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Introduction

The relevance of chimpanzee research

In the search to better understand ourselves and our origins, biologists have since at least the time of Darwin turned to non-human animals for insight. Darwin himself (1874) provided one of the first in-depth comparisons between the behavior of humans, non-human primates, and other animal species. In the past decades, primatologists have pushed particular primate species as models to aid in the reconstruction of the behaviors of our early human ancestors (reviewed in Zihlman, 1996; Strum & Mitchell, 1987; Wrangham, 1987). Early models based on baboons fell to the wayside, as humankinds' closest genetic relatives, i.e., bonobos (*Pan paniscus*) (Zihlman et al., 1978) and chimpanzees (*Pan troglodytes*) (reviewed in Zihlman, 1996), were offered forth as the ideal stand-ins for early hominins (human ancestors). Wrangham & Peterson (1996) proposed that the common ancestor which humans share with chimpanzees and bonobos was probably morphologically and behaviorally chimpanzee-like. Bonobos, despite being equally close genetic relatives to humans as are chimpanzees, have in this view diverged farther from the ancestral condition than chimpanzees. Chimpanzees (and to a lesser degree bonobos) have been proposed to share a number of key behavioral features with humans that were likely present in the common ancestor of *Pan* and *Homo*: a fission-fusion social system in which related males monopolize a community of often unrelated females (Ghiglieri, 1987), monkey-hunting (Stanford 1999), lethal inter-community violence (warfare), and elaborate tool-use traditions (Wrangham & Peterson, 1996). The latter three traits were proposed to have been lost or reduced in bonobos. Other comparisons have been even more specific than this. Moore (1996) examined the utility of using savanna woodland-dwelling chimpanzees as a model to understand early human adaptations.

Recent fossil discoveries have called into question the assumption that the common ancestor of humans and the two *Pan* species shared basic chimpanzee / bonobo adaptations, thus opening a debate on the appropriateness of using any living African ape as a model for early humans (Lovejoy et al., 2009). Several morphological features shared by chimpanzees and bonobos are now claimed by some experts to have been absent from their common ancestor with humans: knuckle-walking and other locomotory adaptations (the possible hominin *Ardipithecus ramidus* was not a knuckle walker: Lovejoy et al., 2009), large canines in males (*Sahelanthropus tchadensis*, another possible hominin, may have had small non-sexually-dimorphic canines: Brunet et al. 2002), and thinly-enameled molars (*A. ramidus* molars were more thickly-enameled than those of a chimpanzee: Suwa et al., 2009). These morphological differences may have been tied to behavioral and ecological dissimilarities between the last common ancestor and modern chimpanzees and bonobos (Lovejoy et al., 2009). To further complicate matters, the lack of elaborate tool-use traditions in bonobos raises the possibility that the evolution of such traditions might have occurred independently in the chimpanzee and human lineages, although two gains of material culture (in chimpanzees and in humans) may be considered less parsimonious than one loss (in bonobos). The same could be said of warfare and monkey-hunting, although one population of bonobos at Lui Kotal in DRC has recently been discovered to hunt monkeys (Surbeck & Hohmann, 2008). It is premature to make generalizations about bonobos when they have not been studied as extensively as chimpanzees.

Contrary to Lovejoy et al. (2009), Whiten et al. (2010) dispute the conclusion that this perceived lack of similarity in some features makes chimpanzees useless for reconstructing

the common ancestor. In addition, claims that *A. ramidus* and *S. tchadensis* were hominins post-dating the split between humans and chimpanzees have been contested (Wolpoff et al., 2002; Sarmiento 2010), leaving open the possibility that the common ancestor of humans and chimpanzees was a chimpanzee-like knuckle-walker. Even if some chimpanzee morphological and behavioral adaptations had been independently-derived following their split from the hominin lineage, and were thus not directly relevant to reconstructions of the life-style of our mutual common ancestor, the fact that these apes show a large and complex repertoire of possibly cultural, or at least socially-transmitted, behaviors means that they are still relevant to the study of the evolution of cultural systems in hominids (including hominins). Even if we discover that our common ancestor with chimpanzees was not an accomplished culture-bearer, and that the elaborate tool and gestural traditions of chimpanzees evolved completely independently from those of humans in the 6-8 million years since we separated from them [the discovery of tool traditions in Sumatran orangutans (*Pongo abelii*) by van Schaik & Knott (2001) makes this unlikely], the species would still be relevant to understanding the emergence of traditions and social systems in large-brained hominids. If we want to understand the factors that led to the emergence of pre-human and human culture in our remote ancestors, then it is crucial that we understand the baseline from which these behavioral systems sprung, or failing that, study the independent origins of similar phenomena in a related lineage. For this reason we must gather as many observations as possible of chimpanzee traditions in their natural habitat.

