).

A *PAN*-CENTRIC APPROACH TO COMPARATIVE COMMUNICATION

So far, much of what I have discussed has been shaped by a direct comparison with human language. In many studies of comparative behaviour, human behaviour is the default position, with similarities and distinctions described based on our understanding of human traits. But while human language is a uniquely rich and powerful system of communication, it is, like any other human behaviour, fundamentally adapted to human needs. Pointing, for example, occurs in many forms and is a culturally universal human trait (Wilkins, 2003) that emerges spontaneously in early infancy (Butterworth, 2003; Franco & Butterworth, 1996). There is almost no evidence from wild apes of a similar gesture (Hobaiter, Leavens, & Byrne, 2014). Thus, it could be argued that apes are not capable of pointing (e.g., Tomasello, 2008). However, evidence from captive, and in particular enculturated, apes shows not only that they can acquire pointing spontaneously, but also that they will then use it with both humans and conspecifics (Leavens & Hopkins, 1999; Leavens et al., 1996; Leavens, Hopkins, & Bard, 2005). There is no fundamental biological difference between wild and captive apes: it is not that wild apes do not have the capacity to point, it is that they do not express it, likely because their socioecological environment does not promote it (Leavens, Bard, & Hopkins, 2017; Leavens, Hopkins, & Bard, 2005). If wild chimpanzee communication formed the basis for comparative studies of communication, would studies have described pointing in humans? I would hope that chimpanzee scientists might have noticed humans' funny tendency to extend their arms and fingers during communication and explored it. But there are likely many more subtle distinctions that reflect the fact the chimpanzee communication is adapted to chimpanzee needs. Many aspects of behaviour previously claimed by scientists to be human species universals subsequently turned out to be Western cultural norms (e.g., Haun, 2007; Levinson, 1996; Levinson, Kita, Haun, & Rasch, 2002). What aspects of chimpanzee communication are we missing by taking human language as our central point of comparison?

One illustration of this point is found in how we distinguish what a gesture is. Researchers across groups and species often approach this question arbitrarily; some consider only hand and finger movements (Leavens & Hopkins, 2007; Pollick & de Waal, 2007; Roberts et al., 2012), while others include limb and body movements as long as they meet the criteria for intentional use (Fröhlich et al., 2017; Genty et al., 2009; Graham et al., 2017; Hobaiter & Byrne, 2011b; Pika et al., 2003; Tomasello et al., 1985). Some studies split at a fine level, distinguishing the position of individual fingers (Pollick & de Waal, 2007); or lump up at increasing levels (e.g., Byrne et al., 2017; Hobaiter & Byrne, 2011b). A decision to split or lump should be driven by the particular research question being addressed (Tinbergen, 1963); however, we need to discriminate appropriate categories. The word "stop" uttered by a young girl from Glasgow may have very different visual-acoustic properties to the same word uttered by a large adult man from Liverpool. Both the consistency (in lexical-semantic meaning) and the variation (in pitch, tone, intonation, accent, etc.) are interesting features. Does raising one hand or both hands change the meaning or the tone of a chimpanzee's gesture? Does it matter if it is the left hand with the fingers extended, or the right with a bend in the wrist? One way to address this is to consider the question from the apes' perspective: does a chimpanzee recipient respond differently to a signaler raising one or both hands, and if so how? With the same category of response, but faster? We recently explored this question in a large dataset of East African chimpanzee gestural communication (Hobaiter & Byrne, 2017). First, we split gestures at the most fine-grained level; then, we lumped them up depending on consistency in their apparent meaning based on the signaler's apparent satisfaction with their outcome. In doing so, we were able to establish that simultaneous (hit, hitting, slap, slapping, etc.) and alternating (drum, drumming) hitting gestures were typically used to achieve the same types of meanings, despite being previously split in the majority of described repertoires. Similarly, the use of one limb or two had little impact on the type of meaning communicated, although it may impact other information, such as emphasis (Hobaiter & Byrne, 2017).

An important step in resituating our description of chimpanzee communication within the socioecological context of chimpanzee behaviour is the increasing number of studies of communication in wild chimpanzees and other apes (Douglas & Moscovice, 2015; Fröhlich, Kuchenbuch, et al., 2016; Fröhlich et al., 2017; Fröhlich et al., 2016b; Graham et al., 2017, 2018; Hobaiter et al., 2017; Hobaiter & Byrne, 2011b, 2011a, 2012; Pika & Mitani, 2006; Roberts et al., 2012). While studies in captivity allow the very detailed investigation of individual life-histories, a captive environment significantly impacts the expression of apes' behavioural repertoires, including their communication (Hebert & Bard, 2000; Hobaiter & Byrne, 2014; Seyfarth & Cheney, 2017).

Compare the lives of captive and wild chimpanzees. In captivity, groups, often hybrids of one or more of the three separate wild subspecies, rarely number more than 10 to 20 individuals, while in the wild, communities, for example of East African chimpanzees, number anywhere from about 30 to over 200. In captivity, the physical and social environment limits the range of behaviour expressed. There are no neighbouring groups to fight with, there are no monkeys to hunt, females are typically on hormonal birth control, there are no predators, and food is abundant and easily available. As a result, they spend much of their time in play. Their enclosures are typically open, with long lines of sight and limited opportunity to use vertical space. Perhaps most crucially for understanding chimpanzee social communication, captive individuals spend much of their day in regular visual, and near constant auditory, contact. The impact on their choice of signals, but also on the information they have or need to find out about others is likely to be profound.

In the wild, parties fission and fuse over dozens of kilometres of dense rainforest; a female East African chimpanzee may not see many of the other individuals in her group for weeks or even months, while others will meet group members almost every day. This fission-fusion social structure allows wild chimpanzee mothers to modify their social environment; one way in which they do so is to increase their gregariousness when they have male offspring (Murray et al., 2014). Chimpanzee social lives are male philopatric, and their hierarchies are male dominated (Goodall, 1986; Hayaki, Huffman, & Nishida, 1989), and as a result male-male social relationships are particularly important for lifetime fitness. Young male chimpanzees exploit these opportunities, with sex-specific differences in social behaviour (Lonsdorf, Anderson, et al., 2014; Lonsdorf, Markham, et al., 2014) reflected in gestural communication differences (Fröhlich et al., 2017; Fröhlich, Wittig, & Pika, 2016a).

In captive groups, play is the dominant context for gestural communication across ape species (Bard et al., 2014; Genty et al., 2009; Liebal, Call, & Tomasello, 2004; Pika et al., 2003, 2005; Tomasello et al., 1985), so much so that it was suggested that gestural communication is typically employed for “less evolutionary urgent functions” (Call & Tomasello, 2007). However, captive apes rarely experience evolutionary urgent contexts. In wild chimpanzee groups play remains an important context for gesture (Fröhlich et al., 2016a; Hobaiter & Byrne, 2011b); however, gesture is also used in contexts in which there is a real risk to life, such as consortship. Here a female and male chimpanzee move away from the main group, sometimes days or weeks in advance of her fertile peak, in order for him to retain exclusive sexual access (Tutin, 1979; Goodall, 1986; Nishida, 1997). In doing so the male in particular risks lethal attack both from neighbouring groups and from males within his own group (Fawcett & Muhumuza, 2000; Wilson et al., 2014). Under these circumstances, gestural communication provides a particularly flexible tool. All vocalizations contain both audible and visual modes of information (a chimpanzee cannot pant-hoot without making the visual facial movements needed to produce the sound). But while all gestural signals contain information in the visual modality, these include visual-silent gestures (an arm raise or hand wave), audible gestures (a branch shake or object drum), and contact gestures (a touch or slap) that themselves can also include audible information. Moreover, most, if not all, chimpanzee vocal signals appear to encode the individual signaler's identity (Crockford, Herbinger, Vigilant, & Boesch, 2004; Herbinger, Papworth, Boesch, & Zuberbühler, 2009; Kojima, Izumi, & Ceugniet, 2003). In contrast, only chimpanzee long-distance drumming gestures appear to encode signaler identity (Arcadi, Robert, & Mugurusi, 2004). Within a visually dense rainforest, where lines of sight may be limited to just a few metres, gestural communication allows the signaler to choose whether or not to reveal their intended goal and their identity to any unknown nearby eavesdroppers. On consortship, as opposed to other sexual solicitations, male chimpanzees select different gestures and use silent-visual or those with a limited audible range (Hobaiter & Byrne, 2012). We find further evidence for chimpanzees' ability to consider multiple audiences in their wider use of gestural and vocal signals across their everyday behaviour, with signalers selectively deploying gestural or vocal signal types depending on the social context and considering the public/private nature of information (Hobaiter et al., 2017).

CONCLUSION

The age, sex, social rank, and biological relationship of a chimpanzee signaler and a chimpanzee recipient impact the shape of their gestural communication. Whether it is in the selection of gesture types or modalities (Fröhlich et al., 2016a), the combination of gestures with other signals (Hobaiter et al., 2017; Hobaiter & Byrne, 2011a; Waller et al., 2013), or the particular way in which a goal (Fröhlich et al., 2016b) or gesture (Bard et al., 2014; Bard, Maguire-Herring, Tomonaga, & Matsuzawa, 2017) is expressed, the rate of social interaction and the variety of communicative partners impacts the frequency and variety of gestures used in infancy (Fröhlich et al., 2016b). Signalers use gestures selectively depending on the costs and benefits of signaling to their current audience and potential audience (Hobaiter et al., 2017; Hobaiter & Byrne, 2012). Forest density has been suggested as a possible explanation for variation in the acoustic structure of their pant-hoot vocalizations (Mitani, Hunley, & Murdoch, 1999); variation in the availability and distribution of large buttressed trees might similarly impact their buttress-drumming gestures. A deeper understanding of chimpanzee gestural communication requires a broader understanding of how their communication is impacted by their socioecological environment. Here, variety may be key. Among wild populations there are dramatic differences in habitat, from savannah grassland communities in Senegal (Bogart & Pruetz, 2008), to dense rainforest communities in Uganda (Hobaiter & Byrne, 2011b; Mitani et al., 1999); in sociality (Lehmann & Boesch, 2004); and in culture (Whiten et al., 1999). Comparisons between different socioecological environments, including captive and (pre-existing) enculturated communities, allow us to better understand the flexibility and potential within chimpanzee gesturing. In recentering our exploration of chimpanzee communication firmly within chimpanzee behaviour, we are better able to explore meaningful similarities and differences with human communication, as well as developing a richer understanding of chimpanzees themselves.

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Chapter 4

PATTERNS IN CHIMPANZEE MARKING AND DRAWING

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ABSTRACT

In humans, aspects of aesthetics appear in balance, respect for boundaries, threeness, and other patterns in markings (Morris, 1962). Two studies of chimpanzee marks systematically analyzed the productions for patterns. In the first study, seven captive chimpanzees (*Pan troglodytes*) produced drawings at the University of Oklahoma between November 1971 and November 1972. Chimpanzees drew on sheets of paper that were either blank or had a stimulus. The stimulus was located either in the centre or offset from the centre. Analysis of digitized

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versions of these drawings tested whether chimpanzee mark placement was contingent on the location of stimulus figures. Centroid locations in drawings significantly changed between stimulus type for all drawing categories and among participants for free choice and central figure drawings. Participants drew in the empty space opposite offset figure drawings. In the second study, titled productions were used. Chimpanzees who were cross-fostered by humans acquired signs of American Sign Language and other behaviours typical of Western human children, such as drawing. The chimpanzees titled many of their drawings. Researchers asked one of the cross-fostered chimpanzees, Moja, to draw pictures of seven objects resulting in 35 drawings. Using this set of drawings, experimenters instructed 77 human participants to sort 28 drawings into stacks based on their similarity to an exemplar. A multidimensional scaling analysis showed that participants perceived form similarity in three objects that Moja drew. Participants frequently sorted Moja's drawings of cup, boot, and banana into separate stacks, indicating they identified patterns that were repeated in each set of drawings. The findings in these studies support previous conclusions that chimpanzee drawings are not random acts on paper, but are deliberate exploratory choices that vary across species and on an individual level (Boysen, Berntson, & Prentice, 1987; Morris, 1962; Schiller, 1951; Smith, 1973; Zeller, 2007). Communicating intent behind the marks of a nonhuman species is fascinating to anthropologists, primatologists, and art historians alike, for it provides further evidence for a continuity of species and the biological basis for aesthetic. Analyzing and interpreting these drawings enlighten us about the behaviour of another species and possibly about the behaviour of early humans, who began to express themselves visually through symbols and figures tens of thousands of years ago (Bahn, 1998, p. xii).

Keywords: schema, chimpanzee, artwork, drawing, cross-fostering

INTRODUCTION

Like human children, chimpanzees show innate interest in drawing. Kohts documented the earliest evidence of ape drawing. She (1935) compared drawings Joni the chimpanzee produced from 1913 to 1916 with drawings her son Roody produced from 1925 to 1929. In comparison of two "first-stage" drawings, both had stylistically similar simple scribbled lines. Kohts compared Roody's age two drawings to Joni's age three and four drawings. From this comparison, she concluded that "the predominance of round and circuitous drawing, while the chimpanzee at age 3 to 4 years, even after extensive exercises in drawing, did not go beyond drawing straight, sometimes crossing, lines haphazardly scattered on paper, which were so characteristic of the first two stages of the child's drawing" (Kohts, p. 327).

Winthrop N. Kellogg and Luella D. Kellogg received infant chimpanzee Gua on loan from the Yerkes laboratory in 1931. At that time, the Kelloggs had a 10-month-old son, Donald, and agreed to raise Gua as their son's companion for nine months. The Kelloggs (1933) performed a drawing test during this experimental period, and both chimpanzee and human infants drew on the page when given a pencil. As with the Kohts (1935) study, Donald surpassed Gua's drawing abilities as he got older, and imitated the examiner's straight line while Gua failed to do so (Kelloggs 1933, p. 266).

Schiller (1951) published the first study primarily focused on chimpanzee drawings. Alpha, an 18-year-old female chimpanzee at the Yerkes Laboratories of Primate Biology, showed a keen interest in drawing. Researchers attached paper to a 12 by 15 in board and inserted it through a narrow space below the caging. Researchers pasted figures from coloured paper onto sheets of contrasting colours and cut openings from paper sheets to paste contrasting coloured sheets behind (p. 101). Alpha received one or two pencils of different colours and drew on the paper from 10 to 180 sec before the experimenter withdrew the board. The stimuli pasted on paper served to study colour preference, figure formation, influence of form, position, size of figure or groups of figures, and tendencies to complete figures (p. 102). Alpha mainly used two strokes: short dashes and nearly parallel broad zigzags.

When presented with a blank sheet of paper, Alpha usually made short marks in each corner and then along the margins, and finally filled in the middle of the paper with coarser marks. In reaction to the various figures, she placed her marks almost exclusively within a single figure, and only diverged from this pattern in three of the 25 large, single figures presented (p. 103). In reaction to the placement of single figures positioned off-centre, Alpha drew in the largest open space, producing a "sort of balance between her markings and the presented figure" (p. 104). When presented with outlined figures, Alpha confined her drawing to the space within the outline in 22 out of 24 examples. She reacted differently to spots scattered at random depending on the size of spots and the distance between them. If the spots were large and spread out, Alpha kept her drawing within each separate figure. If the spots were small and close together, she filled in the space between them or drew over the grouping as if they were one large figure. When presented with a solid figure with a portion cut out, she generally marked the figure and the left the open space blank, leaving the missing portion unmarked. In two of six cases, Alpha carefully filled in the missing portion with few marks made on the solid figure. She did not complete incomplete triangles, squares, polygons, or circles. Alpha consistently completed the figure when presented with a space left among a circle of six or more dots. In reaction to symmetrical figures, Alpha responded to triangular outlines by centring her marks along each side of the triangle five out of seven times. Schiller stated that "the location of the scribblings indicates the dominant aspect of the total configuration presented, and this dominance is quite evidently determined by the physical proportions and arrangement of the elements of the situation and not by selective conditioning" (p. 111). Alpha's drawings in reaction to various stimuli presented a strong argument for inclinations of balance, symmetry, and a self-motivated eagerness to draw, but these results were not quantitatively analyzed.

Morris (1962) devised a similar experiment with Congo, a 1-year-old male chimpanzee at the London Zoo. Morris obtained 172 black and white drawings from Congo. Congo made 40 drawings on blank sheets of paper while the remaining 132 he made on pages that already contained one or more simple stimulus figures. When presented with a blank sheet of paper, Congo kept within the space (40 out of 40 tests), marked where he had not already marked (30 out of 40 tests), marked where he already marked (10 out of 40 tests), concentrated on the centre (24 out of 40 tests), and marked in a series of radiating lines (15 out of 40 tests) (p. 70). When presented with incomplete figures, he treated most figures as if complete and only marked inside the incomplete area once. Congo received a novel stimulus to test whether he would create intersecting lines when presented with a vertical line on the page, and only produced the intersecting response in 1 out of 18 tests. Like Alpha, Congo tended to mark a central figure and positioned marks in the blank space opposite an offset figure. He also marked the corners, far less frequently than Alpha. These results solidified Schiller's findings of central marking and an inclination to "scribble for scribbling's sake," but they were only descriptive.

Smith (1973) first used quantitative methods to analyze chimpanzee drawings. He obtained approximately 100 drawings on paper from three young chimpanzees. Smith presented the chimpanzees with white 8.5 by 11 in sheets of paper with one of 16 different stimulus figure categories (blank sheet, central small square, central large square, central small circle, central large circle, small right offset square, large right offset square, small left offset square, large left offset square, slightly right small square, slightly left small square, two centred horizontal small squares close together, two centred horizontal small squares slightly further apart, two centred horizontal small squares far apart, offset complete circular array of squares, and offset incomplete circular array of squares) printed on them. The blank sheets served as the control (p. 407). Researchers presented five sheets of paper to each chimpanzee per session with either a black or a blue crayon.

Smith analyzed the drawings by fitting a Plexiglas grid over the paper, dividing it into 10 rows and 10 columns, totaling 100 rectangular cells measuring 3 by 2.25 cm. Researchers placed the grid over each drawing and made a tally mark on the corresponding score sheet wherever a grid cell contained a crayon mark. All three chimpanzees marked significantly more in the lower half than the upper half on the blank sheets of paper, and the markings were concentrated in the central 16% of the paper. In categories with one stimulus figure in the centre, all chimpanzees tended to mark the centre of the sheet, which corresponded with earlier findings (Morris, 1962; Schiller, 1951). On sheets that displayed one figure offset from the centre, the chimpanzees marked the available space without attempting to balance the offset figure. In the separated figures category, two of the three chimpanzees practiced a space-filling tendency consistent with earlier findings (Morris, 1962; Schiller, 1951). When the multiple separated stimulus figures were close together, two of the chimpanzees marked each component separately. When stimulus figures were between 6.25 and 10 cm apart, two chimpanzees marked the space between them. When testing for completion of an incomplete figure, the chimpanzees concentrated their marks in the general area of the stimulus array, but these marks occurred closest to the centre regardless of the location of the gap in the array. Smith concluded that chimpanzees respond to different stimulus figures by marking the paper and concentrating their marks in the centre of the page.

Boysen et al. (1987) continued the stimulus-drawing test in chimpanzees by presenting 18 different figures to three chimpanzees. Researchers obtained a total of 618 black and blue ballpoint pen drawings on 8.5 by 11 in white paper and compared results to earlier studies. Categories 1 through 16 were the same as Smith's (1973), while categories 15a and 16a were mirror images of Smith's categories 15 and 16. Researchers analyzed the drawings with a computerized adaptation of Smith's (1973) approach by placing a 10 by 10 Mylar grid over each drawing and recording the marked cells with a graphics pen. Boysen et al. scored and averaged each drawing by stimulus category and created a summary matrix for each category. General results showed a tendency for all three chimpanzees to mark toward the bottom horizontal centre of the page. Like Smith, Boysen et al. found that any presence of a stimulus figure on the page elicited more centralized markings than a blank sheet. There was no evidence of balance among offset figures or closure of incomplete figures. Results also supported Morris's (1962), Schiller's (1951), and Smith's (1973) observations of space filling. As in previous studies, the chimpanzees marked each component in a multiple-stimulus figure when components were close together and marked the space in between figures when they were further apart.

Tanaka and Tomonaga (2003) studied the development of scribbling in infant chimpanzees. Researchers used a notebook computer with a 10.4 in touch-sensitive screen to record strokes produced by three pairs of mother and infant chimpanzees. Each pair entered the experimental booth and accessed the screen for a 3-minute trial. A dot appeared on the screen with an arrow-type mouse pointer at the centre of the white screen. The chimpanzees touched the screen any way they chose for the trial. The monitor provided six colours – black, red, blue, green, yellow, and white – at different sessions for electronic ink. The white electronic ink served as the control condition since it did not produce visible traces on the already white screen. The computer recorded all touches to the screen, and the ink colour remained the same during each session and changed per session to prevent familiarization.

Researchers divided touches between mother and infant based on time-stamped data from the computer and video monitoring. Researchers used "strokes" as the unit analysis and defined them as "a series of consecutive dots, where each dot was recorded less than 100 ms after the one immediately preceding it. When an interval of more than 100 ms passed between the recording of one dot and the next, the first dot became the end of the previous stroke and the second dot the beginning of the next stroke" (p. 247). Researchers calculated the number of strokes in each session per subject and classified each stroke into six types: dot, straight line, curve, hook, loop, and miscellaneous.

