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Summary and Conclusion

**What Have We Learned from the Bili-Uele Chimpanzees?
And What Will Become of Them?**



The results of this 5-year field project in the northern Democratic Republic of the Congo (DRC) have shed light on what was until now a major gap in our knowledge of Eastern chimpanzees (*Pan troglodytes* subspecies *schweinfurthii*). Previously, doubt existed even as to whether chimpanzees inhabited the area; in Chapter 4, we not only confirmed the presence of the apes up to the border of DRC with the Central African Republic (CAR), and documented their nests within a few kilometers of even the largest human settlements, but we also suggested that no less than 35,000 and possibly even 65,000 chimpanzees might inhabit the region. This is more chimpanzees than are currently thought to inhabit all of West Africa (Butynski, 2003). In arriving at this population estimate, we are not taking into account the neighboring Rubi-Tele Domaine de Chasse, surveyed by Hart (2007), nor adjoining regions such as Wapinda, for which we have no survey data, but in which chimpanzees have been confirmed to exist within the past decade. As we saw in Chapter 4, the density of chimpanzees across the Bili-Uele landscape seems to be considerably higher than the average reported for other areas of the northern DRC. That such a potentially large population of chimpanzees has been neglected for so long by researchers and conservationists is understandable due to the inaccessibility of the region and the political turmoil in DRC, but given the dire state of affairs for chimpanzees in much of the rest of Africa, now is the time to take decisive steps to protect this important population.

Conclusions

We can now be sure that the population of great apes inhabiting the forests of northern DRC are Eastern chimpanzees. Debate continues as to whether or not they should be separated into a different sub-species from the Ugandan / Rwandan / Tanzanian chimpanzees (Groves, 2005; Gagneux, 2001). Morphologically, behaviorally, and in terms of diet, the Bili chimpanzees appear to depart little from chimpanzee basics (Chapter 4). Nevertheless, in terms of their traditions and society, we have only just scratched the surface in understanding them.

Our two most exciting findings concern the sheer number of these chimpanzees (Chapter 4), and the behavioral uniformity they apparently maintain across a vast area (Chapter 5). We can now add roughly 30,000 - 60,000 chimpanzees to the world total (it should be stressed that this does not reflect an increase in the number of chimpanzees, a species on the decline everywhere, but a gain in our knowledge). Considering that fragmentation of ape populations and the resulting inbreeding may result in decreased fitness (see Frankham, 1996 for a discussion of the risks of inbreeding on threatened animal species, as well as Ewers & Didham, 2006), the establishment and maintenance of a long-term research and conservation presence at Bili would present us with a golden opportunity to conserve what is likely to be a large and continuous population of chimpanzees.

The behavioral uniformity of the Bili-Uele chimpanzees is an anomaly in need of explanation, and has led me to propose the 'Mega-Culture' hypothesis: the chimpanzees of northern DRC share a set of behavioral traditions which is relatively uniform over hundreds of thousands of square km. The majority of chimpanzee traditions, as can be seen in Table XXVI of Chapter 5, appear to be distributed in an idiosyncratic manner across Africa (i.e., some populations fish for termites, some do not, without any obvious pattern). Even neighboring communities within the same populations, for whom ecological differences are minimum or absent, can show surprising differences in their food-processing techniques and tool-use (Boesch, 2003; L. Luncz, in prep.). In contrast, the traditions shared by the Bili-Uele apes appear to cluster together and are spread across a wide geographic region, possibly covering the whole of northern DRC. More surveys need to be carried out to fully chart the extent of this 'behavioral complex', which includes the frequent construction of night ground

nests, the use of leaf cushions and ant dipping tools, a lack of termite fishing, and the smashing of snails, termite mounds, and tortoises against substrates. One possibility tentatively put forward in Chapter 5 is that the interconnectedness of this chimpanzee population across such a large area has somehow discouraged behavioral innovation, with any new inventions being swamped out by immigrating females from multiple neighboring communities. The situation may be different in areas where chimpanzees are living in more fragmented populations (possibly leading to behavioral innovation). However, other possible explanations should be considered as well, such as genetic or environmental influences on behavior, and the possible impact of prehistoric migrations of chimpanzee populations on the current distribution of these behavioral traits. As interesting as the behavioral uniformity shown by the Bili-Uele chimpanzees are the subtle behavioral differences between the regions, including the frequent construction of ‘half ground nests’ to the east of the Bima River, possible differences in ant prey species-preference on either side of the Uele River, and the presence of fruit-smashing to the north but apparently not to the south of the Uele. It is possible that when we study these regions in more detail we will find that these ‘subtle’ differences in behavior are deeper than currently appears to be the case, and more resemble the diversity of traditions typical in other areas. In addition we do not yet know if the new tool-types we documented to the south of the Uele River, ‘fruit hammer’ and ‘ant scoop’ were merely individual innovations or traditions on their own right. Finally, the possibility that the ‘Mega-Culture’ extends all the way east to Uganda must be confirmed with more surveys.