The study of chimpanzees across widely-different ecological contexts continues to yield fascinating surprises into what this species is capable of (Whiten et al. 2001). Until recently, our knowledge was limited to a few populations of chimpanzees (*Pan troglodytes schweinfurthii*) living at the extreme eastern edge of the species' range (reviewed in Goodall, 1986); the behavior of rainforest chimpanzees was mostly unknown. Studies at Taï Forest in Ivory Coast and other West African sites (*Pan troglodytes verus*) have recently expanded the chimpanzee behavioral repertoire considerably: nut-cracking with hammers, cooperative-hunting, and higher degrees of female interaction than in the east (Boesch & Boesch-Achermann, 2000). Most recently, Boesch has documented a propensity of Taï Forest adult male chimpanzees to adopt apparently unrelated orphans (Boesch et al., 2010) and to actively defend community-members against leopard attacks (Boesch, 2009), behaviors which stand in apparent contrast to the rather more individualistic societies of East African chimpanzees. Add to this the recent discovery that chimpanzees at Fongoli, Senegal fashion 'spears' to hunt bushbabies (Pruetz & Bertolani, 2007) and rest in caves (Pruetz, 2001), that chimpanzees of Ugalla, Tanzania use digging sticks to excavate underground tubers (Hernandez-Aguilar et al., 2007), and that Central African chimpanzees (*Pan troglodytes troglodytes*) of Goualougo, Republic of Congo (Sanz & Morgan, 2007) and Loango, Gabon (Boesch et al., 2009) use tool sets (in the case of Goualougo, for multiple unrelated tasks), and it is clear that a real understanding of what chimpanzees are capable of will require, just as it would with humans, a knowledge of the full scope of their behaviors across their range (Boesch, 2009).

Ideally, of course, information on chimpanzees should come from direct behavioral observations of fully-habituated chimpanzees, but this is not always possible. Fortunately, invaluable studies following the protocol of paleoanthropologists have been carried out on un-habituated chimpanzees [for a pioneering example, see Sept's (1992) study of nest sites at Ishasa, Democratic Republic of the Congo (DRC)]. In addition, the forested habitats of some habituated chimpanzee communities have been excavated as archaeological sites investigating the 'prehistory' of the local apes' material culture (Mercader et al., 2002). Researchers have made inferences from indirect evidence about the geographical distribution of potential great ape cultural behaviors both for chimpanzees (Boesch & Boesch-Achermann, 2000) and Sumatran orangutans (van Schaik & Knott, 2001).

Boesch (2007; 2008) cautioned against using results obtained from chimpanzees living in the extremely altered environment of research laboratories as representative of the species' cognitive and social capabilities. This warning should be extended to studies of free-living chimpanzees as well. Van Schaik (2002), in his disturbance hypothesis, postulates that great ape societies may suffer impoverishment when they collide with growing populations of human settlers. I will present some possible evidence of this phenomenon in the northern DRC in Chapters 3 and 5 of this thesis. If this is indeed the case, then it seems obvious that the more remote and isolated a chimpanzee population is from humans, the less affected its set of traditions should be by human incursions. This highlights the value of studying the Bili-Uele (DRC) chimpanzees, which inhabit some of the most remote wilderness remaining in Africa. As will be demonstrated in Chapter 4, this population is still large and inter-connected, with probable opportunities for gene and meme exchange across vast areas. The forests in which these chimpanzees live have not yet been carved up into isolated patches; when this happens, as it already has across much of Africa, the apes are forced to inhabit isolated genetic / memetic 'islands' (Goodall, 1996). As we shall see in Chapter 2, there are still areas in northern DRC (the Gangu Forest in particular) where the chimpanzees rarely encounter humans, and do not show a strong fear of them when encountered. Such places are becoming rare in the world, and provide us with an excellent opportunity to observe what chimpanzee societies and traditions must have been like across Africa before the species' recent clash with expanding populations of human agriculturalists.

History of the research project

Over the last decade, the Bili-Bondo apes of northern DRC have been the subject of intense speculation, both in science and in the media. CNN heralded the existence of a possible new species of apes, while popular science magazines weighed the likelihood of hybridization scenarios between chimpanzees and gorillas (Young, 2004). Crypto-zoology websites have hyperbolized about the 'giant lion-eating Bili-Bondo apes' alongside reports on Bigfoot and the Florida 'skunk ape'. The Bili population also attracted the attention of primatologists. An unknown population guaranteed discoveries of hitherto unknown traditions.

The Bili apes research project was initiated in 1996 by wildlife photographer and conservationist Karl Ammann (Ammann, 2001). Ammann traveled into the remote forests near Bili, looking for evidence of the 'lost' *Gorilla gorilla uellensis*. The mystery surrounding this disputed taxon had its origins in 1898, when the Belgian colonel Le Marinel collected four gorilla skulls in the Bondo area (Ammann, 2001; Hofreiter et al., 2003). These were later proposed to represent a 'missing link' population bridging *G. berengei* in East Africa to *G. gorilla* in the west (a 600 km gap without gorillas exists to the east and west of Bondo) (Chapter 1, Figures 3 & 4; Hofreiter et al., 2003). During his first visit to the area, Ammann gathered reports from the locals of large, aggressive 'lion-killing' apes, and in the town of Bambillo near Bili he discovered a peculiar chimpanzee skull sporting a gorilla-like sagittal crest (Ammann, 2001). Between 1998 and 1999, Ammann's team established a research center called Camp Louis in the forest 34 km northwest of the town of Bili (Chapter 1, Figure 5). In their search for the resident apes in the gallery forests separating the savannas, the team found a number of ground nests resembling those constructed elsewhere by gorillas. In addition, they discovered ant dip tools measuring over 2 m in length. Ammann speculated that perhaps two ape species might inhabit the forests of Bili: *G. g. uellensis* and chimpanzees. Using hidden robot cameras, he managed to photograph several imposingly robust-looking apes. In addition, a photograph of a dead chimpanzee shot near Bondo indicated that it might be exceptionally large for its species. In 2001, a group of renowned primatologists visited