All three infants drew on the screen without food reward. Two of the three mothers also touched and drew on the screen. Infant chimpanzees drew on the screen for much less time than adult chimpanzees. Researchers classified a total of 1,460 strokes and all infants produced each type of stroke. Chimpanzees made more strokes when the ink colour was visible on the screen. Results supported previous studies (Boysen et al., 1987; Morris, 1962; Schiller, 1951; Smith, 1973) by showing that chimpanzees possessed an intrinsic motivation to draw. Chimpanzee infants aged 13 to 23 months demonstrated motor-control to produce a variety of strokes with their finger. Infant chimpanzees drew with their fingers before they used a mark-making instrument on paper. The same infant chimpanzees showed rapid development at 20 to 23 months when drawing with a marker on paper (Tanaka & Tomonaga, 2003, p. 251).

Zeller (2007) conducted a study of similarities and differences in a collection of 396 paintings made by human children, chimpanzees, gorillas, and orangutans. The researcher analyzed the number of colours used, first and last colour preferences, use of novel colours, respect for boundaries, negative space, and placement pattern to see whether there was any evidence of choice in the production of marks to disprove a null hypothesis of random concatenations of colour and placement (p. 185). All species demonstrated centralized mark placement; chimpanzees placed their marks in the lower central area of the page in agreement with previous studies (Boysen et al., 1987; Schiller, 1951; Smith, 1973). There was evidence of respect for boundaries, with human children showing most respect for boundaries with 52.6% of their marks placed within the edges of the paper, and chimpanzees with 29.2% of their marks within the boundaries of the page (p. 198–200).

This chapter adds to our understanding of chimpanzee patterns of drawing with two systematic experiments.

EXPERIMENT 1: CHIMPANZEE RESPONSE TO STIMULUS

We systematically studied chimpanzee drawings in response to stimulus figures located on the page. Analysis tested whether the location of the chimpanzees' marks on the page were contingent on the location of stimulus figures. Findings support previous studies that chimpanzee drawings show systematic patterns that vary between individuals. These findings have implications for motor play, aesthetics, and the ontogeny and phylogeny of art.

Method

Participants

Seven captive chimpanzees (*Pan troglodytes*), Ally, Booee, Bruno, Cindy, Lucy, Thelma, and Washoe, participated in the drawing study conducted by researchers affiliated with the University of Oklahoma between November 1971 and November 1972. See Table 1 for background information on each chimpanzee.

Drawings

Experimenters obtained a total of 593 drawings from chimpanzee participants between November 1971 and November 1972. Chimpanzees completed drawings on 8.5 by 11 in sheets of white paper with pencil. During drawing sessions, experimenters familiar with the chimpanzees provided them with stimulus sheets and/or blank sheets of paper. (See Figure 1 for stimulus categories.)

When the chimpanzee relinquished the drawing, the experimenter noted the top of the drawing, chimpanzee name, date, and stimulus category on the back. Experimenters also recorded information on “Chimpanzee Art Test” forms, specifying the name, sex, and age of the chimpanzee tested; the name and gender of the human experimenter; place tested; date tested; session start/finish time; number of free choice drawings; hand positions; and additional remarks. There were 81 completed drawings from Ally, 88 from Booee, 47 from Bruno, 70 from Cindy, 96 from Lucy, 70 from Thelma, and 141 from Washoe. Experimenters presented stimulus categories 1 through 22 to four of the participants (Ally, Booee, Lucy, and Washoe) and presented stimulus categories 23 through 31 to all seven participants. All participants produced drawings in the free choice (blank sheet) category.

This study used drawings from only those categories with adequate sample sizes and similar stimulus figures from previous studies. The researcher, AC, combined categories 8, 9, 10, and 12 to represent left- and right-sided offset stimulus figure drawings, and combined categories 27 to 31 to represent central figure drawings. A research assistant scanned drawings and data sheets into digital images.

Analysis

AC initially adapted techniques from Smith (1973) and Boysen et al. (1987) to analyze the drawings. AC and a research assistant placed a clear lamination sheet with a 10 by 10 grid on a tablet computer displaying each drawing. They notated each cell containing a mark with a tally on the lamination sheet. They recorded the total number of marks per cell for each drawing on a score sheet per participant. AC reevaluated and made adjustments if the research assistant obtained a different total from AC. AC completed summary matrices to show overall distribution of marks.

AC converted all drawings into .jpeg files and inputted them into a Python code programmed to provide the mean x and y coordinates (centroids) for each drawing in relation to the physical centre of the image. Python is a programming language widely used in scientific and numeric computing (“General Python FAQ,” 2015).

Statistical evaluations were based on a two-way analysis of variance (ANOVA) that independently compared mean x and y coordinates versus participants and stimulus categories. Since not all participants produced offset figures drawings, the researcher analyzed them separately from the free choice and central figures. Post hoc Tukey’s honest significant difference (HSD) tests examined differences between stimuli and participants’ centroids. Results were considered significant if $p = \leq .05$.

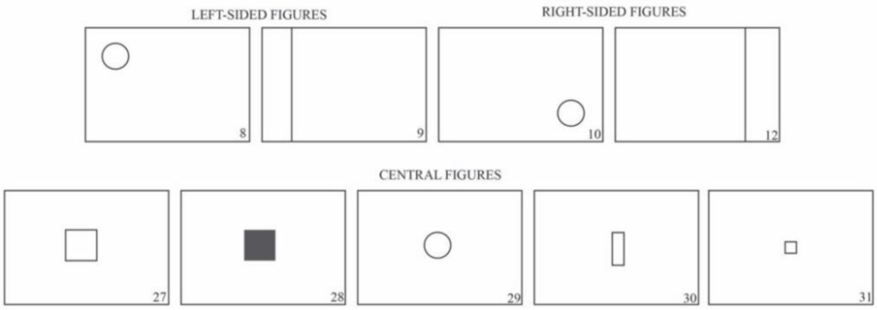

Figure 1. Presented stimulus categories for drawing. Free choice (blank sheet) is not depicted.

Table 1. Background information for each chimpanzee

Name (sex)	Year born (location)	Early rearing	Age during study (yrs)	Art experience	Location during study
Ally (M)	1969 (IPS)	Home-reared in private residence	2–3	Painting	PR
Booee (M)	1967 (NIH)	Home-reared for >30 months in private residence after experimental split-brain operation	4–5	Drawing, painting	IPS
Bruno (M)	1968 (IPS)	Home-reared for 24 months, then partially home-reared for eight months in private residence	3–4	No reports	IPS
Cindy (F)	1966 (wild)	Readily handled by humans in laboratory setting	5–6	No reports	IPS
Lucy (F)	1964 (circus)	Cross-fostered PR	7–8	Drawing, painting	PR
Thelma (F)	1967 (wild)	Readily handled by humans in laboratory setting	4–5	No reports	IPS
Washoe (F)	1966 (wild)	Cross-fostered UNR	5–6	Drawing, painting	IPS

Note. IPS = Institute for Primate Studies; NIH = National Institute of Health; UNR = University of Nevada Reno; PR = Private residence.

Results

Free Choice versus Central Figure Drawings

Mean *x* coordinates were significantly different between stimulus type F(1,340) = 7.09, p = .008 and participants F(6,340) = 2.61, p = .017. Figure 2 displays the central stimulus figure mean (865.15) farther to the right on the x-axis than the free choice drawing mean (820.91). There was a significant interaction between stimulus type and participants F(6,340) = 2.46, p = .024. Tukey's HSD tests showed individual differences between Ally versus Booee and Ally versus Thelma (see Table 3). Figure 3 shows the distribution of means between stimulus types for each chimpanzee. In this figure, the interaction is apparent in that on the *x*-axis, Ally's centroids are farthest from Booee's and Thelma's.

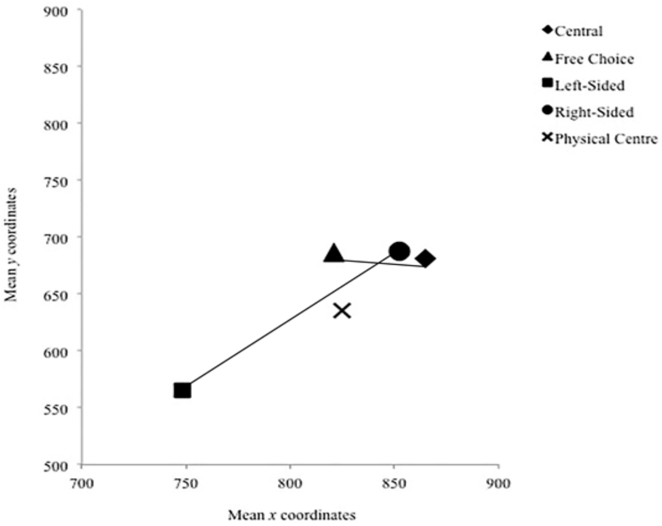

Figure 2. Scatter plot displaying mean *x* and *y* coordinates per stimulus type. Lines connect central figures versus free choice and left-sided versus right-sided figures. The larger X represents the physical centre of the page.

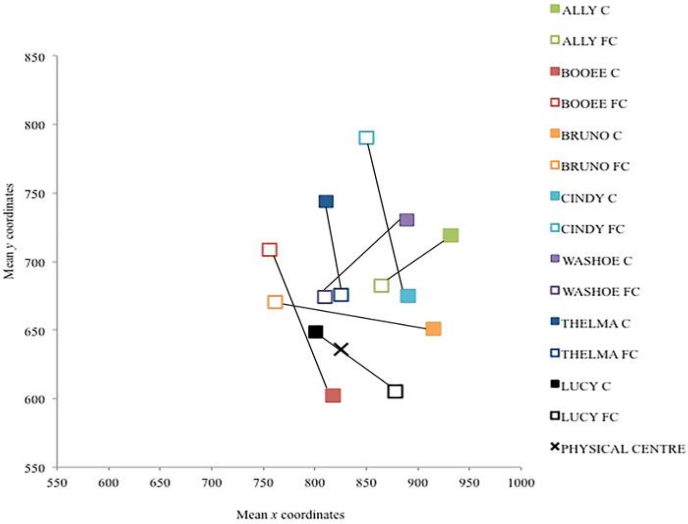

Figure 3. Scatter plot displaying free choice and central figure mean *x* and *y* coordinates per participant. Free choice coordinates are outlined squares and central figure coordinates are filled in squares. The larger X represents the physical centre of the page. Lines connect each individual's free choice and central figure coordinates to illustrate interactions.

Table 2. Tukey Simultaneous Tests for Differences of Mean x Coordinates in Free Choice and Central Figure Categories

Difference of Levels	Difference of Means	SE of Difference	T-Value	Adjusted P-Value
Booee-Ally	-128.05	32.43	-3.95	0.0015
Bruno-Ally	-59.52	35.20	-1.69	0.6222
Cindy-Ally	-46.67	30.92	-1.51	0.7394
Lucy-Ally	-88.09	34.22	-2.57	0.1339
Thelma-Ally	-94.77	30.92	-3.07	0.0354
Washoe-Ally	-81.12	29.33	-2.77	0.0827
Bruno-Booee	68.53	32.71	2.09	0.3556
Cindy-Booee	81.38	28.06	2.90	0.0573
Lucy-Booee	39.96	31.66	1.26	0.8691
Thelma-Booee	33.28	28.06	1.19	0.8996
Washoe-Booee	46.92	26.29	1.78	0.5586
Cindy-Bruno	12.85	31.22	0.41	0.9996
Lucy-Bruno	-28.57	34.49	-0.83	0.9821
Thelma-Bruno	-35.25	31.22	-1.13	0.9193
Washoe-Bruno	-21.60	29.64	-0.73	0.9909
Lucy-Cindy	-41.42	30.11	-1.38	0.8150
Thelma-Cindy	-48.10	26.30	-1.83	0.5282
Washoe-Cindy	-34.46	24.41	-1.41	0.7958
Thelma-Lucy	-6.68	30.11	-0.22	1.0000
Washoe-Lucy	6.96	28.47	0.24	1.0000
Washoe-Thelma	13.64	24.41	0.56	0.9979

Individual confidence level = 99.66%.

Mean y coordinates were significantly different between participants F(6,340) = 3.78, p = .0012. Tukey's HSD tests showed individual differences between Cindy versus Booee and Lucy versus Cindy (see Table 3). Figure 3 shows the distribution of means between stimulus types for each chimpanzee. In this figure the interaction is apparent in that on the *y*-axis, Cindy's centroids are farthest from Booee and Lucy's centroids. Mean *y* coordinates were not significantly different between stimulus type F(1,340) = .12, p = .73. There was a significant interaction between stimulus type and participants F(6,340) = 5.05, p = <.0001.

Offset Figure Drawings: Left-Sided versus Right-Sided Figures

Mean *x* coordinates were significantly different between stimulus type F(1,30) = 4.67, p = .03. Figure 2 displays the right-sided figure mean (852.61) farther right on the *x*- axis than the left-sided figure mean (748.43). Mean *x* coordinates were not significantly different between participants F(3,30) = .70, p = .55. There was not a significant interaction between stimulus type and participants F(3,30) = 1.79, p = .17.

Table 3. Tukey Simultaneous Tests for Differences of Mean y Coordinates in Free Choice and Central Figure Categories

Difference of Levels	Difference of Means	SE of Difference	T-Value	Adjusted P-Value
Booee-Ally	-52.79	29.13	-1.81	0.5397
Bruno-Ally	-50.99	31.62	-1.61	0.6743
Cindy-Ally	30.95	27.78	1.11	0.9240
Lucy-Ally	-74.76	30.74	-2.43	0.1853
Thelma-Ally	-4.21	27.78	-0.15	1.0000
Washoe-Ally	-19.08	26.35	-0.72	0.9912
Bruno-Booee	1.81	29.39	0.06	1.0000
Cindy-Booee	83.75	25.21	3.32	0.0156
Lucy-Booee	-21.96	28.44	-0.77	0.9876
Thelma-Booee	48.58	25.21	1.93	0.462
Washoe-Booee	33.71	23.62	1.43	0.7873
Cindy-Bruno	81.94	28.04	2.92	0.0539
Lucy-Bruno	-23.77	30.98	-0.77	0.9880
Thelma-Bruno	46.78	28.04	1.67	0.6376
Washoe-Bruno	31.9	26.63	1.20	0.8952
Lucy-Cindy	-105.71	27.05	-3.91	0.0018
Thelma-Cindy	-35.16	23.63	-1.49	0.7520
Washoe-Cindy	-50.03	21.93	-2.28	0.2527
Thelma-Lucy	70.54	27.05	2.61	0.1234
Washoe-Lucy	55.67	25.58	2.18	0.3083
Washoe-Thelma	-14.87	21.93	-0.68	0.9938

Individual confidence level = 99.66%.

Mean *y* coordinates were significantly different between stimulus type F(1,30) = 24.17, p = <.0001 and participants F(3,30) = 32.02, p = <.0001. Figure 2 displays the left-sided figure mean (687.55) lower on the *y*-axis than the right-sided figure mean (565.16). There was also a significant interaction between stimulus type and participants F(3,30) = 3.91, p = .01. Tukey's HSD tests showed individual differences between Booee versus Ally, Lucy versus Ally, Washoe versus Booee, and Washoe versus Lucy (see Table 4). Figure 4 shows the distribution of means between stimulus types for each chimpanzee. In this figure, the interaction is apparent in that on the *y*-axis, Ally and Washoe's centroids are farthest from Lucy and Booee's centroids.

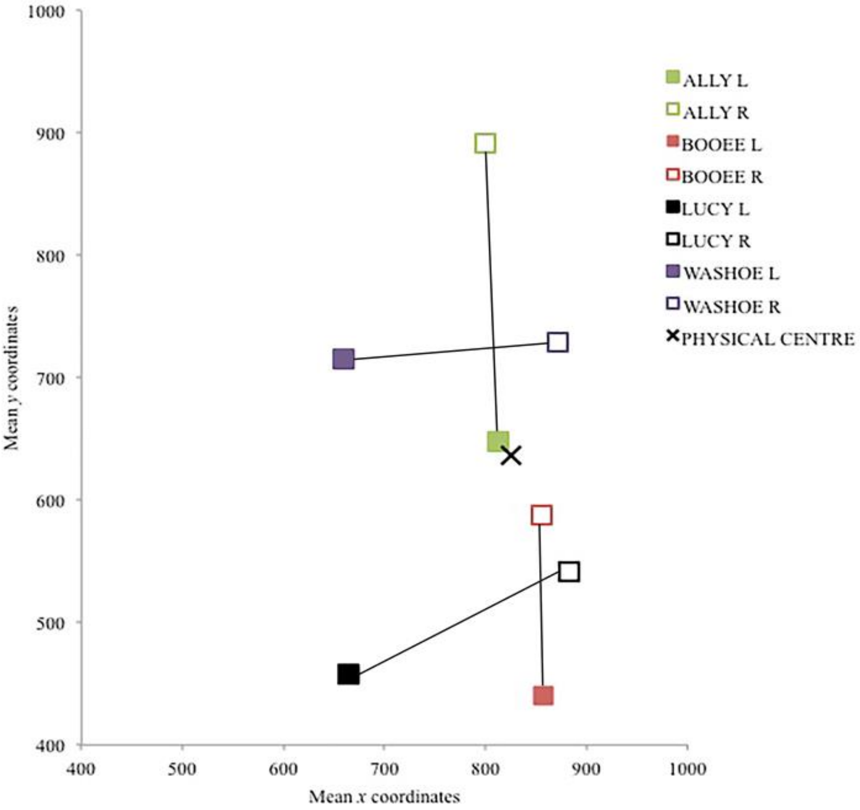

Figure 4. Scatter plot displaying offset figure mean *x* and *y* coordinates per participant. Coordinates from right-sided figures are outlined squares and coordinates from left-sided figures are filled in squares. The larger X represents the physical centre of the page. Lines connect each individual's right-sided and left-sided figure coordinates to illustrate interactions.

Table 4. Tukey Simultaneous Tests for Differences of Mean y Coordinates for Offset Figure Categories

Difference of Levels	Difference of Means	SE of Difference	T-Value	Adjusted P-Value
Booee-Ally	-264.08	49.25	-5.36	<0.0001
Lucy-Ally	-270.18	47.94	-5.64	<0.0001
Washoe-Ally	-46.89	49.25	-0.95	0.7771
Lucy-Booee	-6.11	49.25	-0.12	0.9993
Washoe-Booee	217.18	50.53	4.30	0.0008
Washoe-Lucy	223.29	49.25	4.53	0.0004

Individual confidence level = 98.93%.

Discussion

Mean *x* and *y* coordinates were significantly different between stimulus type for free choice and central figures, which shows that drawings were contingent on figures versus a blank page. For free choice drawings, Ally, Booee, Bruno, Thelma, and Washoe's centroids were slightly above the physical centre of the page, while Cindy and Lucy's centroids were well above or slightly below the physical centre (see Figure 3). For central figure stimuli, all centroids were located slightly above the physical centre of the page, except Booee with a centroid below the physical centre (see Figure 3). Chimpanzees tended to mark in the centre of the blank page, but the centroid changed with the addition of a central stimulus figure. Numerous other studies (Boysen et al., 1987; Morris, 1962; Schiller, 1951; Smith, 1973; Zeller, 2007) also show central marking patterns.

There were significant differences between Ally's versus Booee's pattern and Ally's versus Thelma's pattern (see Table 3). Figure 3 illustrates these differences by showing the distance between centroids per participant. The centroids for left- versus right-sided stimuli were significantly different from each other. Centroids averaged below and to the left of the physical centre of the page for left-sided figures and above and to the right of the physical centre of the page for right-sided figures (see Figure 2). All offset centroids were located in areas absent of stimulus figures, which provided evidence for space filling and balance. Figure 5 shows examples of offset figure drawings. Results also supported previous findings of space filling/balance for offset stimulus figures (Morris, 1962; Schiller, 1951; Smith, 1973). There were individual patterns in centroid placement with lines connecting left-sided versus right-sided centroid pairs per participant. There were significant differences between Ally's versus Lucy's pattern, Ally's versus Booee's pattern, Washoe's versus Lucy's pattern, and Washoe's versus Booee's pattern (see Table 4). Figure 4 indicates the distance between centroids per participant.

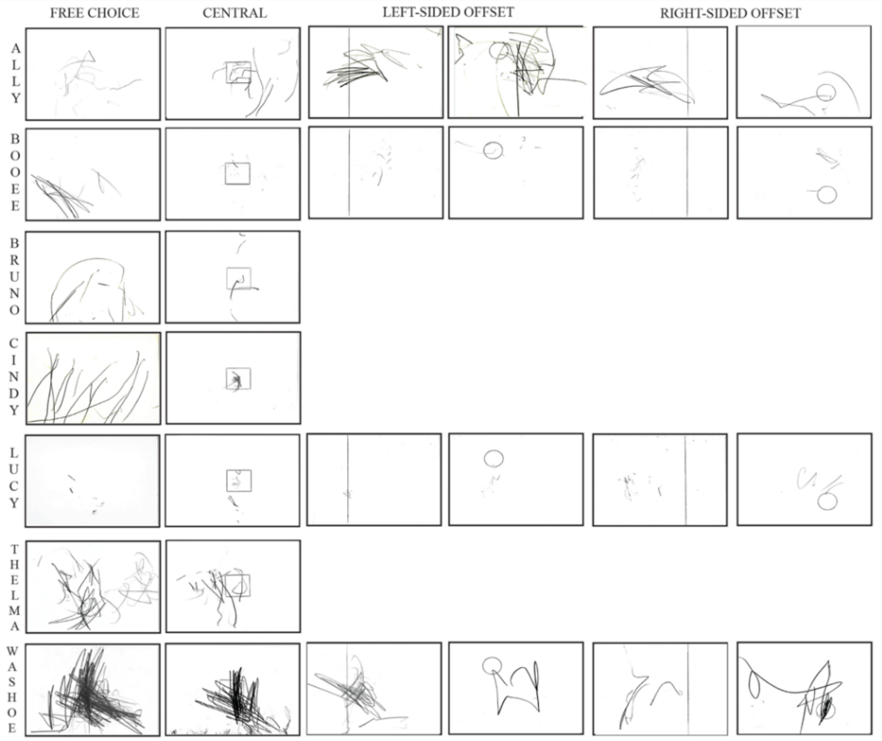

Figure 5. Selected drawing examples from all chimpanzees per category. Bruno, Cindy, and Thelma did not produce drawings for offset figure categories.