Ground nesting presents us with a particularly interesting behavioral trait. In other areas where ground nests have been found, the behavior seems to be quite limited geographically; for instance, although the behavior is common at Nimba (Koops, 2007), it is not so at Bossou less than 10 kilometers away (Matsuzawa & Yamakoshi, 1996). The same apparent disjunction in distribution exists between the nearby sites of Fongoli and Assirik in Senegal (Pruetz et al., 2008; Baldwin et al., 1981), with ground nests common at the former site but apparently not at the latter. At Bwindi, the ground nesting behavior is even more limited in its distribution (Maughan & Stanford, 2001). All three of the ground nesting sites just mentioned have low densities of large predators. The situation is quite different in northern DRC, as can be seen in Figure 63, Chapter 5: in almost all areas surveyed between Tayna in the east and Wapinda in the west, ground nests have been found, and in some areas they represent up to 28% of nests. No significant difference was found between ratio of ground nests to tree nests on opposite sides of the Uele River (Chapter 5). Large predators are common throughout this region, particularly in the Bili area north of the Uele, the savannas, woodlands, and forests of which are prowled by lions, leopards, and hyenas (Chapter 1). This makes the frequency of the behavior all the more surprising.

The primary predictors of ground nest occurrence in the northern DRC were absence of human disturbance and the related factors distance from road, season, and forest density (Chapter 5). Factors such as forest category and elevation above sea level had no significant impact on the probability of the occurrence of ground nests. Considering the difference in eco-type between the two sides of the Uele River (savanna woodland and mosaic forest to the north, moist tropical forest to the south), it is difficult to imagine any over-arching ecological similarity that might facilitate the independent innovation of ground nesting. This might make cultural explanations seem the most likely solution. However, other factors cannot be ruled out, such as genetic influences, large body size, or characteristics of social structure (i.e., mate-guarding).

Certainly our failure (so far) to find any evidence of chimpanzee termite-fishing in the northern DRC cannot be explained by the lack of availability of *Macrotermes* spp. These insects and their mounds appeared to be numerous in all of the forests that we surveyed. Interestingly, these chimpanzees appear to fulfill their ‘termite needs’ using a totally different

technique (mound smashing), and by consuming two different species of termites (*Thoracotermes macrothorax* and *Cubitermes* spec.). Even more interestingly, *Thoracotermes* and *Cubitermes* are widespread genera and are present at many sites where the chimpanzees fish for *Macrotermes* (also a widespread and common genus) but ignore the other two species. It is difficult to interpret this as anything other than particular ‘tastes’ and / or feeding techniques being passed down through the generations by social learning. However, before we can be sure of this, we must test for other explanations: i.e., are the *Macrotermes* mounds in northern DRC thicker and more impervious to tools than elsewhere? Are their soldiers more timid, and less likely to bite onto a fishing tool? Are *Cubitermes* and *Thoracotermes* mounds softer at Bili-Uele than elsewhere? Are their larvae more nutritious? All of these competing explanations must be ruled out before we can be certain that we are dealing with traditions and culture.

Ant dipping provides a confirmation of but also adds a complication to the ‘Mega-Culture’ hypothesis. The confirmation lies in the fact that over the entire region surveyed (and probably in the Aketi region as well, although this has yet to be confirmed) the chimpanzees use short sticks to dip for *Pachycondyla*, *Dorylus* and possibly other genera of ants. The chimpanzees are all dipping for ants and not fishing for termites – a perfect example of behavioral continuity over a large area. The puzzling difference lies in the fact that to the north of the Uele River but not to the south the chimpanzees also construct enormous tools averaging over one meter in length to dip for epigaeic driver ants (*Dorylus wilverthii* and possibly other species). It is difficult to understand why chimpanzees rarely eat epigaeic ants to the south of the Uele and never use long tools to do so, despite what seems to be an equal availability of epigaeic *Dorylus* prey species. We cannot yet be sure whether the ant dipping pattern occurs across the rest of northern DRC, as is apparently the case with ground nesting and probably termite mound smashing. No one has recorded it, but apparently no one has been looking for it either. The nearest site to the southeast where the chimpanzees dip for ants is Kalinzu in Uganda. I predict that future surveys will reveal that the habit is common all across eastern DRC.