Camp Louis and failed to find evidence of any ape other than chimpanzees inhabiting the forest (NPR Radio Expeditions, 2001). Finally, genetic tests on the purported *G. g. uellensis* skulls collected by Le Marinel revealed them to be too similar to Western lowland gorillas to be an intermediate form between the eastern and western species (Hofreiter et al., 2003); thus the more likely explanation is that the skulls had been transported from West Africa to Bondo by traders.

In an attempt to attract the apes and habituate them to the presence of researchers, Ammann's team planted several patches of sugar cane near Camp Louis (Young, 2004). Shelley Williams conducted two field expeditions between 2002 and 2003, for a total of 3.5 months in the field (Young, 2004). Her team managed to acquire the first footage of a Bili ape in the forest, an adult female peering warily at the local trackers. Williams collected some large casts of ape feet measuring up to 34 cm (Young, 2004); the largest prints found by Ammann had measured 30 cm long (Ammann, pers.com., December 2003). Analysis revealed that mitochondrial DNA from hairs / faeces found in Bili ground nests was that of a chimpanzee (Young, 2004; Breeuwer et al., unpublished data), and indeed, its genotype is nested comfortably near the branch point from which several clades of *P. t. schweinfurthii* radiated (Gagneux, 2001). Williams, however, speculated that perhaps these apes were a form of hybrid between chimpanzees and gorillas (Young, 2004), a possibility if the fathers had been gorillas (and thus had not contributed any mitochondrial DNA). This, however, is unlikely, due to the different social systems of chimpanzees and gorillas (Wrangham, 1987), and the fact that, as described above, no solid evidence of gorillas has ever been found in the area. The opening section of Chapter 4 of this thesis will briefly describe what we know about the morphology of the Bili apes, and will make it clear that these animals are behaviorally and morphologically typical chimpanzees.

The current study began in August 2004, when I flew into Bili with Karl Ammann. I was assigned the task of habituating a group of chimpanzees around Camp Louis. This thesis presents the results of the 2.5 years of field work that followed.

Outline of the thesis

Before I describe the Bili chimpanzees themselves, some background is needed. Chapter 1 focuses on the environment in which these chimpanzees (*P. t. schweinfurthii*) live, describing climate and rainfall patterns, the local flora and fauna, human impact, and finally, the conservation history of the area.

Chapter 2 compares the response of chimpanzees to humans in different areas of the northern DRC. We hypothesize that chimpanzees living in remote forests will be found to react in a more relaxed and curious manner when encountering our research team than those chimpanzees living in proximity to roads and villages. This is probably tied to a difference in human hunting pressure on the different communities in the recent past. Chapter 3 details differences in chimpanzee sound production between areas of low and high human disturbance. We predict that chimpanzees living under increased pressure from poachers will reduce their sound-production and restrict it to the early morning hours.

Chapter 4 is a compendium of our basic knowledge of these chimpanzees acquired prior to and during this field study, beginning with a brief review of their morphology and genetics. We then plot their distribution across the landscape of the northern DRC and make rough calculations of their density. Excitingly, an area that just 10 years ago was a 'blank spot' on maps of chimpanzee distribution has now been filled in, and we can be certain that tens of thousands of chimpanzees are still thriving in the woodlands and gallery forests. The chapter also includes a basic description of the chimpanzees' tree-nesting behavior and diet.

In Chapter 5, we present evidence for behavioral continuity, describing a suite of traditions shared by the chimpanzee population across the vast area that was surveyed, and which possibly extends across a much larger area. This pattern stands in contrast to other chimpanzee populations, whose traditions seem to be more idiosyncratically distributed. Different explanations for this phenomenon are explored, including the possibility that it represents a 'Mega-Culture'.

Chapter 6 is a 'call to arms', describing the imminent crisis that the chimpanzees of northern DRC are facing. This area is now one of the last remaining large, continuous populations of the species in Africa. With artisanal gold and diamond mining spreading rapidly across the landscape, the bushmeat trade is now gaining a foothold as it already has elsewhere. Unfortunately, chimpanzees are increasingly being targeted for their bushmeat and for their babies, which in some areas are now frequently offered for sale. With the inevitable decline and fragmentation of this chimpanzee population will vanish one of our last opportunities to understand the species in the context in which it evolved, and not merely as isolated populations of terrified fugitives clinging onto a tenuous existence, which is now the situation across much of tropical Africa.

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