EXPERIMENT 2: COMPARISON OF FORM IN DRAWINGS

This study examined whether humans perceived similarity of form in a chimpanzee's drawings of the same object. Experimenters instructed 77 human participants to sort 28 chimpanzee drawings into stacks based on their similarity to an exemplar. A multidimensional scaling analysis showed that participants perceived similarity of form in three objects that the chimpanzee drew. Participants frequently sorted the chimpanzee's drawings of cup, boot, and banana into separate stacks, indicating they identified unique patterns that were repeated in each set of drawings.

Cross-Fostering and Two-Way Communication

Ethologists use cross-fostering to study the interaction between genetics and environment. Cross-fostering began for the infant chimpanzee, Moja, when she was several days old, at the University of Nevada-Reno (Gardner & Gardner, 1989). In this environment, she was treated in every way like a human child. She wore clothes. She ate meals using a spoon and sitting first in a high chair and later in a chair at a table. She played games, helped with chores, drew, and painted. She interacted with other cross-fosterling chimpanzees at the laboratory. Human caregivers only used American Sign Language (ASL) and encouraged the cross-fosterlings to sign by modeling and molding the signs, expanding on their fragmentary utterances, and asking them questions. In 1979, Moja was moved to the Fouts's project, which was located briefly at University of Oklahoma in Norman and then at Central Washington University in Ellensburg (Gardner & Gardner, 1989).

Moja acquired signs in patterns that resembled human children and used them in conversation with her caregivers (Gardner & Gardner, 1989). Vocabulary size, use of sentence constituents, number of utterances, and proportion of phrases all grew robustly during cross-fostering (Gardner & Gardner, 1998). Moja continued to sign conversationally with human caregivers, and initiated conversations, answered questions, and clarified misunderstandings (Bodamer & Gardner, 2002; Jensvold & Gardner, 2000) at Central Washington University until her death on 6 June 2002.

Moja experienced her childhood life like a human child. She was exposed to balls, flowers, cups, and the myriad of other objects in Western culture. She looked at books and magazines, which further expanded her visual experience. She often labeled and discussed objects and pictures with caregivers. She drew pictures and painted. At age 3, Moja began to name her drawings (Gardner & Gardner, 1978). After Moja made a sparse drawing, Gardner and Gardner recorded the following interaction:

> Because so few lines had been made, the research assistant put the chalk back in Moja's hand and urged her to TRY MORE, but she dropped the chalk and signed FINISH. The reply was unusual, and looking at the drawing the assistant noticed that it, too, was unusual in form. He then asked Moja, WHAT THAT? and she replied, BIRD. Since that time, Moja has labeled additional drawings that she produced and has been consistent in the form of the drawing associated with a given label, e.g., radial shapes for FLOWER and round forms for BERRY. Moja has also drawn and then labeled figures as requested by her teacher (e.g., DRAW BERRY THERE), and she has replied appropriately to questions asking her to name both the artist and the subject, as in Q. WHAT THAT? A. GRASS and Q. WHO DRAW THIS? A. MOJA. (p. 72)

Washoe, another cross-fostered chimpanzee at University of Nevada-Reno, also made drawings with similarity of form. For example "flower was a large centrally placed radial form" (Beach, Fouts, & Fouts 1984, p. 2). Her pictures that she named BIRD also contained similarity of form (Beach, Fouts, & Fouts, 1984). These discoveries were made possible because of a means of two-way communication.

To test if a chimpanzee used similarity of form in her drawings, Beach, Fouts, and Fouts (1984) asked 11-year-old Moja to draw six objects in six conditions: (a) asked vocally; (b) asked vocally and in ASL; (c) asked vocally and in ASL and shown a line drawing of each object; (d) asked vocally and in ASL and shown a colour slide image of each object; (e) shown the actual object and asked vocally and in ASL; and (f) shown the actual object, watched the experimenter make a line drawing of the object, and asked vocally and in ASL. Moja produced drawings in each condition. The researchers reported that Moja used a consistent pattern in her drawings of brush, cup, and ball. Her drawing pattern for brush was a "series of vertical strokes crossing a series of horizontal strokes, placed centrally on the page" (Beach et al., 1984, p. 3). Her drawing pattern for cup was a "vertical fan shape mass of strokes of nearly the same length which was placed centrally on the page" (Beach et al., p. 3). Her drawing pattern for ball was a "zig-zag stroke placed centrally on the page" (Beach et al., p. 3).

The present study used a subset of drawings collected in Beach, Fouts, and Fouts (1984), since they were uniform black and white and all contained labels. This provided a useful dataset for the present study since there were multiple exemplars with similar labels, void of other variation such as colour and medium. The objective of the present study was to examine how human judges using an exemplar sorting task (Kindler, 1990) grouped Moja's drawings from Beach, Fouts, and Fouts (1984), thereby providing evidence for similarity of form between drawings. The hypothesis was that the judges would sort drawings with the same labels into groups.

Method

Participants

This study had 77 participants, recruited from Earthwatch volunteers at the Chimpanzee and Human Communication Institute and the student body of a variety of departments on the Central Washington University campus. All participants were 18 years of age or older.

Drawings

This study used 35 drawings created by Moja during the Beach, Fouts, and Fouts (1984) study from all experimental conditions. In five of the six drawing sessions, Moja drew with white chalk on black 9 by 12 in construction paper. In the sixth session, she drew on white paper. Only the drawings on black paper were selected for this study; this eliminated the confounding variable of colour. For each drawing, Beach, Fouts, and Fouts asked Moja to draw a single specific object: an apple, ball, banana, boot, brush, or cup. This resulted in five drawings of an apple, ball, boot, brush, and cup, and seven drawings of a banana, and all of these were used in this study. Three additional drawings by Moja, labeled BIRD, were also used in this study. Like the Beach, Fouts, and Fouts drawings, these drawings also were on black 9 by 12 in construction paper with white chalk marks. The researchers included these drawing because they hypothesized that drawings labeled as bird had similarity of form.

The researchers assigned a code to each drawing, consisting of the name of the object that Moja was asked to draw in that trial and a number. For example, Moja made three drawings of a bird and for the study and they were assigned the codes bird1, bird2, and bird3. The participants did not see these codes. The researchers randomly assigned each drawing a consecutive number (1 to 35), which was marked on the back of each drawing. The top of the each drawing was labeled “Top” on the front. A single drawing of each object was selected as an exemplar for all of the drawings of that object. Two judges familiar with the drawings jointly came to a consensus on which drawing was the best exemplar for each object. Their criterion for selection was based on the Beach, Fouts, and Fouts (1984, p. 3) description of the drawings and visual inspection of each drawing and its label.

Sorting Task

This study used an exemplar sort task replicated from Kindler (1990) to examine the way humans categorize chimpanzee drawings. Kindler studied human development of perception of nonobjective paintings that were made by humans. Participants grouped paintings using one of two types of sorting conditions: exemplar sort and free sort. In the exemplar sort condition, experts selected six paintings that best represented the remaining 24 paintings. Participants sorted the 24 paintings into the six categories based on similarity to the exemplar. In the free sort condition, participants sorted 30 colour paintings into categories based on similarity with no exemplar as a reference. The participants represented three developmental groups and included third graders, seventh graders, and college-level students. Each groups' sorting was compared to that of experts. Kindler found that younger subjects did not perform as well as the college students in the free sort condition. However, all participants across developmental stages performed similarly well in the exemplar sort condition.

In this study, before participants entered the room, researchers laid out the seven exemplars on each table and set a packet of the 28 drawings at the end of each table. Next to each exemplar was a sheet that stated how many drawings belonged in its category, as per Kindler (1990). Participants completed the task individually in a room with up to six other participants. At the beginning of the trial the researcher instructed each participant to stand next to a table with a packet of 28 drawings and to sort the drawings into one of seven categories based on similarity of form to the exemplar: "You will be asked to sort a number of drawings into piles based on similarity of form using an exemplar. Any drawings that appear to be similar in form to the exemplar should be placed in the same pile." Participants could look at all of the drawings before sorting them. They could only place a drawing in one pile, but they could move it to another pile as many times as they wanted before they completed the task. Participants were instructed how many total drawings should be sorted with each exemplar. Experimenter delivered instructions in the informed consent form that participants read and signed. The time allotted was up to 45 minutes. The researcher remained in the room while participants completed the task. The researcher answered participants' questions if the question was already addressed in the scripted instructions. The researcher did not provide any additional information or direction to participants before or while they completed the task.

Analysis

JM calculated the probability of sorting drawings with the corresponding exemplar and compared that to the participants' actual performance. The number of drawings that a participant sorted with the corresponding exemplar is their sorting score. The distribution of sorting scores shows the number of people that received each score. Then, the researcher calculated the number of participants who sorted each drawing with the corresponding exemplar.

Multidimensional scaling (MDS) is "a useful mathematical tool that enables us to represent similarities of object spatially as in a map" (Schiffman, Reynolds, & Young, 1981, p. 3). MDS provides a visual representation of similarities or dissimilarities among a set of objects using patterns of proximity. For this study, the MDS analysis determined perceived similarity and dissimilarity between Moja's drawings. To do this, the participants' sorting patterns were condensed into an input matrix. Each cell of the input matrix contained the number of times a pair occurred. A pair would occur when two drawings were placed in a stack together. For example, if drawings 5, 9, and 11 were in a stack together, this would result in three pairs: 5 and 9, 5 and 11, and 9 and 11. The number in each cell of the input matrix indicated the number of participants who placed a particular set of two drawings in the same stack, which was the number of times that pair occurred. Thus, the number in the cell is an indicator of the degree to which the two drawings were perceived as similar (Kruskal & Wish, 1978, p. 30).

The output of an MDS analysis is an MDS map that locates each drawing in relation to the other drawings based on the number of times drawings were paired, which means they occurred together in a stack. Thus, the distance between drawings on the map represents the participants' perceived similarity and dissimilarity of Moja's drawings. Drawings that participants frequently sorted into the same stack would appear close together on the MDS map. Drawings that participants rarely placed into the same stack would appear far from one another on the MDS map.

Results

Table 5. Number of participants who placed each drawing with its corresponding exemplar

Drawing	No. of participants	Percentage
Exemplar: Cup 1		
Cup2	44	57
Cup3	18	23
Cup4	10	13
Cup5	15	19
Exemplar: Boot1		
Boot4	39	51
Boot5	24	31
Boot3	20	26
Boot2	6	8
Exemplar: Banana1		
Banana3	26	34
Banana5	20	26
Banana6	13	17
Banana4	11	14
Banana7	10	13
Banana2	9	12
Exemplar: Apple3		
Apple4	39	51
Apple5	3	4
Apple2	2	3
Apple1	2	3
Exemplar: Ball1		
Ball3	30	39
Ball2	8	10
Ball4	8	10
Ball5	1	1
Exemplar: Brush4		
Brush3	26	34
Brush5	19	25
Brush2	17	22
Brush4	3	4
Exemplar: Bird2		
Bird3	11	14
Bird1	9	12

Table 5 shows the number of participants who placed each drawing with its corresponding exemplar. Participants performed particularly well on the following three pairings: 44 of the 77 participants paired cup2 with the corresponding exemplar for cup; 39 of the 77 participants paired boot4 with the corresponding exemplar for boot; and 39 of the 77 participants paired apple4 with the corresponding exemplar for apple. Participants frequently sorted boot3, boot4, and boot5 with the corresponding exemplar for boot. Participants frequently sorted cup2, cup3, and cup5 with the corresponding exemplar for cup. Participants frequently sorted banana3, banana5, banana6, and banana7 with the corresponding exemplar for banana. Participants frequently sorted brush2, brush3, and brush5 with the corresponding exemplar for brush.

While participants were instructed to place drawings with the corresponding exemplar, they instead may have grouped the drawings by similarity to other drawings. For example, a participant may have grouped the four drawings of cup together but placed them in the ball exemplar stack. The MDS analysis would show these groupings.

MDS Analysis

Figure 6 is the MDS map. The researcher embedded circles on the MDS map to make the clusters of drawings more apparent. Stress was S = .34269 for a two-dimensional model. The addition of a third dimension reduced the stress to S = .19345.

In Figure 6, the lower left quadrant shows a cluster that contains drawings of cup. Specifically, participants frequently grouped combinations of cup1, cup2, cup3, and cup5 together. Figure 7 shows a layer with only the cup drawings. All but one cup drawing are located in the cluster.

In Figure 6, the lower right quadrant shows a cluster that contains all of the drawings of boot. Participants frequently grouped combinations of boot1, boot2, boot3, boot4, and boot5 together. Figure 8 shows a layer with only the drawings of boot, which shows all the drawings of boot were in this cluster.

In Figure 6, the upper right quadrant shows a cluster that contains four of the drawings of banana and the lower right quadrant shows a cluster that contains the other three drawings of banana. Figure 9 shows a layer with only the drawings of banana, clearly showing the two clusters.

Figure 10 shows a layer with only the drawings of apple. Apple2 and apple5 are in close proximity, and the other drawings are scattered. Figure 11 shows a layer with only the drawings of ball. Ball2 and ball5 are in close proximity, and the other drawings are scattered. Figure 12 shows a layer with only the drawings of brush, which are scattered. Figure 13 shows a layer with only the drawings of bird, which are scattered. Participants overall did not perceive similarities between the drawings of ball, bird, and brush.

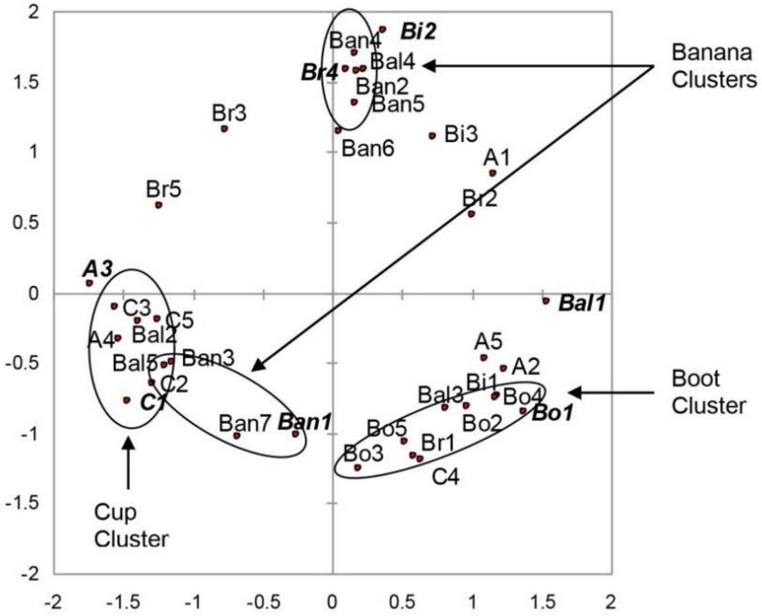

Figure 6. Multidimensional scaling map of all drawings based on (dis)similarity. Bolded text indicates exemplar drawings. Embedded circles show clusters of the same drawings. A = apple; Bal = ball; Ban = banana; Bi = bird; Bo = boot; Br = brush; C = cup.

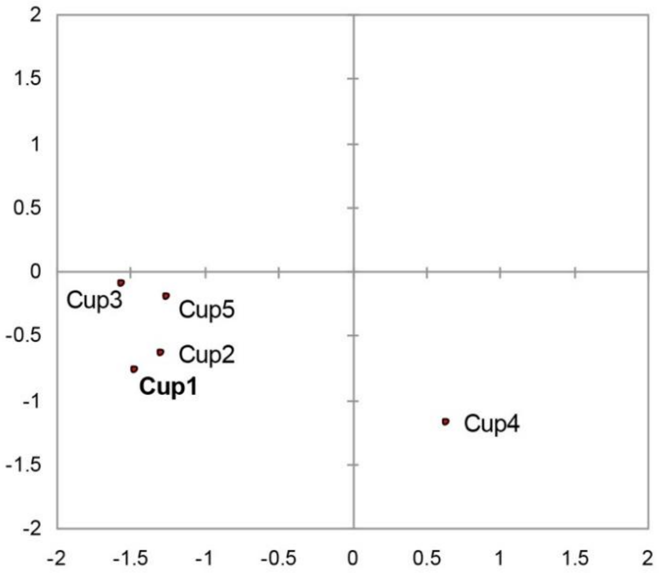

Figure 7. Multidimensional scaling map of drawings of cup. Bold text indicates the exemplar.

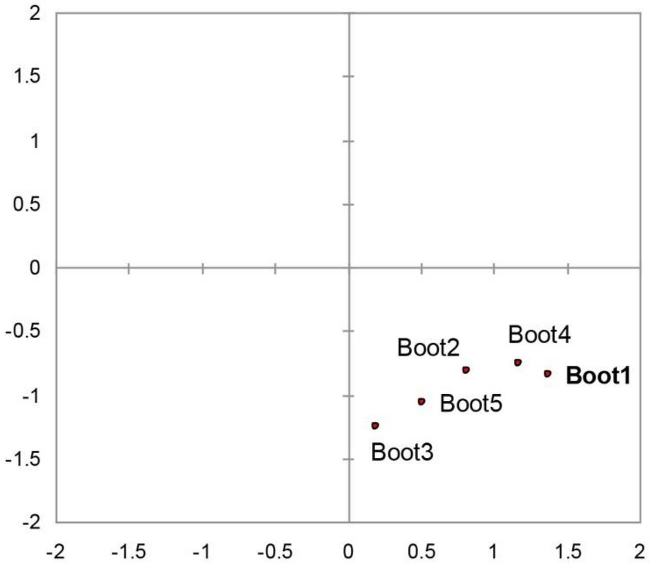

Figure 8. Multidimensional scaling map of drawings of boot. Bold text indicates the exemplar.

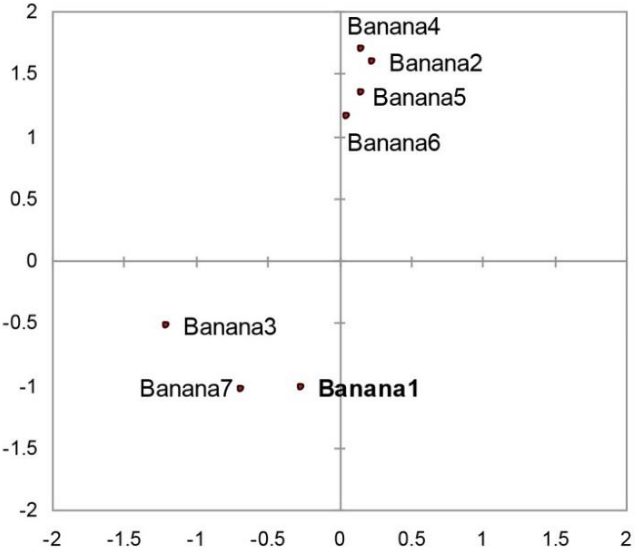

Figure 9. Multidimensional scaling map of drawings of banana. Bold text indicates the exemplar.

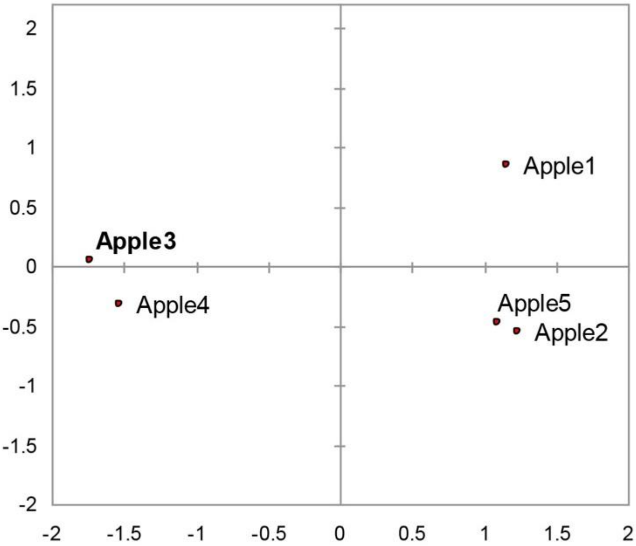

Figure 10. Multidimensional scaling map of drawings of apple. Bold text indicates the exemplar.

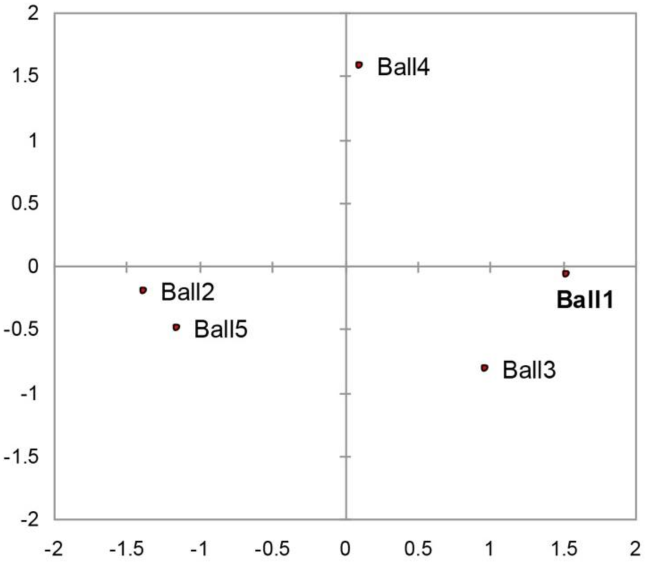

Figure 11. Multidimensional scaling map of drawings of ball. Bold text indicates the exemplar.