Finally, the food smashing behavior shown by the northern DRC chimpanzees is an interesting extension of a basic chimpanzee propensity for smashing fruits. This tradition has been recorded at multiple sites in East and West Africa, but the smashing has always been limited to fruits [see Table XXVI, Chapter 5; the exception is one isolated termite mound smashing community in the Taï Forest, Ivory Coast (Boesch, 2003)]. In northern DRC the chimpanzees seem to have extended the fruit-smashing behavior to other objects as well, such as termite mounds, giant snails, and even tortoises. Might this be an example of the ‘ratchet effect’, i.e., one innovation facilitating the discovery of another (Lycett et al., 2009)? One complication is that the South Uele chimpanzees, who smash termite mounds, snails, and tortoises, do not seem to smash open fruits. What we have discovered in the northern DRC raises questions that can only be answered with further research. But how much more time do we have?

What of the future?

In the Bili-Uele area we have been fortunate enough to have been offered a view into what chimpanzee populations must have been like until the recent past, when their habitat spanned most of the tropical belt of Africa and they must have numbered in the millions. As we have seen, this window may now be closing, as more and more tracts of formerly remote chimpanzee habitat are exposed to anthropogenic disturbances such as deforestation for agriculture and charcoal-production, habitat degradation caused by artisanal mining, and the bushmeat trade (Figure 1; Chapters 1 & 6). As these processes progress, we will lose our

opportunity to understand the ecological and evolutionary significance of the unique behaviors that we documented in Chapter 5. As chimpanzees come into increasing contact with humans and their habitat becomes more fragmented, it is probable that their traditions and behaviors will be transformed, making it imperative to protect, document, and study these traditions.

In this thesis, I have provided evidence for several unique behaviors shown by a large and continuous population of chimpanzees hundreds of kilometers distant from any other community to have been studied. It is my hope that the data presented will contribute to broadening our understanding of the diversity of chimpanzee behavior across Africa, as well as documenting the behavioral profile of a hitherto unknown population of chimpanzees in a particular time and place; especially important as these chimpanzees, as do all others, face an uncertain future. What we are learning has the potential to help us to understand the past migrations of *P. t. schweinfurthii* across the African landscape. Finally, the patterns revealed may have much to teach us about the general spread and maintenance of behavioral systems in large-brained hominids, with potential relevance to understanding the cultural evolution of the bipedal variety.

Socially-transmitted behaviors, or traditions, have presumably developed over millennia in great ape populations and are particularly vulnerable to human disturbance (van Schaik, 2002). Because of this, we face the distinct possibility that increased access to great ape habitat by humans are impoverishing or destroying the very traditions that cultural primatologists are attempting to document. We may be currently underestimating the extent to which free-living chimpanzee populations have had their social systems and traditions degraded by contact with humans. An example is the ground nesting behavior which we have documented in the northern DRC. As seen in Chapter 5, if one were to survey only the forests adjacent to roads and in proximity to cities and towns, one might conclude that the local chimpanzees do not construct ground nests, and in this respect are no different from many previously-documented chimpanzee populations. But this would be an inaccurate conclusion and entirely an artifact of human disturbance. Likewise, to assume that the northern DRC chimpanzees have low rates of vocalization based only on the study of populations living near cities or in heavily-hunted areas would be an artifact of human disruption and not reflect the true nature of their communicative systems. Other human influences could lead to the deterioration of chimpanzee social traditions as well. For example, we have provided preliminary evidence for the existence of a snail smashing tradition never before documented in any chimpanzee population (Chapter 5). One could imagine, however, that as human population densities increase, they may begin to gather and consume more and more giant snails, leading to this food source decreasing in availability, resulting in the potential extinction of the tradition in chimpanzees.