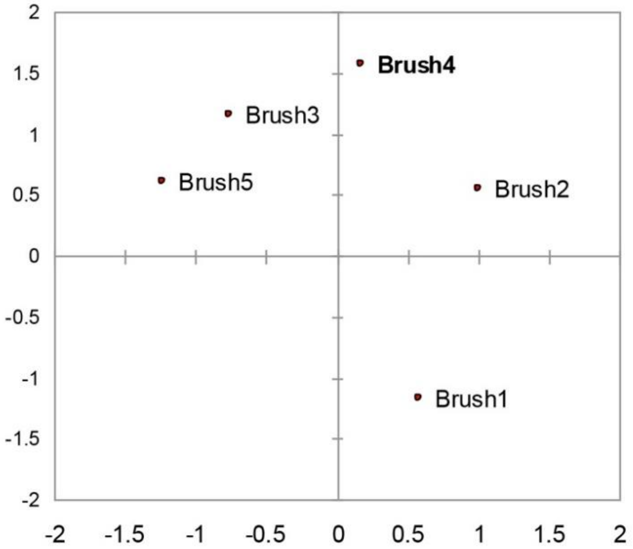

Figure 12. Multidimensional scaling map of drawings of brush. Bold text indicates the exemplar.

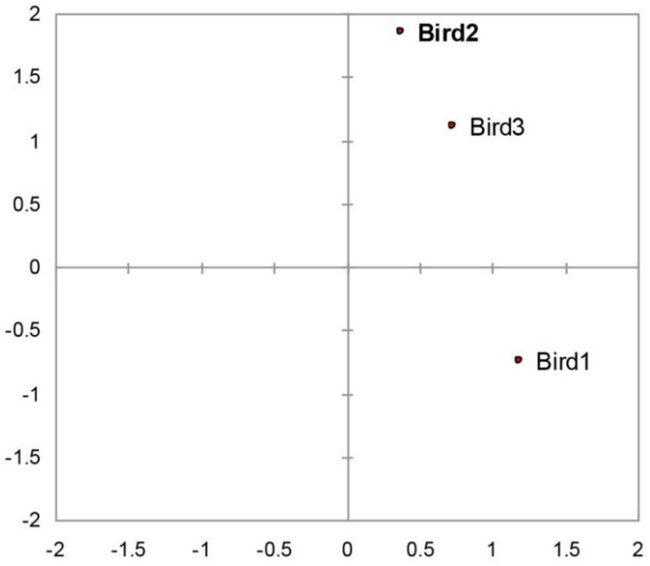

Figure 13. Multidimensional scaling map of drawings of bird. Bold text indicates the exemplar.

Figure 6 shows that each cluster contains drawings of other objects. For example, the boot cluster also contains ball3, bird1, and brush1. Figures 11, 12, and 13, respectively, show that these three drawings are not clustered with any other drawings of the same object. More specifically, other drawings of the same object are scattered on the MDS map. For example, ball3 is in the cluster of drawings of boot. However, ball3 is far from any other drawing of ball, and the other four drawings of ball are scattered. Thus, participants perceived dissimilarity among the drawings of ball in general. The drawing of ball that is near the cluster of drawings of boot is not part of a larger pattern of ball drawings. This is the same for drawings of bird and brush. Distances between objects in MDS space mean they are dissimilar. Therefore, participants did not perceive similarities between the drawings of balls, birds, and brushes overall, and this is reflected by the fact that they are scattered throughout the MDS map.

Discussion

Sorting Patterns

This study used an exemplar sorting task that showed that humans sorted drawings based on similarity of form for three of the seven objects that Moja drew: cup, boot, and banana. Beach, Fouts, and Fouts (1984) were able to subjectively detect similarity of form in banana, boot, and apple. The authors' detection of similarity of form was based on their inspection of the drawings and their knowledge of the drawing label. This study lends objective support to Beach, Fouts, and Fouts's findings by using an experimental paradigm. Like in the Beach study, the participants also inspected the drawings and examined them for similarities yet the participants were unaware of the labels.

Participants frequently sorted three drawings of cup with the corresponding exemplar. Upon further analysis, the MDS map shows a cluster that contains four of the five drawings of cup. Table 5 shows 57% of participants sorted cup1 and cup2 together, making them two of the most similar of all 35 drawings. Figure 14 shows all five drawings of cup. Moja predominantly used multiple vertical and multiple diagonal lines in her drawings of cup. Marks on cup1, cup2, and cup5 radiate from the base, upward and outward. Cup4 was separate from the other four drawings of cup and Figure 14 shows it has a different pattern than the other drawings. The frequency data and MDS analysis show that participants found form similarity among four of the five drawings of cup.

Participants frequently sorted three of the drawings of boot with the corresponding exemplar. This is further supported with the results of the MDS analysis. Participants frequently sorted all five drawings of boot together as evidenced by their close proximity on the MDS map. This indicates that participants saw similarities among the drawings of boot. This suggests that there is similarity of form for boot. Figure 15 shows Moja's five drawings of boot. Moja made sparse marks in her drawings of boots as compared to her other drawings. Using Kellogg's (1970) chart of scribbles for nomenclature, Moja drew a single crossed circle in boot1, boot2, boot3, and boot4. There are several marks in each drawing of boot, and the chalk was lifted between each of the marks in a single drawing. Using the frequency data and the results of the MDS analysis, it is evident that participants perceived the most consistent similarity of form among all of Moja's drawings of boot.

Figure 14. Moja's five drawings of cup.

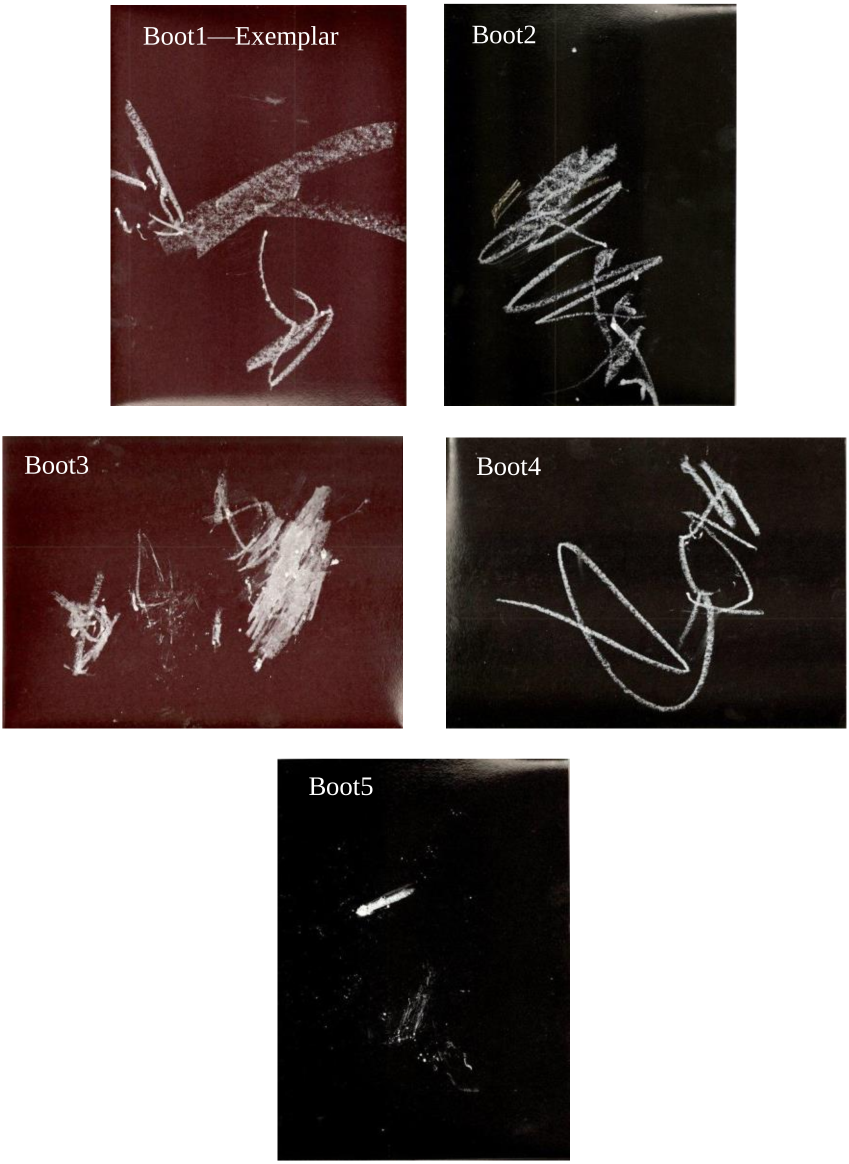

Figure 15. Moja’s five drawings of boot.

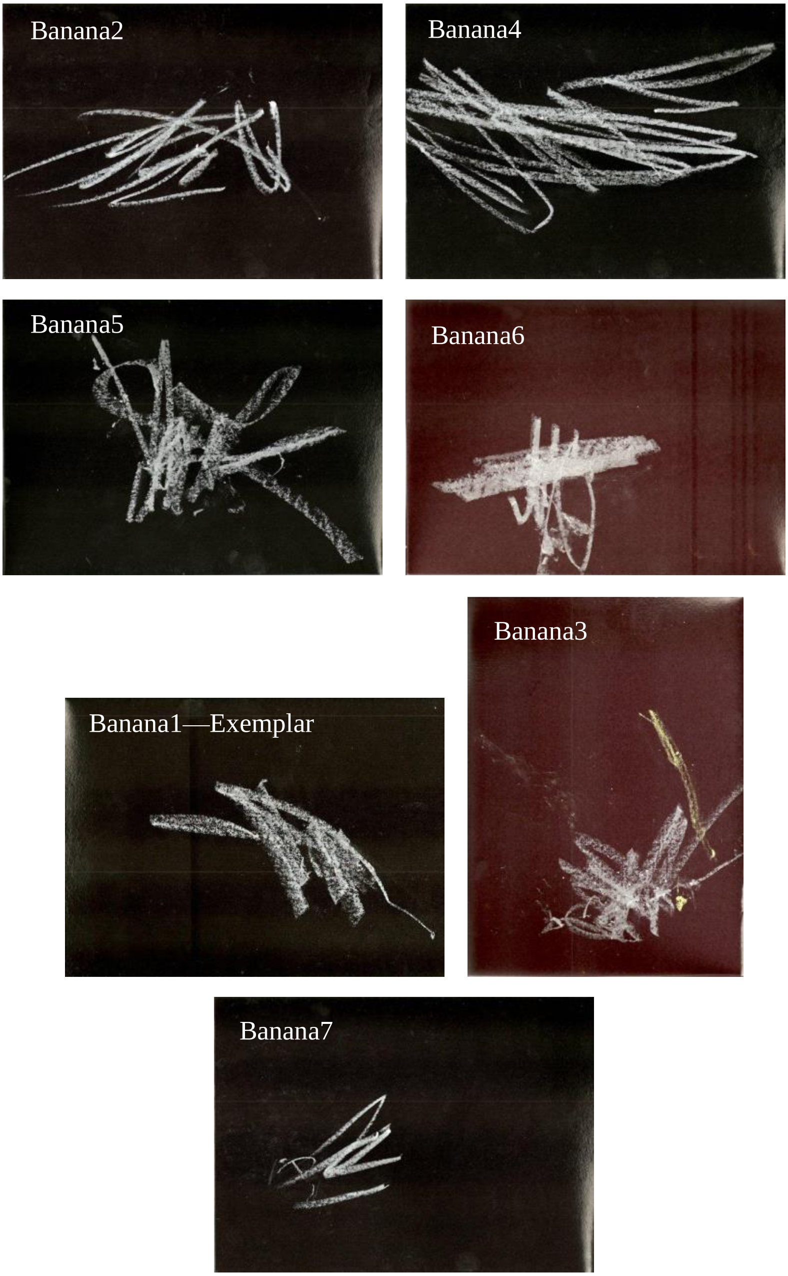

Figure 16. Moja's seven drawings of banana. Individual drawings separated based on clusters in Figure 6.

Banana3, banana5, and banana6 were frequently sorted with the corresponding exemplar, banana1. However, the MDS analysis provides a deeper understanding of the data by accounting for a drawing's similarity or dissimilarity to all other drawings, not only the exemplar. The MDS map shows there are two separate clusters of bananas: one that contains four drawings and another that contains three drawings. Banana2, banana4, banana5, and banana6 are clustered in the upper right quadrant, apart from the exemplar. The cluster of these four drawings is the tightest compared to distances between drawings in other clusters. This indicates participants saw a great deal of similarity among these four drawings.

Figure 16 shows all seven drawings of banana. Moja made relatively long straight marks and used most of the page in the drawings in this cluster. The second cluster of drawings of banana is in the lower left quadrant of the MDS map and includes banana1, banana3, and banana7. Figure 16 shows the marks in these drawings are primarily restricted to one corner of the sheet of paper. Moja used multiple vertical and diagonal lines. Participants found similarity of form among four of the drawings of banana: banana2, banana4, banana5, and banana6. They also found similarity of form among the other three drawings of banana: banana1, banana3, and banana7. However, the two clusters of drawings of banana differ in form from each other.

It is important to note that the three clusters of drawings of cup, boot, and banana are far from each other in different quadrants. The drawings of cup are in one quadrant, the drawings of boot are in a second quadrant, and one group of drawings of banana is in a third quadrant. This indicates that participants considered drawings of cup to differ from boot, both of which were, in turn, different from banana.

The drawings of apple are scattered on the MDS map; however, there are two clear pairs. Apple2 and apple5 are in close proximity on the MDS map. Therefore, participants see similarity of form between these two drawings. Figure 17 shows all five of Moja's drawings of apple. Moja used isolated curved lines in apple2 and apple5. Over half of the participants paired apple4 with the corresponding exemplar, apple3. Apple3 and apple4 are in close proximity on the MDS map, but are in a different quadrant than apple2 and apple5. This suggests that despite instruction to place drawings with similar exemplars, participants also placed like drawings together. Figure 17 shows Moja used very dense marks on apple3 and apple4 and focused all marks on one side of the paper. There are no extraneous marks outside the locus of the drawing. Although participants did not perceive similarity of form among all drawings of apple, there are clear pairs.

The drawings of ball are scattered; however, there are two clear pairs. Ball1 and ball3 are in close proximity on the MDS map. Thirty participants sorted ball3 with the corresponding exemplar, ball1. Ball2 and ball5 are also in close proximity but appear in a different quadrant from ball1 and ball3 on the MDS map. Figure 18 shows all five drawings of ball. Moja used multiple vertical lines in ball2 and ball5. One unique aspect of Moja's drawing of ball is that it appears she forcefully struck the paper with the chalk. Ball5 provides the clearest example of this occurrence.

Table 5 shows participants frequently sorted brush2, brush3, and brush5 with the corresponding exemplar. The MDS map is particularly valuable in this instance because it shows the relationship that drawings have with each other and not just their similarity to the exemplar. Figure 19 shows that four drawings of brush are loosely clustered in the upper half of the MDS map. Figure 6 shows there are few other drawings near brush3, brush4, and brush5 in the upper left area of the MDS map. Although these drawings of brush are not tightly clustered, they are relatively isolated on the MDS map. This indicates that humans perceived brushes to have a relatively unique pattern as compared to other drawings. Figure 19 shows all drawings of brush.

The drawings of bird are scattered, yet they only appear on the right half of the MDS map. Figure 20 shows all drawings of bird. Based on the frequency data and the MDS analysis, it does not appear participants saw similarity of form among these drawings. Only three drawings were used to represent bird, while the other objects had more drawings to represent them. Perhaps with more drawings of bird a clearer pattern would emerge.

Participants found varying levels of similarity among Moja's drawings. They found the greatest similarities in drawings of cup, boot, and banana.

Participants did not seem to discern a pattern in drawings of ball, brush, and bird. Moja's drawings of apple fall in the middle of this spectrum, with similarities between sets of drawings but no patterns among all of the drawings.

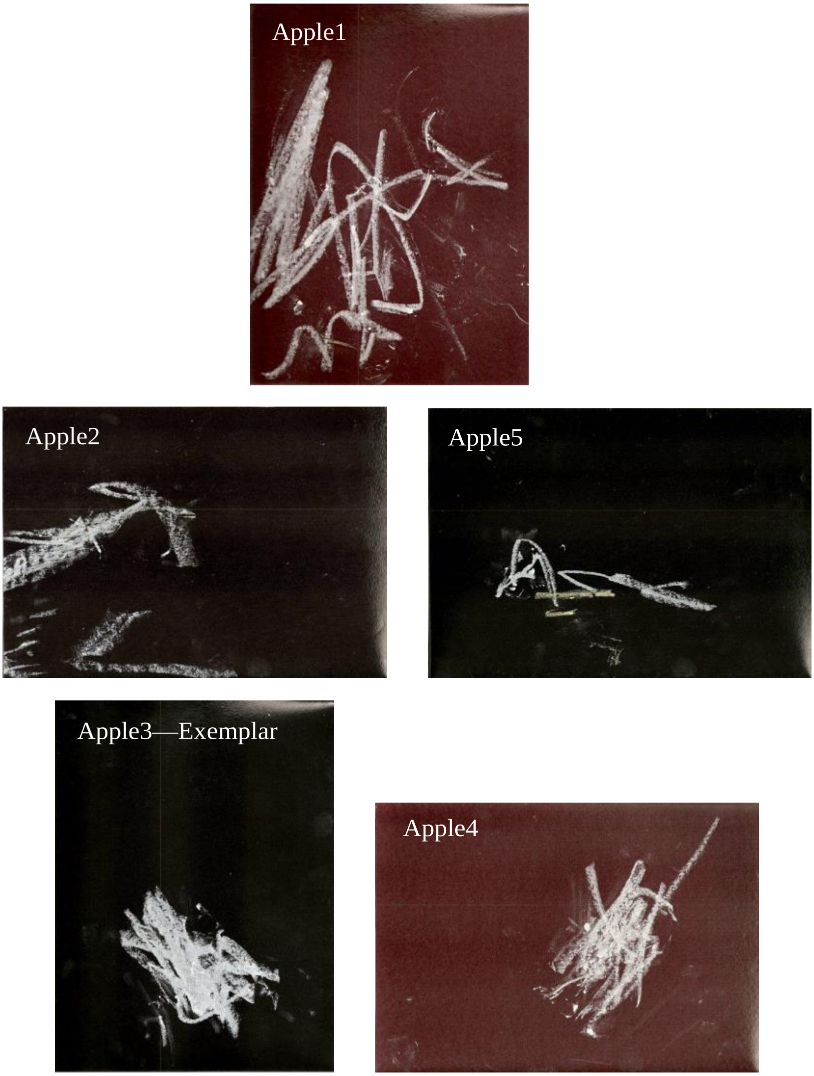

Figure 17. Moja's five drawings of apple. Individual drawings separated based on clusters in Figure 6.

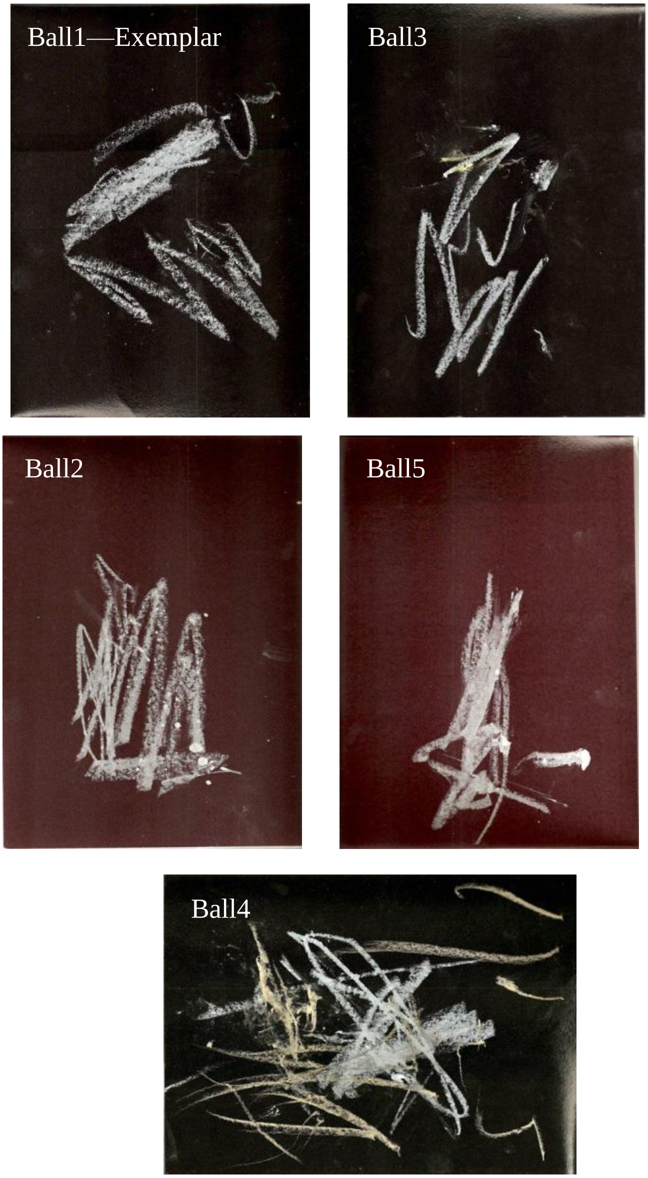

Figure 18. Moja’s five drawings of ball. Individual drawings separated based on clusters in Figure 6.

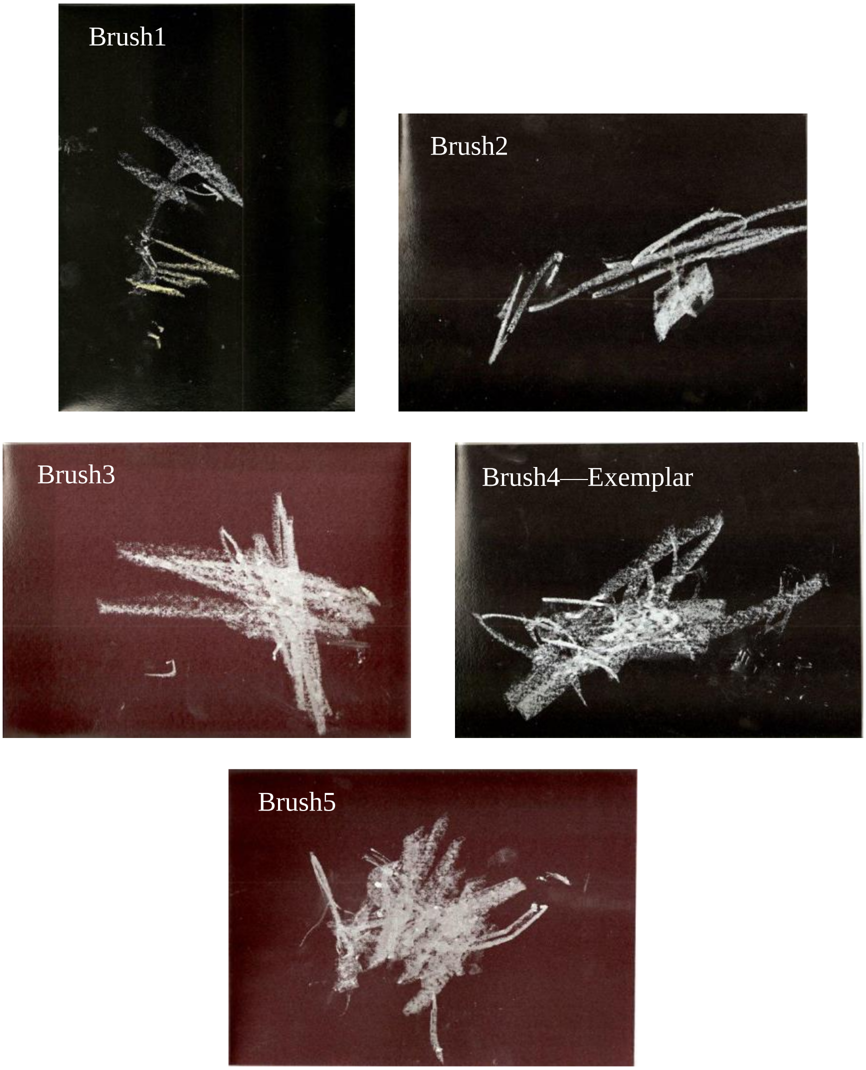

Figure 19. Moja’s five drawings of brush.

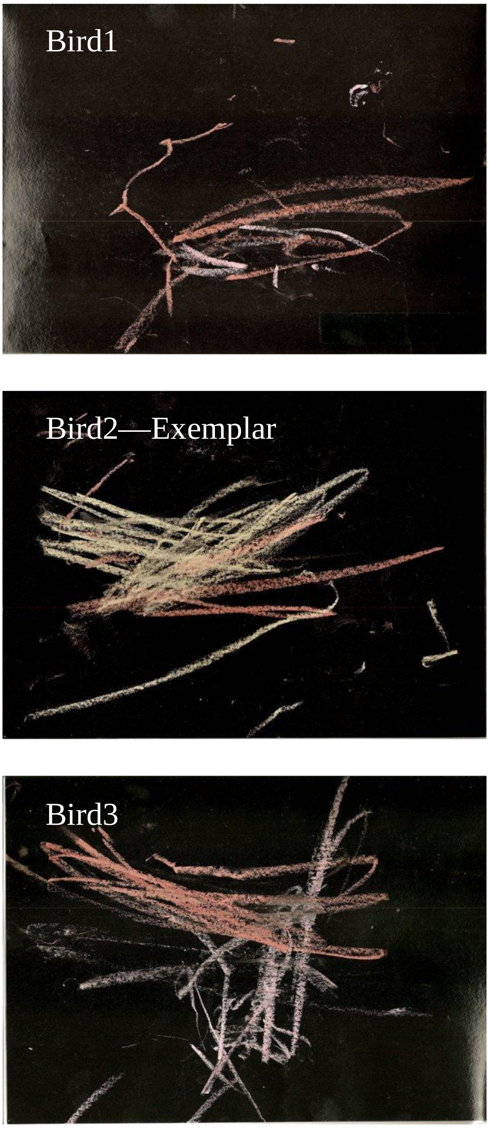

Figure 20. Moja's three drawings of bird.

Implications for Children's Drawing

Chimpanzees in drawing studies all participate in exploratory motor play while making marks for "mark's sake," suggesting an intrinsic motivation to draw. Human children begin making marks on paper as early as 12 months by first exhibiting the motor sensations of the drawing utensil on paper (Gardner, 1980, p. 10).

Piaget (1948) described three principal stages characteristic of children's drawing that begin after stage zero, in which "pure scribbles" show no purpose or aim up until age two (p. 599). Stage one is divided into two substages. The first shows variations depending on the model being copied; a substage begins around age three when children can talk about actual shapes and representational forms, but accuracy is not yet developed (p. 600). Stage two begins around age four and is marked by the progressive differentiation of Euclidean shapes at increasing levels of accuracy (p. 600). Children enter stage three around age six or 7 and can distinguish and independently represent shapes and concepts. As stated in the chapter's introduction, chimpanzees and human children have similar mark making, but the abilities of human children reach beyond that of the chimpanzee after age two (Kellogg & Kellogg, 1933; Kohts, 1935).

Matthews (1989, p. 128) theorizes that children draw the motion of the object, as opposed to the representation of the object's physical properties. In the early phase of representational drawing, "the child begins to perceive a relationship between the structures he/she is generating and the structures in the perceived environment." Matthews proposes there are two modes of representation: configurative and action. Configurative representations convey the shape of an object. Action representations convey the movement or action of the object. These two modes are sometimes combined in a single drawing. For example, a 3-year-old child made two parallel strokes to represent arms (configurative), and then made rotational strokes (action) at the end of the vertical strokes and named the drawing "Someone Washing." In experiment 2, Moja's drawings that were scattered on the MDS map were of objects that move: balls bounce, brushes brush, and birds fly.

Implications for Aesthetics

Researchers in West Africa recently observed chimpanzees habitually banging and throwing rocks against trees or tossing them into tree cavities, resulting in "conspicuous stone accumulations" (Kuhl et al., 2016, p. 2). A possible explanation for this behaviour is that the chimpanzees were “triggered by thoughts of awe, wonder” at magnificent natural features or events (King, 2016, p. 2). Meanwhile humans participate in aesthetic experiences when erecting Cairns or skipping rocks on water. Chimpanzees, too, may create an aesthetic experience by placing rocks in piles. Human artists practice personal aesthetics by choosing colour, composition, balance, and subject matter. Chimpanzees in these studies showed central marking, balance, and similarity of form, which may similarly demonstrate aesthetic experience.

Implications for Early Hominids

Art behaviour has traditionally been regarded as “selectively neutral,” or as having no effect on the selection pressures that shape the way in which species evolve. However, art behaviour can be traced to early human ancestors in the Paleolithic in the surviving parietal rock wall carvings and drawings (Barton, Clark, & Cohen, 1994). There is a greater number of surviving Middle-Paleolithic rock wall art than Upper-Paleolithic rock wall art, which implies that art was produced before physiologically modern humans appeared (Bednarik, 2008). Evidence of representational art dates to 45,000 to 35,000 years ago, while nonrepresentational art such as red ochre pigments and shell ornaments can be dated to 100,000 years ago (Zaidel, 2009). In nonhumans, a 50,000-year-old Iberian site reveals evidence for Neanderthal body adornment with shells and pigment (Zilhão, 2010). While contemporary chimpanzees are not early hominids, certainly the drawing ability in early hominids, Neanderthals, contemporary humans, and chimpanzees implies that aesthetic behaviours may have been present in hominids earlier than archaeological evidence has revealed. From an ontological perspective, Kindler and Darras (1998) suggest that “the roots of pictorial representation can be traced back to first icons of gestures” (p. 166). From this perspective, Moja’s use of a representational gestural language, ASL, would facilitate her drawing representationally. While representation is not our suggestion, the similarity of form would be the roots of a representational system of drawing.

The findings in this chapter support previous conclusions that chimpanzee drawings are not random acts on paper, but deliberate exploratory behaviours that vary across species and individuals (Boysen et al., 1987; Morris, 1962; Schiller, 1951; Smith, 1973; Zeller, 2007). Communicating intent behind the marks of a nonhuman species provides further evidence for a continuity of species. Analyzing and interpreting these drawings enlighten us about the behaviour of another species and possibly about the behaviour of early humans, who began to express themselves visually through symbols and figures tens of thousands of years ago (Bahn, 1998, p. xii).

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Chapter 5

SIGN LANGUAGE IN CHIMPANZEES ACROSS ENVIRONMENTS

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ABSTRACT

Sign language studies with chimpanzees are a way to study the fuzzy boundaries between species and among behaviours. Washoe, Tatu, Dar, and Moja were reared as infants in R. Allen and Beatrix Gardner's pioneering cross-fostering laboratory at the University of Nevada, Reno. Loulis was adopted by Washoe and acquired signs from her and other chimpanzees. As adults at Central Washington University (CWU), the chimpanzees signed to each other and to themselves. In conversations with humans the chimpanzees' patterns of interaction resembled humans for initiation, eye gaze, and response to questions. They signed to each other when no humans were around. As in childhood, caregivers used ASL in all conversations. In 2013 the remaining chimpanzees, Tatu and Loulis, moved to Fauna Foundation (FF) near Montreal. They joined

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other chimpanzees with no sign language exposure. Tatu and Loulis signed to humans, each other, and the other chimpanzees who did not use signs at FF. Signing caregivers systematically recorded signs at both locations. Tatu produced more vocabulary items at CWU than at FF. Loulis produced an equal number of items at both locations. High frequency signs changed some between locations. Written logs of chimpanzee-to-chimpanzee signing shows these interactions occurred in a variety of contexts such as social, reassurance, and greeting and included a variety of partners at FF who had no sign language exposure. Chimpanzees who acquire signs robustly communicate with that modality throughout life in a variety of environments.

Keywords: cross-fostering, American Sign Language, chimpanzee-to-chimpanzee signing

INTRODUCTION

Sign language studies with chimpanzees are a way to investigate the fuzzy boundaries between species and among behaviours.[1] Ethologists use cross-fostering to study the interaction between environmental and genetic factors by having parents of one genetic stock rear the young of a different genetic stock. It seems as if no behaviour is so fundamental or so distinctively species-specific that it is not deeply sensitive to the effects of early experience. Ducklings, goslings, lambs, and many other young animals learn to follow the first moving object that they see, whether it is their own mother, a female of another species, or a shoebox. The mating calls of many birds are so species-specific that an ornithologist can identify them by their calls alone without seeing a single feather. Yet as distinctive and species-specific as these calls may be, they, too, depend upon early experience (Slater & Williams, 1994; West, King, & Freeberg, 1997):

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> Cross-fostering a chimpanzee is very different from keeping one in a home as a pet. Many people keep pets in their homes. They may treat their pets very well, and they may love them dearly, but they do not treat them like children. True cross-fostering – treating the chimpanzee infant like a human child in all respects, in all living arrangements, 24 hours a day every day of the year – requires a rigorous experimental regime that has rarely been attempted (Gardner & Gardner, 1998, p. 292).

Chimpanzees are an obvious choice for a cross-fostering study. They share with humans a long evolutionary history and many adaptations for communication. In blood chemistry, for example, the chimpanzee is not only the closest species to the human, but is also closer to the human than to the gorilla or the orangutan (Ruvolo, 1994; Stanyon, Chiarelli, Gottlieb, & Patton, 1986), and 98% of human and chimpanzee DNA shares the same structure (Sibley & Ahlquist, 1984). Maturation also shows similarities between species. Infant chimpanzees are quite helpless; adults must provide warmth, bodily care, and food (Plooij, 1984). Under natural conditions in Africa, infant chimpanzees depend on their mother's care almost completely until they are age 2 or 3. They cannot survive if their mother dies before they are three, even when older siblings attempt to care for them. Weaning only begins between age 4 and 5. The change from milk teeth to adult dentition begins at about five. Young males usually live with their mothers until they are seven, and females until they are 10 or 11. Menarche occurs when females are 10 or 11, and their first infant is born when they are between 12 and 15 (Goodall, 1986, pp. 84–88, 443). While the average age of death is in the 30s, some chimpanzees do live into their 60s (Stanford, 2018).

Cross-Fostering Laboratory: University of Nevada, Reno

In 1966, a 10-month-old chimpanzee named Washoe arrived in a cross-fostering laboratory in Reno, Nevada. Drs. Beatrix Gardner and R. Allen Gardner created the cross-fostering laboratory using their unique combination of backgrounds in experimental psychology and ethology.

They used rigorous methodology while allowing the individual to behave naturally in an appropriate environment. While previous researchers had attempted to teach chimpanzees to talk (Hayes & Hayes, 1951; Kellogg, 1968), they had failed to realize that chimpanzees do not produce voluntary vocalizations but have no such restriction in their ability to gesture. The innovation of Project Washoe was the use of gestures as a medium of communication in an immersive sign language environment.

The cross-fostering procedure was not that different than the life of a deaf child being raised by his or her sign-language-using family. However, it was very much different from the life of a chimpanzee raised in a typical laboratory cage. Early in the project, the Gardners endeavored to provide a stimulating environment that elicited conversation:

> We tried to make Washoe's life as interesting as possible. She lived in a furnished house-trailer in the large backyard of a suburban home. The living areas were stocked with furniture, tools, and toys of all kinds and there were frequent excursions to other interesting places. We reasoned that, if you want your chimp to talk to you, you have to give her interesting things to talk about. Washoe's human companions were, of course, the most interesting things in her life. They had to be something more than laboratory technicians, they had to be good friends and amusing playmates. We reasoned that, if you want your chimp to talk to you, you have to give her good friends to talk to (B. Gardner & Gardner, 1974, p. 148).

The procedure was successful as Washoe's size of vocabulary, number of utterances, proportion of phrases, variety of phrases, length of phrases, complexity of phrases, and inflection all grew throughout 5 years of cross-fostering (B. Gardner & Gardner, 1994; R. Gardner & Gardner, 1998). The growth was patterned, and the patterns were consistent across chimpanzees. In 1970, Washoe left the cross-fostering laboratory and Reno for the Institute of Primate Studies at the University of Oklahoma.

Table 1. Chimpanzee biographical information

	Washoe (F)	Moja (F)	Tatu (F)	Dar (M)	Loulis (M)
Date and place of birth:	9/65[a] West Africa	11/18/72 NY, USA	12/30/75 OK, USA	8/2/76 NM, USA	5/10/78 GA, USA
Location and dates of residency:					
University of Nevada, Reno	6/66–10/70	11/72–12/79	1/76–5/81	8/76–5/81	-
University of Oklahoma	10/70–9/80	12/79–9/80	-	-	3/79–9/80
Central Washington University	9/80–10/07[b]	9/80–6/02[b]	5/81–8/13	5/81–11/12[c]	9/80–8/13
Fauna Foundation, Quebec	-	-	8/13–present	-	8/13–present
ASL vocabulary:					
Reliable signs[c]	188	171	157	125	13
Observed signs[c]	57	38	58	50	65

[a] This is an estimated date since Washoe was wild-caught. [b] Washoe died in October 2007. Moja died in June 2002. Dar died in November 2012. [c] According to sign check lists, as of 2005 for Washoe, 2000 for Moja, and 2010 for Dar.

The Gardners began a second cross-fostering project with four other infant chimpanzees. Moja, Pili, Tatu, and Dar were born in American laboratories and each arrived in Reno within a few days of birth. Moja arrived in November 1972 and cross-fostering continued for her until winter 1979 when she left for the Institute of Primate Studies. In 1980, Washoe and Moja moved with Roger and Deborah Fouts to the Chimpanzee and Human Communication Institute on the campus of Central Washington University (CWU) in Ellensburg, Washington. Tatu arrived in Reno in January 1976 and Dar in August 1976. Cross-fostering continued for Tatu and Dar until May 1981, when they left to join Washoe and Moja in Ellensburg. (Table 1 shows the dates for residencies for each of the chimpanzees.) Pili arrived in Reno in November 1973 and died of leukemia in October 1975.

Systematic Records of Signs

The human caregivers were with the chimpanzees throughout the day. They used sign language in all interactions with the chimpanzees and with each other. In the second project, many caregivers were native signers or had at least “a serviceable command of ASL, as well as training in experimental psychology, primatology, and related fields” (Gardner & Gardner, 1989, p. 15):

> Each human member of a foster family had to have a long and thorough acquaintance with the cross-fosterling. This was an essential ingredient of the family environment and an essential requirement if the observers were to respond appropriately and to record observation in their proper context. Some turnover was inevitable, but most of the personnel participated on a long-terms basis (p. 8).

The developmental progress of the cross-fosterlings was recorded using rigorous observation techniques. The caregivers on the cross-fostering project doubled as human observers, and made systematic records of the chimpanzees’ behaviours and signing in the form of diary records, inventories of phrases, and samples of utterances. They recorded signs with descriptions of their shape and contextual use. Each sign in the chimpanzees’ vocabulary had to meet criteria to be included, and periodically old signs were reassessed to make sure they were still part of the vocabulary (see B. Gardner, Gardner, & Nichols, 1989 for review).

Besides observation techniques, Gardner and Gardner also used systematic experiments (R. Gardner & Gardner, 1984; R. Gardner, Gardner, & Drumm, 1989; R. Gardner, Van Cantfort, & Gardner, 1992). These procedures, including systematic controlled manipulation of independent variables, were embedded in the daily routine, making the chimpanzees’ participation in the experiment no more forced than American children saying “trick-or-treat” on Halloween.

Later analysis of these questions and responses revealed that the Washoe, Moja, Tatu, Dar, and Pili replied to Wh-questions with appropriate sentence constituents (B. Gardner & Gardner, 1975; R. Gardner et al., 1992):

> One way to demonstrate the functional roles of these categories is to ask a series of questions about the same object. When Greg G. asked Washoe a series of questions about her red boot; her reply to WHAT THAT? was SHOE, to WHAT COLOR THAT? was RED, and to WHOSE THAT? was MINE (Jensvold & Gardner, 2007, p. 242).

A sign is the production of a gloss. The gloss is the word for the sign. (Glosses appear in all capital letters in this chapter.) Longitudinally, Moja, Tatu, and Dar followed the same developmental sequence in their responses to Wh-questions as would human children (Van Cantfort, Gardner, & Gardner, 1989).

Since the chimpanzees frequently named objects, R. Gardner and Gardner (1984) used naming to test if the chimpanzees could communicate information otherwise unknown to a human observer. A hidden experimenter projected slides onto a screen that only the chimpanzee could see. There were two human observers; one with the chimpanzee and another hidden in a room with a view of the chimpanzee. The human observers could only see the chimpanzee signing and could not see the screen. The chimpanzee began a trial by sliding open a door or pressing a button, which made the slide appear. If the chimpanzee failed to sign, then the observer asked her or him to sign again.

The agreements between the two observers and between the signs reported by the two observers were high, and ranged from 70% to 95%. Using a procedure that required voluntary chimpanzee participation, Gardner and Gardner showed that the chimpanzees could communicate novel information and that their signs were distinct and intelligible. Additionally, this procedure provided a control for cueing. Interlocutors can unwittingly lead subjects to correct or incorrect responses, as the horse Clever Hans famously demonstrated (Gardner, Scheel, & Shaw, 2011 for review). Controls for cueing are essential in tests of language and intelligence and this study provided such a control.

In ASL, place modulation is a type of directional modulation in which the signer modifies the location of the sign. Dar modulated the location of his signs in three ways: by placing the sign on the body of the addressee, by placing the sign on an inanimate object, or by placing the sign on his own body in an alternate location than the citation form. When asked questions such as WHO TICKLE or WHAT WANT?, Dar replied by signing TICKLE on the body of the addressee, indicating the appropriate response YOU TICKLE. In response to questions such as WHERE GROOM?, Dar replied by signing GROOM on his own body, indicating the appropriate response GROOM THERE (Rimpau, Gardner, & Gardner, 1989, p. 259). Functional categories of signs were classified as nouns/pronouns, locatives, markers, modifiers, common nouns, nouns/verbs, or verbs. Dar used directional modulation mostly on verbs such as TICKLE and GROOM and noun/verbs such as BRUSH. He used directional modulation most commonly in response to "who" questions such as WHO YOU?. The modulation was contingent on the type of question and the functional category of the sign.

Chalcraft and Gardner (2005) examined film recordings of Tatu signing with a human interlocutor. Like Dar, she used directional modulation mostly on verbs and noun/verbs in response to "who" questions. She used quantitative modulation evenly across all seven categories. Tatu used 1,023 single quantitative modulations, including enlarged size, increased speed, reiteration, duplication, and extended duration. She occasionally combined multiple modulations, such as enlarged size and holding the sign for an extended duration; reiteration and holding the sign for an extended duration; and enlarged size, reiteration, and holding the sign for an extended duration. Tatu used more turns in conversations on favored topics such as GRAPES. Quantitative modulation was positively correlated with favored topics. For example, she used the sign GRAPES in 51 consecutive turns, of which 29 had quantitative modulation (Chalcraft & Gardner, p. 123).