Similarly, the burning of forests by agriculturalists may result in an impoverished insect fauna, potentially leading to the loss of the ant dipping and termite mound smashing traditions also documented across the region. In order to understand what the region's chimpanzees really do, at least in relation to ground nesting and vocalization patterns, it is necessary to 'leave the beaten path' and survey more remote areas. Of course, as artisanal mining enterprises and the bushmeat trade expand into these areas, we can expect chimpanzee behavioral diversity to become more and more homogeneous and degraded. Chimpanzee adaptations to human encroachment might be seen as interesting behavioral responses in their own right; however, they do not aid us in understanding the origin of chimpanzee traditions under anything but aberrant circumstances.

Campbell et al. (submitted for publication) have provided evidence that the long-term presence of field researchers at great ape study sites has a positive impact on great ape survival. Tranquilli et al. (in prep.) point out the crucial importance of law enforcement

presence in protected areas to safeguard great ape populations. We have our work cut out for us. It is time that we put aside the conservation setbacks of the past few years and return to the Bili-Uele region for the long haul, working together with local and foreign non-governmental organizations, the DRC government, local villagers, and research institutes to assure a future for the Bili-Uele chimpanzees. The potential benefits to our scientific knowledge, the people of the DRC, and, of course, the chimpanzees themselves are incalculable. But without action taken now, the opportunity will slip quickly through our fingers.

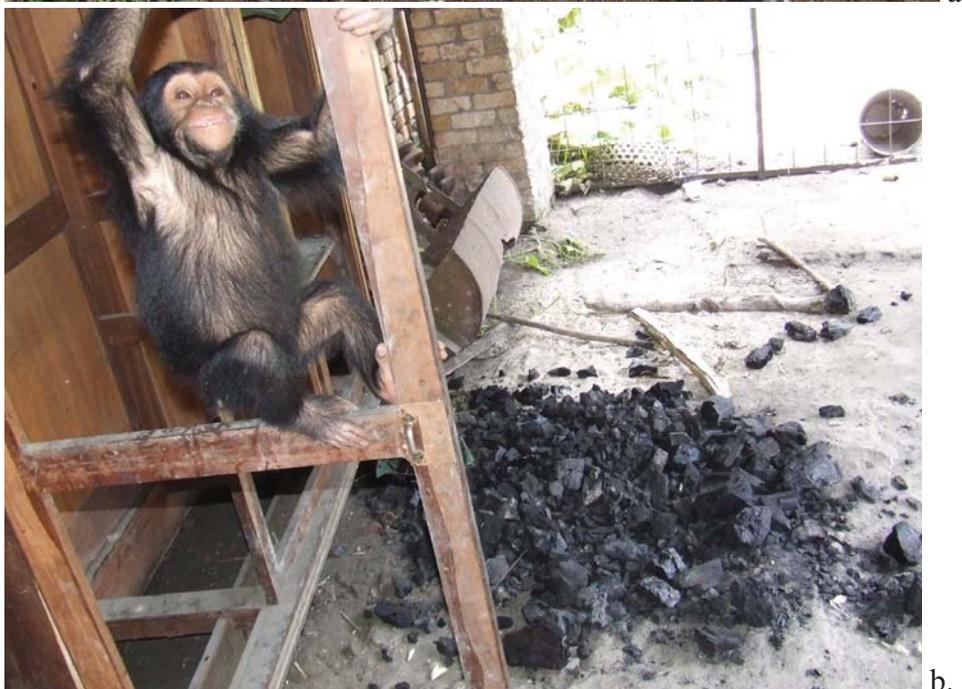


Figure 1 (a). Forest cleared for agriculture in the vicinity of Buta, northern DRC. (b). A chimpanzee orphan in Aketi perched above a pile of charcoal from a burned forest.

The Bili-Uele chimpanzee population provides us with one of the last remaining places to study the exchange and maintenance of socially-learned traditions in a non-human hominid species, occurring across an enormous area and multiple interconnected communities. Further study may help us to understand large-scale patterns of innovation and dissemination of ape behaviors across time and space. In turn, this understanding may help us to pinpoint why one group of these apes, our ancestors, began to develop more and more elaborate tools and traditions. In addition, an understanding of baseline patterns of ape cultural evolution may help us to identify what factors led to the elaboration of ratchet effects, which may not be uniquely human (Lycett et al., 2009) but seem to be something humans have taken to an extreme (Tennie et al., 2009). It is crucial to carefully document and protect these imperiled chimpanzee behavioral systems before they collide with the modern human ‘Mega-Culture’ and are forever diminished or lost entirely.

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