Project Loulis

In 1979 at the Institute of Primate Studies, Washoe adopted a 10-month-old son, Loulis. To determine whether or not Loulis would learn signs from Washoe and other signing chimpanzees without human intervention, human caregivers restricted signing when Loulis was present except for seven specific signs: WHO, WHAT, WHERE, WHICH, WANT, SIGN, and NAME. Instead of signing, humans used vocal English to communicate with both chimpanzees and each other in his presence. Loulis began to sign 7 days after the project began. At the end of the project at 73 months of age, his vocabulary had grown to 51 signs (R. Fouts, 1994; Fouts, Fouts, & Van Cantfort, 1989; Fouts, Hirsch, & Fouts, 1982). At 15 months of age, he combined signs and his phrase development paralleled that of cross-fostered chimpanzees and children (Fouts, Jensvold, & Fouts, 2002). In June 1984, when Loulis was 60 months of age, the signing restriction around Loulis ended. The control showed that chimpanzees easily transmitted ASL, just as free-living chimpanzees acquire the gestures of their community (Hobaiter & Byrne, 2011). Loulis lived with Washoe throughout her life.

Sign Language Studies at CWU

Tatu and Dar joined Washoe, Moja, and Loulis at CWU in 1981. For the first years there, the chimpanzees lived on the third floor of the psychology building. In 1993 they moved to a new building, named the Chimpanzee and Human Communication Institute, on the CWU campus (Jensvold & Fouts, 2008). At CWU, the chimpanzees continued to sign spontaneously and interactively with each other (D. Fouts, 1994) as well as with human familiars (Bodamer & Gardner, 2002; Jensvold & Gardner, 2000; Leitten, Jensvold, Fouts, & Wallin, 2012). Conversational interaction is a fundamental characteristic of human face-to-face communication in words and signs and always has been a primary objective of sign language studies of cross-fostered chimpanzees. Records of the chimpanzees' signs and conversations continued at CWU with the same detail and rigor as in Reno.

Caregiver Researchers

Caregivers at the Chimpanzee and Human Communication Institute were comprised of student interns, faculty, and volunteers, all of whom doubled as researchers. They were responsible for caregiving duties such as cleaning, meal services, and enrichment preparation, and researcher duties such as recording signs and behaviours during conversations and observations. They were trained in ASL, including at least one course and a proficiency test. Proficiency was demonstrated by completing a video test of each individual chimpanzee's sign use with an accuracy of at least 85% (Jensvold & Fouts, 2008).

Vocabulary

B. Gardner and Gardner (1994) developed criterion to include signs onto each chimpanzee's vocabulary list, which they describe:

> After three separate and independent reports of a well-formed, unprompted, and appropriate observation of a new sign by three different observers, we placed the new sign on the list of candidates for reliability. A sign remained on this list until there was at least one report of a well-formed, unprompted, and appropriate observation on each of 15 consecutive days. We restarted the count after any day without a qualified report. After meeting the 15-day criterion, the sign was added to the list of reliable vocabulary items (p. 225).

For the cross-fosterlings at CWU, researchers followed this same procedure for inclusion on new signs. For Loulis the procedure was different: "Before it was counted as a sign in Loulis' vocabulary, the gesture had to be reported by three different observers as occurring in an appropriate context" (R. Fouts, 1994, p. 261).

Sign check lists tracked each chimpanzee's vocabulary. When a chimpanzee signed, a human caregiver checked off that sign on the sign check list. No matter how many times per day a chimpanzee made a sign, caregivers recorded that sign only once that day.

Signs in Conversational Context

Sign logs were a more detailed record of signs. The purpose of sign logs was to record the chimpanzees' signed and nonsigned behaviours, including chimpanzee-to-human interactions, chimpanzee-to-chimpanzee interactions, private signing, and other interesting interactions or behaviours. Sign logs documented each chimpanzee signed utterance during an interaction, along with the nonverbal behaviour of the signer and conversation partner. They included the individual signs in each utterance, the form of each sign, the hand used to form each sign, and utterance frequency. They also included the behavioural context of each interaction (i.e., play, grooming, feeding, affinitive social, etc.), body orientation, physical location in the building, eye gaze, vocalizations, arousal, and any other nonverbal behaviours. Lastly, they contained a written description of the signed interaction (Leeds & Jensvold, 2013).

Sign logs provided opportunity for analysis of communicative function, which is the intention or motive for an utterance (Dore, 1975). For example, an utterance can be a declarative, question, request, or politeness marker. The chimpanzees used seven categories of communicative functions and did so in ways that resembled patterns in human children. The chimpanzees' utterances functioned to answer questions, request objects and actions, describe objects and events, make statements about internal states, accomplish tasks such as initiating games, protest interlocutor behaviour, and as conversational devices to maintain and initiate conversation (Leeds & Jensvold, 2013).

Remote Videotaping

Before camera traps and wireless recording devices, D. Fouts (R. Fouts et al., 1989; D. Fouts, 1994) developed a remote videotaping technique (RVT) to record the chimpanzees' behaviours with no humans present. Cameras mounted in and focused on the chimpanzee enclosure were connected to television monitors and a VCR in another room away from the chimpanzees. Only one camera recorded at a time, and the VCR operator could control which camera recorded. During recording sessions no humans entered the chimpanzee quarters, surrounding hallways, or adjacent rooms. All humans stayed out of view and kept silent, and all laboratory activities that might be a distraction ceased (D. Fouts).

Data collection with RVT initially occurred during a 15-day period at the end of July and the beginning of August 1983 in a study that focused on Loulis' use of signs with Washoe, Moja, Tatu, and Dar. Every day during the 15-day study period had two 20-minute recording periods between 9:00 a.m. and 5:00 p.m. There were 45 recording periods, so that each hour of the day was sampled randomly either five or six times. On the videotapes there were 189 chimpanzee-to-chimpanzee signed interactions. Dar and Loulis were the most frequent dyad with 167 signed interactions and Loulis and Tatu were the second most frequent dyad with 76 signed interactions. Most of the interactions occurred in the affinitive social (33%) and play (38%) contexts (Jensvold, Wilding, & Schulze, 2014).

In the 45 hours of videotape, D. Fouts (1994) reported 115 private signs that Loulis made when his face and body were not oriented toward another chimpanzee. In a second analysis of the videotapes, Bodamer (1987) found 90 instances of private signing by the other chimpanzees. Private signs were made in the absence of interactive behaviours such as looking toward another individual. Bodamer classified these into categories of private speech that humans use (Furrow, 1984). A later study recorded 56 more hours of RVT, with 368 instances of private signing (Bodamer, Fouts, & Jensvold, 1994). In both samples one of the most common categories of signing was referential (59% in the 56-hour sample). In this category, the chimpanzee signed about something present in the room, for example naming the pictures in a magazine. The informative category, an utterance that refers to an object or event that is not present, accounted for 12% in the 56-hour sample and 14% in the 45-hour sample. An example of this category was when Washoe signed DEBBI to herself when Debbi was not present.

One category of private signing was imaginative (Furrow, 1984), which accounted for 17 instances in the 56 hours of RVT. A later study recorded 15 hours of RVT while the chimpanzees' enclosure was filled with toys. There were six instances of imaginary play classified into categories of imaginary play that human children use (Matthews 1977). There were four instances of animation in which the chimpanzee treated an object as if it was alive. For example, Dar signed PEEKABOO to a stuffed bear. There were four instances of substitution in which the chimpanzee treated one object as if it were another. For example, Moja wore a shoe and signed SHOE. She then removed the shoe, put a purse on her foot, and zipped it up (Jensvold & Fouts, 1993). A later sample of 17 hours of adventitiously recorded videotape contained 21 instances of imaginary play (Egan & Jensvold, 2015).

Video Recorded Experimental Conversations

Like in the Gardner cross-fostering laboratory, experimenters at CWU embedded scripted probes into routine conversations. Experimenters video recorded these conversations, which allowed for detailed analysis. Bodamer and Gardner (2002) systematically explored initiation of interactions. The chimpanzees had access to a suite of enclosures, and one was across the hall from a human workroom. When a caregiver was in the workroom, the chimpanzees often came to the nearby enclosure to request objects or activities. They often made noises if the human was facing away. During trials, the interlocutor sat in the work room with his back toward the chimpanzees' enclosure. When the chimpanzee made a noise, the interlocutor turned and faced the chimpanzee immediately or after a 30-second delay. When the interlocutor was facing away, the chimpanzees made noises, such as bronx cheers, and rarely signed. The few times the chimpanzees signed, they used signs that made noise, such as DIRTY, in which the back of the hand hits the bottom of the jaw and which with force is noisy. In the delay condition the noises became louder and faster. Once the interlocutor faced the chimpanzees, signing began and noises ended. Using a naturally occurring situation this experiment showed the chimpanzees initiated interactions and signed spontaneously. They adjusted appropriately to the partner's attentional state.

After the trial the interlocutor continued in unscripted interaction and the cameras continued to record. Hartmann (2011) further analyzed these corpora to investigate turn-taking. The chimpanzees generally overlapped turns at the same rate as the interlocutor. Additionally, they showed a developmental pattern, overlapping less as adults than as infants.

In Jensvold and Gardner (2000), during systematic interactions with Washoe, Moja, Tatu, and Dar, an interlocutor responded to the chimpanzees with either general requests for more information (WHAT? or HUH?), on topic probes, off topic probes, or negative statements (CAN'T). The chimpanzees incorporated and expanded their responses as appropriate to the probe condition. For example, when the interlocutor signed the on-topic probe WHOSE BERRY? Tatu incorporated the sign BERRY into her response (p. 340). When Washoe signed GIMME, the interlocutor responded with the general probe WHAT? Washoe expanded her responses by signing ME GIMME and then FOOD GIMME (p. 337). For off-topic and negative probes, the chimpanzees either failed to respond or responded with novel signs. For example, when Tatu signed EAT? the interlocutor responded with the negative probe CAN'T and Tatu signed the novel utterance IN (p. 342).

The chimpanzees depended on their caregivers to fulfill many of their needs, and often used signs to request objects and activities from humans. Typical interactions between caregivers and chimpanzees included games, such as chase and peek-a-boo; activities, such as colouring and looking at books; and chores, such as cleaning; and meals (R. Fouts et al., 1994). The objective of Leitten et al., (2012) was to experimentally manipulate caregiver responses to the chimpanzees' requests and determine if changes in the chimpanzees' signing were contingent upon this interlocutor input. Following the chimpanzee's request, a human interlocutor either complied with the request, provided an unrequested item or activity, refused to comply, or did not respond to the request. When requests were satisfied, the chimpanzees most often ceased signing. However, when requests were misunderstood, refused or not acknowledged, the chimpanzees repeated and revised.

Sanctuary at Fauna Foundation

Moja died in 2002, Washoe in 2007, and Dar in 2012. On 30 August 2013, Tatu and Loulis moved to Fauna Foundation (FF) near Montreal, Quebec, Canada. FF is a sanctuary for chimpanzees, monkeys, and a variety of farm animals. Tatu and Loulis were the only chimpanzees there who used signs. The other chimpanzees were retired from biomedical research and zoos and had no previous sign language exposure. At FF, the chimpanzees lived in compatible subgroups with access to a suite of indoor and outdoor enclosures. The occupant subgroup in a suite usually moved to a different suite each week. Tatu and Loulis spent their first months in the mezzanine suite. After an initial quarantine they were introduced to two chimpanzee residents, Spock and Sue Ellen. These two were consistent subgroup members with Tatu and Loulis during the first years at FF. Other chimpanzees were introduced to Tatu and Loulis' suite for brief periods but, for the vast majority of the time, the other chimpanzees at FF were in adjacent enclosures.

Four caregivers from CWU continued to care for Tatu and Loulis and the other chimpanzees at FF. They recorded daily sign check lists and sign logs as they had at CWU. The other caregiving staff did not use ASL. On most days there were at least one signing and two or more nonsigning caregivers. Tatu and Loulis continued to sign to humans and chimpanzees at FF. This analysis explores patterns in that output.

ANALYSIS

This analysis uses sign check lists and sign logs from CWU and FF to explore Tatu and Loulis' signing behaviour at FF.

Vocabulary Use

Sign check lists provided a systematic way to compare Tatu and Loulis' vocabulary use between CWU and FF. For CWU we selected the years 2004–2007. For FF we selected the years 2014–2017. We were interested in the number of different vocabulary items, rather than the gross number, each chimpanzee signed in a day. The mean number of vocabulary items that the chimpanzees produced each year appears in Table 2. Tatu produced significantly more items at CWU (M = 19.75, SD = 1.26) than at FF (M = 14, SD = 1.63), t (6) = 5.58, p = .0014. Loulis produced an equal number of items at CWU (M = 4.50, SD = 0.58) as at FF (M = 4, SD = 0), t (6) = 1.732, p = 0.134. The range of different vocabulary items for each year appears in Table 2. For Tatu, there were some days when caregivers recorded only one sign and other days as many as 58. The year with the largest range was at FF. Loulis had a smaller range than Tatu, but like Tatu his largest range was at FF.

Table 2. Mean and range of vocabulary items each year

	Tatu		Loulis	
	Range	$\bar{x}$	Range	$\bar{x}$
2004	1–42	18	1–10	4
2005	2–40	20	1–9	5
2006	1–41	21	1–12	5
2007	2–40	20	1–12	4
2014	1–58	16	1–12	4
2015	1–33	12	1–8	4
2016	1–32	14	1–9	4
2017	1–46	14	1–13	4

Note: CWU was 2004–07. FF was 2014–17.

Table 3 shows the most frequent five vocabulary items for each year. For Loulis CHASE was the most frequent vocabulary item every year. HURRY also was in the top five for each year. In an analysis of Loulis' early signing in 1983, HURRY was his most frequent sign (D. Fouts, 1994, p. 278). Other signs may be more a reflection of the environment.

Table 3. Most frequent five signs by year

	Tatu	Loulis
2004	SMELL MASK CRACKER BLACK THAT	CHASE THAT HURRY GIMME FOOD/EAT
2005	SMELL MASK THAT ONION BLACK	CHASE THAT HURRY GIMME FOOD/EAT
2006	SMELL ONION MASK THAT DRINK	CHASE THAT HURRY GIMME FOOD/EAT
2007	THAT SMELL GUM RED CARROT	CHASE THAT HURRY FOOD/EAT GIMME
2014	MILK DRINK YOU THAT THERE	CHASE HURRY THAT YOU THERE
2015	MILK CHEESE PERSON THAT YOU	CHASE THAT YOU THERE HURRY
2016	THAT THERE DRINK APPLE YOU	CHASE THAT THERE HURRY YOU
2017	THAT THERE DRINK PERSON YOU	CHASE THAT THERE HURRY YOU

Table 4. The number of Tatu's signs each year

	2004	2005	2006	2007	2014	2015	2016	2017	Total
APPLE	116	142	172	136	137	138	154	154	1149
BABY	11	10	5	3	12	12	4	5	62
BAG								1	1
BANANA	175	169	174	176	125	95	92	136	1142
BART H.				1					1
BED	1	3	1			1	1		7
BELT		1							1
BERRY	59	56	55	67	32	17	27	16	329
BIRD	33	31	19	32	1	10	4	4	134
BLACK	255	271	241	140	89	92	100	119	1307
BLANKET	28	22	22	40	13	9	11	7	152
BLOW		8	15	2					25
BOOK		1	1						2
BOY	1	3	1		8	3	2	5	23
BREAD		8	5	19	2		3	14	51
BROWN		1							1
BRUSH	6	9	6	3	1	2	2	2	31
BUG	3	1	2		3	5	1	1	16
CANDY	2	3		3	3		1	22	34
CAN'T	1	4						2	7
CAR		1		2					3
CARROT	76	153	150	251	92	34	81	102	939
CAT	13	9	10	6	5	3	1	2	49
CATCH			1	1					2
CEREAL	136	182	177	216	108	121	48	13	1001
CHASE	45	31	29	4	18	6	13	34	180
CHASED								1	1
CHEESE	205	207	185	140	147	182	95	27	1188
CIGARETTE		1							1
CLEAN	9	3	1	12	9	8	9	8	59
CLOTHES	116	143	117	92	4	3	7	5	487
COFFEE	100	87	55	29	107	54	48	48	528
COLOR								1	1
COME	8	32	25	26	18	2	3	1	115
COOKIE	33	29	15	40	13	4	3	5	142
CORN	43	50	34	17	28	25	32	12	241
COW	6	7	7	4	9	3	1	2	39
CRACKER	282	259	239	185	113	28	87	140	1333

	2004	2005	2006	2007	2014	2015	2016	2017	Total
CRY	5	2	7	1	2			1	18
CUP		1							1
DAR	5	11	9	7	3	1			36
DEBBI F.	1	1		1			1		4
DIRTY	3		2	4	1				10
DOG	13	7	7	3			4		34
DRINK	159	202	274	250	235	153	169	195	1637
EARRING	3	1	3	1	5	1	1		15
EAT/FOOD/ TASTE	119	132	153	140	43	18	22	34	661
ENOUGH			1						1
EXCITING				1					1
FINISH	2	1	2						5
FLOWER	65	59	67	91	10	11	16	19	338
FRIEND	8	12	20	7	32	9	5	12	105
FRUIT	45	66	83	207	67	17	21	5	511
FUNNY							1		1
GARBAGE/ CABBAGE		2	4	2	2		1		11
GIMME	173	142	142	118	124	87	65	79	930
GIRL	22	18	25	4	19	2	3	4	97
GLASS	4	3							7
GLASSES		1							1
GLOVE			1	1	1				3
GO	182	190	189	187	156	107	126	154	1291
GOOD	32	21	19	14	2	1	1	1	91
GRAPES	4	8	6	8	7	6	4	13	56
GRASS	29	35	25	25	50	33	35	32	264
GREEN			1		1				2
GROOM	86	95	72	42	75	63	50	17	500
GUM	99	187	249	258	10	8	7	11	829
HAIR					3				3
HAT	2	1	2	1					6
HEAR/LISTEN	1			1	2	5	1		10
HORSE			5	1				1	7
HOT	2	6	3	6	3	1	1		22
HUG	2		1	1	1				5
HUNGRY	3	6	3	2	1		1		16
HURRY	128	168	183	189	178	113	113	129	1201
HURT	39	36	35	13	23	6	7	16	175
ICE CREAM	45	38	24	28	11	2	14	9	171

Table 4. (Continued)

	2004	2005	2006	2007	2014	2015	2016	2017	Total
ICE/COLD	123	157	145	123	26	6	3	2	585
IN/ENTER	29	30	19	38	114	103	102	112	547
KEY	12	7	5	3	18	4	8	6	63
KISS	8	27	87	17			5		144
LAUGH	22	10	15	8	16	22	17	8	118
LETTUCE	2								2
LIGHT		1	1						2
LIKE	1								1
LIPSTICK	28	128	95	99	14	23	61	63	511
LISTEN			1						1
MARK L.		1							1
MARTI G.			1						1
MARY LEE J.	2	1	1		1				5
MASK	303	295	307	104	47	54	84	178	1372
ME	10	8	15	2	3	2	1	3	44
MEAT	47	53	64	188	31	61	60	58	562
MEDICINE	27	6	1	14	76	14	31	37	206
METAL							1	1	2
MILK	194	247	221	240	258	210	136	154	1660
MINE/MY	2		1	2	4				9
MORE	163	170	171	155	91	31	54	70	905
NICE		1							1
NO				2		1			3
NOSE								1	1
NUT	93	85	86	67	37	77	94	86	625
OIL/LOTION	40	13	13	3	28	64	68	75	304
ONION	205	283	309	236	14	42	79	62	1230
ORANGE	10	20	33	44	6	11	15	9	148
OUT	148	134	71	41	2	1	1	6	404
PAINT	28	21	19	9	8	18	5	9	117
PEA/BEAN	4	10	9	47	7	4	2		83
PEACH					150	37	59	9	255
PEAR				22	8	10	6	20	66
PEEKABOO		1							1
PEN/WRITE		1		2					3
PERSON	98	153	140	164	139	158	137	192	1181
PIPE			1						1
PLANT	49	57	91	95	2	1			295
PLEASE	18	19	15	11	5	1	2		71

	2004	2005	2006	2007	2014	2015	2016	2017	Total
POPCORN	21	15	26	43	6	7	13	4	135
POTATO	198	159	232	109	3	6	10	8	725
POTTY	3	4	4	2	11	2	3	1	30
PRETTY		1							1
QUIET	20	11	2	2	2	2	6	26	71
RADIO					2	1			3
RED	196	235	221	254	65	37	82	59	1149
RICE	53	65	75	128	13	5	3	2	344
ROCK		1							1
ROGER F.	1	2	7	2			1		13
SANDWICH	22	48	73	119	13	7	4	10	296
SANTA CLAUS		1			1				2
SEE		2		1					3
SHIT		1						1	2
SHOE	8	10	6	1	1		2	1	29
SICK								1	1
SLEEP	24	13	10	3					50
SLICE				1	5		37	1	44
SMELL	308	329	325	271	143	113	112	163	1764
SMILE				1					1
SODAPOP	57	54	25	32	42	20	10	24	264
SOON					1				1
SORRY	42	21	21	15	24	3	6	3	135
SOUR	1								1
STUCK						1			1
STUPID	5	3	1	1	1	2			13
SURPRISE		1					1		2
SUSAN N.	1								1
SWALLOW	2	10	20	43	13	1		4	93
SWEET	91	96	80	125	54	25	17	53	541
TATU	73	53	43	12	65	12	8	12	278
TEA	35	32	58	57	70	12	17	4	285
THAT	225	287	295	298	191	157	180	213	1846
THERE	177	215	219	220	180	143	171	204	1529
THINK								1	1
THIRSTY						1			1
TICKLE	3	3	5	1	1		4	8	25
TIME	5		1		1				7
TOMATO	1			15			1		17
TOOTHBRUSH	28	53	124	199	5	7	28	28	472
TOOTHPASTE	1			2			5		8

Table 4. (Continued)

	2004	2005	2006	2007	2014	2015	2016	2017	Total
TREE	57	52	56	19	16	25	27	34	286
UP						2	11	5	18
VEGETABLE				5					5
WANT			5	8					13
WASHOE		1							1
WATER	19	18	68	172	3	6	16	10	312
WHITE	4	4	7		3	1	1	3	23
WHO		1						1	2
WOOD				1					1
WRISTWATCH	3	1			1				5
YELLOW								1	1
YOU	186	257	246	138	198	154	140	187	1506

For example, Tatu signed CRACKER more often at CWU than at FF. The chimpanzees used the sign CRACKER to refer to primate chow, which they ate more often at CWU than at FF. At FF, MILK became a high frequency sign for Tatu and caregivers served milk more often at FF than at CWU. Tables 4 and 5 show each vocabulary item and the number of days caregivers recorded it each year.

Indexical signs are signs that include a point and have a variety of functions. For example, “Often a signer will indicate the location of an entity (a person, or a thing or a place) using a sentence such as MAN THERE, in which THERE is an index finger pointing downward toward a specific place” (Valli & Lucas, 1995, p. 75). Additionally, “indexical signs have some of the same general functions as free-standing pronouns” (Klima & Bellugi, 1979, p. 277). While signers use indexical signs grammatically and systematically, these signs are easily intelligible to both signing and nonsigning individuals. The only indexical signs on Tatu’s and Loulis’ lists are THAT, THERE, ME, and YOU. In Table 3, Tatu and Loulis each only had one of these signs in the top five list at CWU. This changed at FF, where they each had three indexical signs in the top, with the exception of 2015 when Tatu had only two.

Table 5. The Number of Loulis' Signs Each Year

	2004	2005	2006	2007	2014	2015	2016	2017	Total
CHASE	361	357	346	327	233	170	158	299	2251
COME	12	13	6	3	10		2	1	47
CORN						3			3
DIRTY	1	1	1						3
DOG			1						1
DRINK	45	33	54	71	58	26	47	106	440
FOOD/EAT	162	165	161	142	45	29	45	72	821
GIMME	178	220	203	123	51	7	3	7	792
GO							1		1
GOOD			1	2		1	2	6	12
GUM				1					1
HUG								1	1
HURRY	234	272	250	211	196	100	106	203	1572
KISS						5	1		6
MASK							1		1
NO					1				1
OUT		1							1
PERSON	4	6	3				1		14
THAT	318	323	327	324	193	153	151	275	2064
THERE	127	127	144	110	76	119	124	207	1034
TICKLE	72	63	88	71			7	24	325
TOOTH-BRUSH							1	5	6
YES				2					2
YOU	62	78	106	105	141	123	94	142	851

The cross-fostered chimpanzees used THAT as the demonstrative. For example, in response to the question WHAT THAT?, the reply was THAT (indicating a hairbrush) BRUSH (B. Gardner & Gardner, 1994, p. 246). They used THERE as a locative. For example, in response to WHERE BRUSH? the reply was BRUSH THERE (p. 246). Gardner and Gardner (1994) analyzed the placement of the indexical THAT/THERE sign in response to WHAT versus WHERE questions, and reported:

> Wherever there is independent evidence to distinguish between the two cases, the cross-fosterlings mostly used THAT/THERE before other terms in demonstrative phrases and after other terms in locative phrases. Locative phrases were numerous and varied, e.g., WRITE THERE, GROOM THERE, FRIEND THERE, and IN THERE. Demonstrative phrases were even more numerous and varied, e.g., THAT BIRD, THAT RED, THAT MORE, THAT NAOMI. The variety of signs and consistency across subjects, shows that they used order as a structural device to distinguish demonstrative THAT/THERE from locative THAT/THERE (p. 248).

Chimpanzee-to-Chimpanzee Signing

Tatu and Loulis signed to humans and to other chimpanzees at FF. Tatu had never before encountered a sign-naïve chimpanzee, and Loulis had been around only signing chimpanzees since he had moved to CWU at about age two. We expected Tatu and Loulis to sign to the other chimpanzees at FF. Caregivers at FF completed sign logs when they observed chimpanzee-to-chimpanzee signing, just as they had at CWU. Caregivers at FF completed sign logs when they observed chimpanzee-to-chimpanzee signing using the same protocols as at CWU.

At FF between 1 September 2013 and 31 May 2018 (45 months), there were 80 utterances with chimpanzee-to-chimpanzee signed interactions. At CWU from 2000 to 2003 (36 months) there were 44 utterances in chimpanzee-to-chimpanzee signed interactions (Leeds & Jensvold, 2013). At FF Tatu signed 42 utterances, most frequently SORRY (see Table 6 for the frequency of each):

> 10/18/13
>
> The day after they first met, Tatu and Spock were playing tickle and wrestle in Jeannie's front Room 1. Chance came into [the adjacent enclosure] and began screaming. Tatu sat up startled ... she looked at Chance and signed SORRY.

> 9/12/14
>
> Loulis and Jethro [in an adjacent enclosure] were fighting through the plexiglass between the long tunnel and Yoko's Tunnel. ... Jethro started screaming and Loulis offered reassurance. Tatu ran back to Jethro and signed SORRY toward him and then offered him reassurance. Things finally calmed down after lots of screaming.

> 11/12/14
>
> Sue Ellen had grabbed something off the trolley and it upset Toby [in an adjacent enclosure] and he banged on the plexiglass really hard. Sue didn't seem to care but Tatu saw Toby and signed SORRY over and over again. She then moved closer and Toby wasn't engaging with her and she began to whimper and sign SORRY toward Toby with a fear grimace. He finally offered her some reassurance. However, Loulis was nearby and almost began to display but calmed down after Tatu did.

At CWU, the chimpanzees used SORRY as statements and conversational devices (Leeds & Jensvold, 2013). The longest utterance followed an interaction with Chance in a neighbouring enclosure:

> 12/30/13
>
> Tatu and Spock were both sitting in the tunnel. The door to the Apartment [enclosure] was closed and Chance was at the other side [of the door]. A few seconds before there had been lots of screaming and grabbing at Chance's fingers from Tatu and Spock. Spock had gotten up and walked a few feet away when Tatu signed [to Spock]: HURRY YOU COME THERE ([pointing] towards the door where Chance was sitting).

Loulis signed 61 utterances with the other chimpanzees (see Table 7 for the frequency of each). HURRY was the most frequent utterance, followed by YOU. He made one multisign utterance after an exciting introduction with Maya in 2017:

> They had a quiet time sitting in Jeannie’s area. Loulis [with] piloerect [hair] sat up oriented toward Maya. Loulis: HURRY YOU HURRY. Loulis approached Maya. Loulis embraced Maya. Maya embraced Loulis.

At CWU, the sign HURRY appeared in a variety of communicative functions most often in request action and performative reassurance (Leeds & Jensvold, 2013).

Table 6. Tatu Chimpanzee-to-Chimpanzee Utterances

Utterance	Number
CHASE	5
COME	2
GIMME	1
GROOM	2
HUG	2
HURRY	2
HURT	1
MILK	1
PERSON	3
SODAPOP	1
SORRY	10
THERE	1
YOU	6
GO THERE	1
HURRY YOU	2
HURRY YOU COME THERE	1
YOU HURRY	1

Table 7. Loulis Chimpanzee-to-Chimpanzee Utterances

Utterance	Number
CHASE	3
HURRY	52
YOU	5
HURRY YOU HURRY	1

Chimpanzee Sign Recipients

Figure 1 shows the recipients of Tatu's signs (Borgatti, 2002). She signed to Spock 10 times, and signed six or more times to Jethro, Chance, or Toby. She signed less often to Loulis, Binky, and Regis. She never signed to Maya or Sue Ellen. Figure 2 shows the recipients of Loulis' signs. He signed by far most often to Spock at 29 times, followed by Binky at nine and Jethro at seven. Within three months of their arrival at FF, Tatu and Loulis were living in an enclosure with Spock and Sue Ellen. While Tatu and Loulis both signed most often to Spock, neither signed to Sue Ellen. Tatu and Loulis both signed often to Jethro and Binky, who were in adjacent enclosures. All the other chimpanzees in adjacent enclosures were equally likely to be sign recipients. Signing partner was not a result of simply spending time with another individual. Tatu signed often to Chance, while Loulis never signed to her. Tatu often signed to Toby but Loulis only signed to him once. Tatu and Loulis were never inside enclosures with Chance or Toby. These patterns show individual preferences, since Tatu and Loulis were in the same enclosures and they both had the same partners in adjacent enclosures.

Contexts

Tatu and Loulis primarily signed to other chimpanzees in affinitive social (36%), reassurance (23%), and greeting (17%) contexts. Cianelli and Fouts (1998) analyzed signs in videotape records of Washoe, Tatu, Loulis, Dar, and Moja during 60 high arousal interactions. The chimpanzees signed in 15 of the interactions and used 40 utterances, most often in feeding (39%), play (27%), reassurance (15%), and affinitive social (15%) contexts. None were in greeting. Loulis was in 63% of the interactions and signed in 15% of those. Tatu was in 57% of the interactions and signed in none of them. The interactions at CWU were among a stable group of chimpanzees while those at FF were among relative strangers.

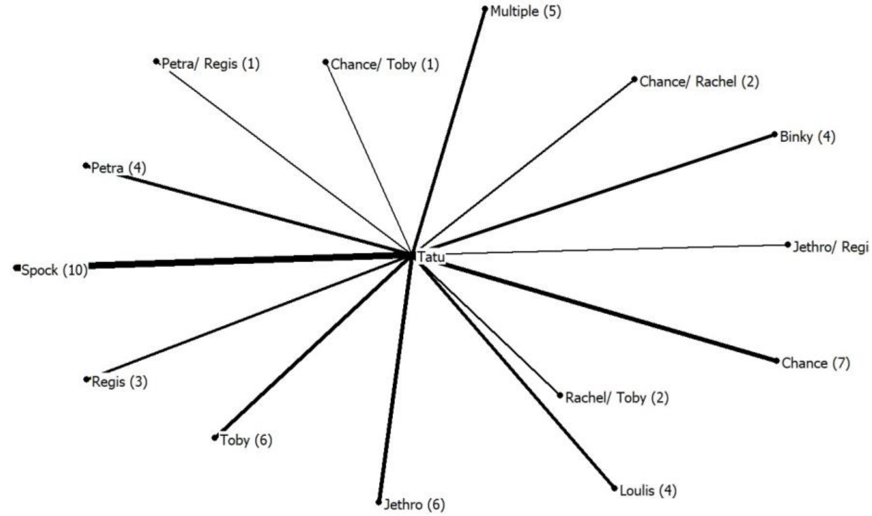

Figure 1. Tatu's sign recipients. Multiple recipients were when Tatu signed to more than two individuals and includes Binky, Chance, Jethro, Petra, Rachel, Regis, Spock, Toby, and Yoko, or an unknown recipient. Number in parenthesis is number of records to that recipient.

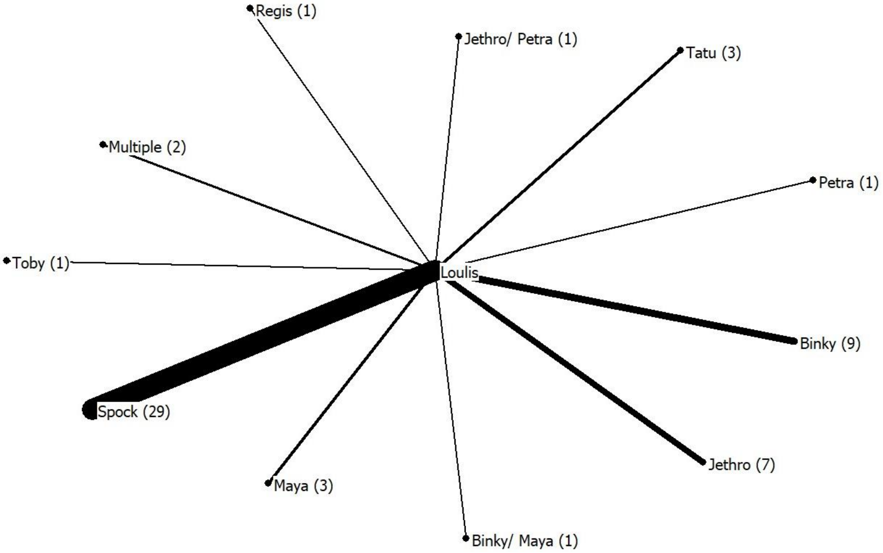

Figure 2. Loulis' sign recipients. Multiple recipients was when Loulis signed to more than two individuals and includes Chance, Jethro, Regis, and Yoko, or an unknown recipient. Number in parenthesis is number of records to that recipient.

When Washoe left Reno for Oklahoma, for the first time since infancy she encountered other chimpanzees with no ASL. In a reassurance context, “Washoe would often sign COME HUG when some of the other juvenile chimpanzees became upset” (R. Fouts, 1994, p. 259). Tatu also signed in reassurance with signs such as SORRY to Jethro. In other situations and with different partners the context was play. For example, with Binky, Tatu signed only CHASE. Likewise, “[Washoe] often signed HUG to the young chimpanzees, but after Washoe was introduced to the adult population the sign she used most was TICKLE” (Fouts, p. 259). Washoe and Tatu adjusted their signing to the different audience.

Frequency of Chimpanzee-to-Chimpanzee Signing

The number of sign logs with chimpanzee-to-chimpanzee signs at FF decreased over time. From September to December 2013 there were 30 logs, in 2014 there were 67, in 2015 there were six, in 2016 there were two, and in 2017 there were four. This decrease could be a result of the ad libitum method or could be evidence that Tatu and Loulis signed less to the other chimpanzees. In a systematic study of the chimpanzees’ conversational behaviours with humans who knew sign language or not, the chimpanzees signed less often to nonsigners (Hartel, Jensvold, Fouts, & Fouts, 2007). The vocabulary use analysis indicates that signing is robust with human partners who sign, but the log analysis suggests it occurs less with partners who do not sign, for example the other chimpanzees at FF. This provides further evidence that chimpanzees who acquire signs communicate persistently with this modality throughout life in a variety of environments.

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Chapter 6

RELATIONSHIPS BETWEEN CAREGIVERS AND CHIMPANZEE SANCTUARY RESIDENTS

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ABSTRACT

The relationship between humans and sanctuary residents is critical to animal welfare. Different organizations, such as zoos, laboratories, and sanctuaries, have different missions, which may affect the nature of this relationship. No matter the type of organization, the relationship between residents and caregivers is omnipresent and is an avenue to improve quality of life and wellbeing. To promote wellbeing, caregivers should consider the unique needs of each individual resident. The individual's history, personality, preferences, health, social network, and social skills contribute to these needs. Caregivers also are part of the social network. They should understand the hierarchy and politics of the chimpanzee group and work within it, and should use appropriate behaviours in interactions to improve the caregiver-chimpanzee relationship. An

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empathic approach in which the caregiver considers the special needs of each individual is advised. Practices in comparable human institutional settings, such as hospitals, prisons, retirement homes, and orphanages, provide models to emulate or avoid. Recently there have been retirements of chimpanzees from research, elephants from the circus, and cetaceans from entertainment, but the individuals still remain in the same facilities. This raises a question about the nature of the relationship. Can relationships that have roots in training and domination change within the new context of sanctuary? The practices suggested in this chapter constitute a culture of compassionate care that seeks to improve the welfare of residents as its singular mission.

Keywords: sanctuary, species-typical behaviours, husbandry, caregiving, chimpanzee, *Pan*

TYPES OF CAPTIVE ENVIRONMENTS

In 2013, the National Institute of Health (NIH, 2015) in the United States announced it would no longer fund invasive chimpanzee research. This announcement, along with the Convention on International Trade in Endangered Species of Wild Fauna and Flora upgrading captive chimpanzees to endangered status, essentially ended invasive research with chimpanzees in the United States. At the time of writing in early 2019, sanctuaries are preparing to accept hundreds of chimpanzees from about five laboratories. Thus, chimpanzees and their care are currently of prime importance in the sanctuary community and this chapter will focus primarily on chimpanzee care.

Chimpanzees live in captive environments such as laboratories, zoos, sanctuaries, and entertainment and breeding facilities. The missions of these are distinct. Biomedical facilities generally serve the needs of human health. This often is demonstrated in their mission statements. For example, the Southwest National Primate Research Center (n.d.) aims “to improve the health of our global community through innovative biomedical research with nonhuman primates.” The MD Anderson Cancer Center (n.d.), which holds over 100 chimpanzees, aims “to eliminate cancer in Texas, the nation, and the world through outstanding programs that integrate patient care, research and prevention, and through education for undergraduate and graduate students, trainees, professionals, employees and the public." Zoos generally have a mission of conservation and education and some include a statement about the care of residents. For example, the Lincoln Park Zoo (n.d.) "is dedicated to connecting people with nature by providing a free, family-oriented wildlife experience in the heart of Chicago and by advancing the highest quality of animal care, education, science and conservation." The San Diego Zoo Global (n.d.) is "committed to saving species worldwide by uniting our expertise in animal care and conservation science with our dedication to inspiring passion for nature," while the Honolulu Zoo Society (n.d.) says its zoo "is to inspire the stewardship of our living world by providing meaningful experiences to our guests. The Zoo emphasizes Pacific Tropical ecosystems and our traditional values of malama (caring) and ho'okipa (hospitality)." With a blended mission, zoos try to balance animal welfare on the on hand with conservation efforts and serving the needs of the public on the other hand.

Sanctuaries generally have missions that centre on their residents' wellbeing. Save the Chimps' mission is "to provide and build support for permanent sanctuary for the lifelong care of chimpanzees rescued from research laboratories, entertainment, and the pet trade" (Save the Chimps, n.d.). The Chimpanzee Sanctuary Northwest (n.d.) "provides lifetime quality care for formerly abused and exploited chimpanzees while advocating for great apes." For sanctuaries, resident wellbeing is the first priority and the caregiver-resident relationship is critical to it.

The husbandry practices and emphasis on the caregiver-chimpanzee relationship will vary among labs, zoos, and sanctuaries, which in turn will affect an individual chimpanzee's experience.

AN ESSENTIAL RELATIONSHIP

No matter the type of organization, the relationships between residents and caregivers are omnipresent. These relationships are an avenue to improve quality of life and wellbeing. Hemsworth, Barnett, and Hansen (1987) compared domestic pigs who caregivers stroked and petted to pigs who caregivers shocked and slapped. The pigs in the friendly condition were more likely to approach caregivers, while those in the aversive condition showed decreased growth and reproduction rates and higher corticosteroid levels, even when humans were absent. Similarly, cows produced more milk if their caregiver was friendly as determined by a self-questionnaire (Seabrook, 1984, p. 84). Laboratory rabbits exposed to systematic petting, holding, and play with a caregiver had reduced aortic atherosclerosis (Nerem, Levesque, & Cornhill, 1980, p. 1475). In another study, when caregivers spent just two minutes a day interacting with and distributing food treats to laboratory rhesus macaques, abnormal behaviours were reduced as compared to when caregivers did not spend the extra time (Bayne, Dexter, & Strange, 1993, p. 6).

Positive relations can improve quality of life and agonistic relationships can decrease it. Captive nonhuman primates often react fearfully and aggressively toward their caregivers (O'Neil, 1989, p. 145), and sometimes the mere presence of the caregiver can have a negative affect (Line, Markowitz, Morgan, & Strong, 1991, p. 160; Bloomsmith, Baker, Ross, & Lambeth, 1999, p. 35; Chelluri, Ross, & Wagner, 2013, p. 306). In addition to relationship quality, the activities associated with the captive environment also can affect its residents. During caregiving activities, such as cleaning and meal times, chimpanzees have higher wounding rates (Lambeth, Bloomsmith, & Alford, 1997, p. 327). Monkeys (Alford, Nash, Fritz, & Bowen, 1992) and chimpanzees (McGrew & McLuckie, 1984, p. 1) are more likely to give birth over weekends when caregiving activities are decreased. Caregiving activities are associated with elevated heart rates in laboratory monkeys (Line et al., 1991, p. 160). These examples suggest that caregivers' attitudes and behaviours can have a significant impact on the quality of life of those in their care. In this chapter, I propose best practices in care to improve welfare and pitfalls to avoid.

GUIDELINES FOR CARE

There are several resources for husbandry standards in chimpanzee care. The US Department of Agriculture (USDA) standards are minimal and primarily describe enclosures, food storage, handling, and hygiene covered in a few paragraphs of more than 200-page Animal Welfare Regulations (APHIS, 2017). These regulations only address interactions with personnel as a form of environmental enrichment (p. 175). Similarly, the National Research Council (2010) also emphasizes handling and medical protocols and states: “Dogs, cats, rabbits, and many other animals benefit from positive human interaction” (p. 63). In both of these standards, there is little emphasis on relationships between caregivers and residents. The Association of Zoos and Aquariums (AZA) recognizes the importance of social relationship but advocates a minimum intervention strategy from caregivers to chimpanzees, and instead emphasizes the relationships between chimpanzees (AZA, 2010, p. 58). The Global Federation of Animal Sanctuaries (GFAS), which accredits sanctuaries globally, requires that “positive relationships between apes and caregivers are maintained. Apes are not fearful or aggressive in response to human presence or routine care procedures” (GFAS, p. 38). This guideline recognizes the importance of positive relationships, although it lists what to avoid rather than specific actions to improve relationships.

Positive Reinforcement Training

The GFAS, the AZA, and the NRC advocate for positive reinforcement training (PRT) to manage behaviour in a variety of nonhuman primates. PRT increases compliance with voluntary movement, encourages social behaviour, reduces caregiver-directed aggression, reduces self-injurious behaviour, and increases compliance with injections (Perlman, Bloomsmith, Whittaker, McMillan, Minier, & McCowan, 2012). Baker surveyed its use in laboratories and wrote: “[P]ositive reinforcement training programs employ the technique of using a positive stimulus after the performance of a behaviour in order to increase the likelihood of the behaviour occurring again. However, 74% of participants in the current survey report also employing negative reinforcement training (NRT) techniques (the withdrawal of a negative stimulus after the performance of a behaviour in order to increase the likelihood of the behaviour occurring again (Baker, 2016, p. 793)." With the presence of aversive stimulus, stress is inevitable in NRT.

Several studies have examined the effect of PRT during interactions between chimpanzees and caregivers. Bloomsmith, Lambeth, Stone, and Laule (1997) found that training sessions increased social interaction among captive chimpanzees and that unstructured interactions with a caregiver reduced solitary and inactive behaviours. Chimpanzees interacted with caregivers more during training sessions and showed increased conspecific social behaviour during and after those sessions. Bloomsmith et al. (1999) later compared the behaviours of chimpanzees during training interactions versus nontraining interactions versus matched control sessions with no caregivers present. Chimpanzees interacted more with caregivers during training than nontraining, and showed more agonism in training sessions versus a baseline. Finally, Carrasco, Colell, Abelló, Velasco, and Posada (2009) found that a combination of training and play therapy significantly decreased abnormal and visitor-directed behaviours and conspecific aggression, and increased affiliative and play behaviours in zoo-living western lowland gorillas. These studies show the benefits of positive training and natural unstructured interactions.

Natural unstructured interactions are ones in which the caregiver simply spends time with the chimpanzees for no specific purpose – no food service, no training, no cleaning, etc. They resemble interactions between chimpanzees with grooming or play for example. They also may include other activities that chimpanzees acquired as youngsters such as colouring, looking at magazines, brushing teeth, or painting nails. In a study by Baker (1997), caregivers increased unstructured interactions with 12 laboratory chimpanzees by approximately 10 minutes per chimpanzee per day. The increase in unstructured interaction time led to a significant decrease in agonistic displays, inactivity, reaction to conspecifics' vocalizations and displays, and abnormal oral behaviours such as regurgitation and reingestion as compared to baseline. Interactions also increased grooming behaviours. In a study with marmosets when caregivers spent an extra 20 minutes interacting, there was a significant decrease in locomotion and self-scratching, and a significant increase in grooming and play behaviours (Manciocco, Chiarotti, & Vitale, 2009). A singly housed gorilla who had one-on-one interactions with a caregiver had a complete reduction of aggressive behaviours and an increase in browsing behaviours over the 5.5-year study period (Pizzutto, Nichi, Corrêa, Ades, & Guimarães, 2007).

Caregivers should have a strong knowledge of the species for which they care (Fouts, Abshire, Bodamer, & Fouts, 1989). This knowledge should include natural diet, social organization, cognition, and behaviours (Joint Working Group on Refinement, 2009 S1:1). Knowledge of a particular species' behaviours allows caregivers to understand an individual's state and recognize arousal level, aggression, affiliative interactions, etc. As Estep and Hetts (1992) describe, "knowledge about the normal signals used in agonistic, affiliative, sexual, parental, and predator-prey interactions is extremely useful in manipulating the animal's behavior and in helping to create a desirable relationship with the animal" (p. 22). This information can be imparted via a taxonomy of behaviours in which the individual behaviours are described and their associated behavioural context (see McCarthy, Jensvold & Fouts, 2013, supplemental information). For example, in chimpanzees a bipedal stance occurs in threat and agonistic contexts. A playface and playslap occur in a play context.

Caregivers also can use appropriate species-typical responses. For example, if a chimpanzee headnods, a friendly greeting, the caregiver can reciprocate the greeting with a headnod and a breathy pant. For many taxa, caregiver use of species-typical behaviours can change the nature of the interaction. For example, Fulani herdsmen in Africa use cattle behaviour to manage the herd. The herdsmen take the role of high-ranking cattle by breaking up fights within the herd and take on the role of the leader to guide the herd's movements (Lott & Hart, 1979). Additionally, to strengthen bonds they stroke cattle on the inside of the rear leg, a place where mothers lick their calves. The cattle approach and lick the herdsmen in return, indicating a friendly relationship. These men are able to manage the herd with cooperation by using their knowledge of cattle and incorporating their behaviours.

Jensvold (2008) tested the effect of using species-typical behaviours with chimpanzees. Caregivers at a zoo either used chimpanzee behaviours or not during interactions. On some days of data collection (chimp condition), the caregiver presented chimpanzee behaviours and vocalizations typical of the practices at the institute. For example, upon greeting, the caregiver would present a pronated wrist and breathy pant and in play interactions she would present a playface and playslaps. On other days of data collection, the caregiver presented only human behaviours and avoided using chimpanzee behaviours (human condition). Overall, the chimpanzees engaged in significantly more friendly behaviours such as play when caregivers used chimpanzee behaviours compared to when they used human behaviours. They were significantly less interactive when caregivers used human behaviours. Jensvold, Buckner, and Stadtner (2010) replicated this study in a group of sanctuary chimpanzees in which caregivers regularly used species-typical behaviours. The chimpanzees were also sensitive to the differences in caregivers' use of species-typical behaviours.

Care for Individual Needs

To promote wellbeing, caregivers should consider each individual resident's unique needs. The individual's history, personality, preferences, health, social network, and social skills contribute to these needs. Captive chimpanzees can be wild caught or home reared, and might have lived in solitary confinement, laboratory, zoo, or entertainment conditions. These histories may have included traumatic or other experiences resulting in psychological disorders (Bradshaw, Capaldo, Linder, & Grow, 2008, p. 9; Ferdowsian & Merskin, 2012, p. 448) and may have manifested in dysregulated, self-abusive, or stereotypical behaviours (Brüne, Brüne-

Cohrs, McGrew, & Preuschoft, 2006, p. 1246). Chimpanzees will react to individual situations with a blend of their history and personality (Kalcher-Sommerguter, Preuschoft, Crailsheim, & Franz, 2001, p. 77). Experiences craft their individual preferences. For example, some chimpanzees prefer blankets for bedding while others prefer straw, and some chimpanzees may have used bowls and spoons in their past and may prefer to receive food this way. Individual preferences point to the need to provide options. For example, both blankets and hay can be provided and individuals can decide which bedding to use. Caregivers should know as much as possible about individual histories and preferences to provide activities that are relevant and attractive to each chimpanzee. Individualized care plans can be developed much like they are in schools that offer individualized study plans for students.

As Goodall (1986) describes, wild chimpanzees are embedded in a community with social hierarchies and fluid subgroupings. They have some degree of choice in their participation in subgroups. An individual can spend time on the periphery of the community or in a different subgroup for a time, and females usually leave the community when they reach sexual maturity. This social flexibility is absent in captive environments and is determined wholly by caregivers. Most captive situations have relatively stable groups and the recommendation is for a minimum of seven individuals in a group (National Institute of Health, 2013, p. 21). This is a valuable recommendation because group life allows a multitude of interactions, and the potential for a variety of interactions grows exponentially as the group size increases.

Not all chimpanzees have histories with group rearing. Some chimpanzees have spent a lifetime alone or with one other chimpanzee. These experiences can affect social skills later in life (Brüne et al., 2006, p. 1253). Jeannie was a chimpanzee who spent much of her life in biomedical research before going to sanctuary. She was alone in a cage all of her life and was unable to later live in a social group. At sanctuary she only was able to have visits for a few hours at a time with other chimpanzees (Westoll, 2011; Bradshaw et al., 2008). The issues with chimpanzees who are unable to cope with group living raises issues of what the best plan for that individual might be. Chimpanzees should live in groups, but what if that arrangement leads to injuries? Creative solutions include adjoining enclosures that allow protected contact, or short visits with compatible individuals (Bradshaw et al., 2008).

Caregivers also are part of the social network. They should understand the hierarchy and politics of the chimpanzee group and work within it (Estep & Hetts, 1992, p. 7). Dominant chimpanzees, for example, should be served and greeted first to acknowledge their social status. Caregivers also should be sensitive to the relationships between individuals. For example, if two chimpanzees are grooming, the caregiver should not disturb them as grooming fosters the bond between individuals.

Insight into the social network helps caregivers to understand reactions and respond to them in ways that can help to deescalate tense interactions. For example, when caregivers performed submissive behaviours such as crouching and offering a pronated wrist when chimpanzees fought among themselves, there was a lower wounding rate in chimpanzees than at other facilities without this policy (Jensvold et al., 2010, p. 5). Caregivers should remain calm around chimpanzees, particularly when chimpanzees are aroused. Yet caregivers can show excitement and enthusiasm in greetings or prior to positive events and incorporate appropriate behaviours such as pant grunts and pant hoots respectively.

AZA guidelines (AZA Tag, 2010, p. 11) explicitly remind caregivers to be mindful of noise. The environment itself tends to be loud with cement walls, clanging metal enclosures, loud pressure washers, spraying water, food grinders, and beeping trucks. Human prisoners report that this kind of noise creates stress in their lives (Bryant, Davis, Haywood, Meikle, & Pierce, 2014). Chimpanzee vocalize when they are aroused, for example during aggression or excitement when eating, but when they are calm they are very quiet. When humans use loud voices, chimpanzees often vocalize in response, which indicates increasing arousal level. Arousal can be a positive situation such as prior to a favoured meal, but a constant state of arousal increases stress hormones and ultimately is deleterious. Thus, as a matter of practice, caregivers should be mindful of noise and use quiet rather than loud voices.

Chimpanzees understand spoken languages and what caregivers say. Caregivers can therefore communicate to residents the plan of activities, meals, etc. When serving food, caregivers can ask chimpanzees to wait for a turn, and explain, “I’ll serve you next,” “I’ll be right back,” or, “Billy, I will serve you after Betty.” When moving into other areas caregivers can say, “Billy please move to the next room.” At the same time, caregivers should be aware that chimpanzees also understand derogatory statements and moods. Caregivers should avoid negative comments to the chimpanzees such as “you’re in a bad mood” or “you’re being bad.” Verbal communication can be used to benefit or inadvertently damage relationships between caregivers and chimpanzees.

How caregivers speak about their charges to other individuals is relevant as well. Derogatory comments such as the chimpanzees are “misbehaving,” “dirty,” or “mean,” whether the chimpanzees can hear or not, is detrimental to the relationship. Our language in reference to others shapes how we view them. Dehumanization is

> …whenever some human beings consider other human beings to be excluded from the moral order of being a human person ... by identifying certain individuals or groups as being outside the sphere of humanity, dehumanizing agents suspend the morality that might typically govern reasoned actions toward their fellows ... this is a central process in prejudice, racism, and discrimination (Zimbardo, 2007, p. 307).

The work of Bandura, Underwood, and Fromson (1975) in experimental psychology showed how moral disengagement, which is a part of dehumanization, can occur simply by hearing one individual use negative labels about another. A caregiver’s language and reference to their charges can affect both their own perceptions and those of their colleagues and peers.

Caregivers should follow through on promises made to their charges and adhere to the organization’s prescribed protocols of husbandry. This creates a consistency among caregivers that ultimately supports a reliable and dependable routine, which is critical to generating a safe secure predictable environment. Gazzola (2014), an incarcerated human, described her prison experience: “The unpredictability, frequent changes, and mounting deprivations piled on top of me, compressed my lungs, shortened my breath ... [it] was driving me crazy” (p. 125). Parenting plans call for consistency within and between caregivers so the child knows what to expect; this is particularly true for children from traumatic backgrounds (Siegel & Bryson, 2014, p. 239). Sanctuary caregivers are not parents, and should not confuse the roles. Adult chimpanzees are not human children. Parenting psychology, however, contains techniques that caregivers can borrow to foster healthy relationships. These practices contribute to healthy professional boundaries, which ensure that caregivers act in ways that fulfill the chimpanzee’s needs rather then their own emotional needs (Paternelj-Taylor & Yonge, 2003).

The sanctuary is a home for its residents, and caregivers should be mindful to treat it as such. This is in contrast to other types of workplaces; a factory is a different type of workplace than an assisted living facility. The sanctuary is like the latter. Caregivers should be mindful that the sanctuary resident is incarcerated and lacks the freedom to leave the situation. Many behaviours may be elicited by this situation, such as spitting, poking, throwing feces, banging, or aggressive displays. Chimpanzees, like humans, can be aggressive. Caregivers must tolerate these behaviours and accept them as part of the job. Caregivers never should punish or seek revenge for these behaviours. Chimpanzees have good days and bad days and this difference in moods should be recognized and allowed in caregiving interactions in a quiet and respectful way. Caregivers should treat residents with dignity and respect. One way to do this, Gruen (2014) argues, is by creating sight distance: “The dignity of the captive is enhanced when the individual is provided with opportunities for choice about who to spend time with, including captors and observers, but crucially, captives must be provided with the ability to escape the gaze of others” (p. 245). In psychology this objectifying gaze, “the visual inspection of the body by another person” (Gervais, Vescio, & Allen, 2011, p. 6), is related to offset in power, poor self-image, poor performance (Gervais et al., 2011, p. 6), and feelings of paranoia, anger and resentment (Gruen, 2014, p. 243; Bryant et al., 2014, p. 105). Looking into the eyes of the social partner is different than looking at the body of the social partner. Fostering respect in relationships by providing chimpanzees with opportunities to avoid gaze such as privacy space and by asking humans not to stare can increase cooperation and decrease antagonism.

Caregivers should treat all chimpanzees with equal respect and avoid favouritism. Inequality in treatment could upset the dynamic within the social group, and could create inconsistent care among chimpanzees. If a caregiver spends more time with a favoured chimpanzee, then an unfavoured chimpanzee receives less care than others.

Relationships between caregivers also may be reflected in patterns of interaction between caregivers and chimpanzees. Coworkers who are disrespectful or aggressive to each other may have problematic ways of interacting with residents. Chimpanzees are incredibly sensitive to humans' nonverbal behaviour (Kano, Yamanaski, & Tomonaga, 2012, p. 9; Parr, 2001, p. 223), so even microaggression may affect their wellbeing. Chimpanzees should be protected from witnessing, or being the brunt of, aggression or negativity between staff. Organizations can develop programs to promote positive behaviours, mutual respect, and courtesy among staff to create a positive workplace for caregiving staff and ultimately improve resident wellbeing.

Nursing takes an empathic approach to caregiving. Empathy is "the capacity to comprehend the affective and emotional states of others in relation to oneself" (Decety, 2011, p. 1). Gruen (2015) describes "entangled empathy" as "a type of caring perception focused on attending to another's experience of wellbeing" (p. 3). Mercer and Reynolds (2002) describe empathic care as a "core aspect of effective, therapeutic consultations in general" (S9). It is a form of professional interaction with skills and competencies. Nursing care outcomes are improved in patients with empathetic nurses (La Monica, Madea, & Oberst, 1987). Caregivers in sanctuary settings can draw from this approach as chimpanzees, too, are emotional beings. Key aspects of empathic care include supportive communication, empowering the patient, and reducing or resolving the patient's problems (Mercer & Reynolds, 2002, p. 10). Communication is at the core, when the patient’s needs are recognized. In chimpanzees, this type of empathic care involves understanding behaviours, histories, and communication verbally and nonverbally. Additionally, caregivers must be empowered to advocate for residents. They must articulate observations and concerns about residents to management. Policies should be in place to record and address any issues. For example, caregivers and behaviour managers should regularly receive and read daily moods and interactions reports.

WHEN CARE GOES WRONG

Sometimes the inherent invasiveness in captive settings is taken to an extreme and the relationship between the caregiver and nonhuman primate becomes that of a dominator and subordinate (Estep & Hetts, 1992). Boundaries are completely violated. Sometimes this can involve physical punishment or abuse. For example, in 2009, the Humane Society of the United States (2009) published video footage of neglectful, aggressive, and harmful behaviours from care staff to nonhuman primates at New Iberia Research Center in Louisiana. Examples from human institutions suggest perhaps it is not so difficult to arrive in this situation. In the Stanford prison experiment, college students played the role of inmates or prison guards in a mock prison. The experiment ended after 6 days when inmates became pathologically depressed and helpless-feeling while the guards embraced their power and became dominating and abusive (Zimbardo, 2007). This provides some experimental evidence to explain abuse in real institutional settings.The Abu Ghraib prison and the Magdalene institutions in Ireland are real-world examples of torture and abuse in institutions that are part of large organizations, the US military and the Catholic Church respectively. They speak to the human potential to slip to extreme forms of abuse, torture, or simply daily teasing and haranguing when in dominant-subordinate relationships despite oversight from large organizations. They are cautionary tales for institutions holding nonhuman animals.

These types of relationships are described in an HSUS investigation report. For example: “An employee struck one monkey three times in the mouth with a hard metal pole in order to make him open his mouth for the tube” (HSUS, 2009, p. 3). The whistleblower in this report described an “employee burning some of the chimps with a lighter. He had also thrown a 5-gallon bucket of very hotwater on Chimp Dali” (HSUS, 2009, p. 9). From entertainment there are similar reports: “I saw Yost kick and punch these baby chimpanzees in the face, hit them with sticks and metal objects, and subject them to mental and psychological abuse. Even worse, this horrifying treatment of chimpanzees appears to be an industry standard” (Baecker & Spano, 2006).

Often, caregivers wear personal protection devices (PPD), which can range from gloves to a full Tyvek suit with face shield and full body coverage. The Stanford prison experiment included guards wearing eyeglasses and uniforms. Zimbardo suggests one of the situational factors that contributed to the abuses was the anonymity, which was created by the uniform (2007, p. 444). It could be that PPDs contribute to anonymity and degrade the interaction. While PPDs are important for reducing zoonotic transmission, protocols should require only what is necessary. Chimpanzees with known clean histories can be treated differently than those who have exposure to diseases. Laying a foundation that emphasizes individuals, relationships, and communication is a start to steer away from these negative potentials.

IN SITU SANCTUARIES?

Practices and policies of an organization constitute a culture of care characterized by the daily interactions between caregivers and residents. Many chimpanzees retired from research remain at the laboratories, and some have suggested retiring them in place rather than moving them to sanctuaries (Speaking of Research, 2016; Buckmaster, 2016, p. 271). At the time of this writing, NIH (2018) is evaluating the safety of moving at-risk chimpanzees from laboratories to sanctuaries. If the chimpanzees remain in place, the staff at the laboratories would remain the same. The daily routine and procedures would remain the same. The culture of care would remain the same. This is a culture rooted in biomedical research in institutions designed to facilitate invasive experimental procedures. These institutions continue to practice research with other primate species.

Similarly, Ringling Brothers Circus ended its elephant shows in 2017 and the elephants remain at its Center for Elephant Conservation. The website for the organization (Ringling Bros. and Barnum and Bailey Center for Elephant Conservation, n.d.) features pictures of elephants doing tricks, unprotected contact between caregivers and elephants, and baby elephants, which promotes breeding. Ringling Brothers uses bullhooks in its caregiving practices (Aria, 2014). Doyle (2014) describes this practice:

> Training never ends for performing elephants. Handlers reinforce tricks and routines at the point of the bullhook, even though the elephants have performed these maneuvers hundreds of times. The bullhook is often embedded in sensitive areas of the elephant's skin, including inside the ear or mouth, behind the ears, in and around the anus, and in tender spots under the chin and around the feet (p. 47).

SeaWorld phased out its shows with orcas and instead now offers educational programs (Siegel, 2016). The orcas remain in their small tanks with the same protocols and procedures for care. Can relationships and captive environments that have roots in training and domination change within the new context of a sanctuary simply because it is called a sanctuary? Can dignity and respect be instilled in settings originally based on utilitarian relationships? The experience of the individual living within those confines and in that relationship likely will remain the same, so a new label will do little to improve welfare.

The practices suggested in this chapter constitute a culture of compassionate care that seeks to improve the welfare of residents as its singular mission. Changing organizational culture is difficult, but a key component is participation in and inspiration for the mission. If caregivers are driven by residents' wellbeing, they are already inspired by the mission of a well-run sanctuary. The rest is easy.

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Mary Lee Jensvold currently is the Primate Communication Scientist and Associate Director at Fauna Foundation in Carignan, Quebec. She is former director of the Chimpanzee & Human Communication Institute and is a Senior Lecturer in the Primate Behavior and Ecology Program and Anthropology Department at Central Washington University. She has over 30 years experience working in chimpanzee sanctuaries in care, management, and design. Her expertise is in behaviour and communication, including American Sign Language in chimpanzees and other apes. Her research includes conversational behaviours between chimpanzees and humans, private signing, phrase development, chimpanzee-to-chimpanzee conversation, and imaginary play. Other research includes caregiving practices, zoo visitor effects, and public education about chimpanzees. She is a member of the board of directors of the Animal Welfare Institute, Fauna Foundation, and Friends of Washoe. She is an alternate on the North American Primate Sanctuary Alliance steering committee. She is past Sigma Xi distinguished lecturer. She has numerous journal article and book chapter publications.

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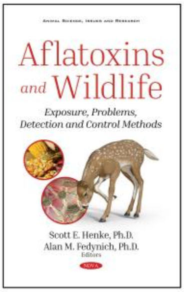

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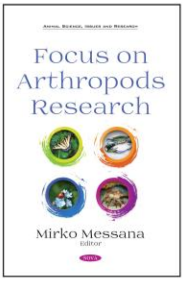

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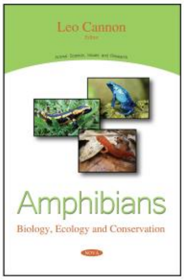
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