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Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo

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Abstract

With the exception of humans, chimpanzees show the most diverse and complex tool-using repertoires of all extant species. Specific tool repertoires differ between wild chimpanzee populations, but no apparent genetic or environmental factors have emerged as definitive forces shaping variation between populations. However, identification of such patterns has likely been hindered by a lack of information from chimpanzee taxa residing in central Africa. We report our observations of the technological system of chimpanzees in the Goualougo Triangle, located in the Republic of Congo, which is the first study to compile a complete tool repertoire from the Lower Guinean subspecies of chimpanzee (*Pan troglodytes troglodytes*). Between 1999 and 2006, we documented the tool use of chimpanzees by direct observations, remote video monitoring, and collections of tool assemblages. We observed 22 different types of tool behavior, almost half of which were habitual (shown repeatedly by several individuals) or customary (shown by most members of at least one age-sex class). Several behaviors considered universals among chimpanzees were confirmed in this population, but we also report the first observations of known individuals using tools to perforate termite nests, puncture termite nests, pound for honey, and use leafy twigs for rain cover. Tool behavior in this chimpanzee population ranged from simple tasks to hierarchical sequences. We report three different tool sets and a high degree of tool-material selectivity for particular tasks, which are otherwise rare in wild chimpanzees. Chimpanzees in the Goualougo Triangle are shown to have one of the largest and most complex tool repertoires reported in wild chimpanzee populations. We highlight new insights from this chimpanzee population to our understanding of ape technological systems and evolutionary models of tool-using behavior.

Keywords: Chimpanzee; *Pan troglodytes troglodytes*; Tool use; Tool manufacture; Human evolution

Introduction

Although tool use has been observed in various taxonomic groups, complex and flexible tool use seems limited to the order Primates, with humans showing extraordinary talent in using objects to achieve their goals or change the environment. There is a great deal of variation among primate species that van Schaik et al. (1999) attributed to differences in manual dexterity, capacity for social learning, and opportunities for social learning. Boesch and Boesch-Achermann (2000) further suggested that an understanding of causality between external objects is a key component for inventing and developing flexible tool repertoires, such as those of humans and chimpanzees. With the exception of humans, chimpanzees show the most diverse and complex tool-using repertoires of all extant species and are often used as models for the development of tool use in our common ancestors. It is essential that we have an understanding of intraspecific behavioral diversity in tool-using behaviors before this information is

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used in comparative research or for constructing evolutionary models. Although chimpanzee tool use has been well documented at sites in western and eastern Africa, detailed information on tool-using behavior of the Lower Guinean subspecies (*Pan troglodytes troglodytes*) has not been available. The aim of this paper is to describe the chimpanzee tool-using repertoire from the Goualougo Triangle, located in the Ndoki forests of the Republic of Congo. We provide detailed descriptions of each tool and compare the overall tool repertoire to those reported from other chimpanzee sites.

Field research on chimpanzees spanning the past four decades has shown marked differences in tool technology within and between populations (Goodall, 1973; McGrew, 1992; Boesch and Boesch-Achermann, 2000). Goodall (1964) first documented the tool-using behavior of wild chimpanzees in Tanzania, and as reports accumulated from other sites, it became clear that chimpanzee tool use was common and widespread across their range (Teleki, 1974; Boesch and Boesch, 1981; Nishida and Hiraiwa, 1982; McGrew and Rogers, 1983; Boesch and Boesch, 1990; Tutin et al., 1995). Tool-using behaviors vary among populations in tool forms, materials used, and goals of tool-using behaviors. These differences in tool diversity and complexity between sites are not easily attributable to phylogenetic or ecological determinants (Boesch and Boesch, 1990; McGrew, 1992). One challenge to discerning patterns in the material culture of wild chimpanzees has been the distribution of field sites, which are found predominantly in western and eastern Africa. Reports on the tool repertoires of the Lower Guinean and Nigerian subspecies are needed to further our understanding of the tool technology of chimpanzees.

Several researchers have proposed regional differences in chimpanzee tool technology (summarized by McGrew, 1994). In most of these scenarios, the nut cracking of west African chimpanzees is contrasted with the technology used by *P. t. troglodytes* and *P. t. schweinfurthii* to gather social insects (Struhsaker and Hunkeler, 1971; Nishida, 1973; Teleki, 1974; McGrew, 1992). However, all of these hypothesized regional differences in tool use have subsequently been challenged with evidence contradictory to predicted regional patterns. For example, Boesch et al. (1994) hypothesized that nut cracking was associated with the historical forest refugia on the west side of the Sassandra River, Ivory Coast. Researchers reported that ecological conditions on the eastern side of this natural geographic boundary could support nut-cracking (Boesch et al., 1994; McGrew et al., 1997), but the behavior had not been observed beyond this river until recent reports from Cameroon (Morgan and Abwe, 2006). Although the hypothesis of separate origins of termite fishing proposed by McGrew et al. (1979) has been shown to be invalid, the fact remains that only chimpanzees within the Congo Basin seem to use tool sets involving stout sticks and herbaceous probes to access and extract subterranean termites (Sanz et al., 2004). Further research is needed to determine if tool behavior is related to the distribution of specific termite fauna or local knowledge of the chimpanzees in this region. Hicks et al. (2005) recently suggested that honey hammering may be a regional tradition of *P. t. troglodytes*. Chimpanzees in Republic of Congo and Central African Republic use large clubs to open the hives of stingless bees (Fay and Carroll, 1994; Bermejo and Illera, 1999; Hicks et al., 2005), whereas chimpanzees in other regions use different types of tools to access honey. Boesch and Boesch (1990) reported that chimpanzees in the Tai Forest used tools to kill bees, inspect beehives, and fish for honey. Chimpanzees in the Bwindi forests of Uganda use specific types of tools when preying upon different bee species, but the diameter of these tools was relatively small compared to tools recovered from central Africa (Stanford et al., 2000).

Aside from particular ecological opportunities or constraints of some environments, it does not seem that particular habitat types have fostered or hindered tool-using dispositions in wild chimpanzees. Early models of human evolution and initial documentation of tool use by chimpanzees in open habitats promoted the idea that key human innovations were driven by a transition to savanna habitats. However, recent geological and palaeontological data indicate that the earliest hominids inhabited wet and wooded environments (Wolde-Gabriel et al., 1994, 2001). The largest tool repertoires of chimpanzees are manifested by populations residing in different habitats, such as the rainforests of Tai in western Africa and the savanna-woodlands of Gombe (Boesch and Boesch, 1990; Boesch-Achermann and Boesch, 1994). Further examination of the patterns of tool expression across ape populations may provide insights for reconstructing the context of tool behavior of our last common ancestor.

We report our observations of the technological system of wild chimpanzees in the Goualougo Triangle, Republic of Congo. This study is the first to compile a tool repertoire from prolonged, direct observations of identified individuals representing the Lower Guinean subspecies of chimpanzee that resides throughout the Congo Basin. We provide detailed descriptions of use, manufacture, and modifications of each tool type. The complete tool repertoire of this population is compared to those from other sites to summarize our current understanding of intraspecific variation in tool-using behaviors of wild chimpanzees.

Methods

Study site and population

The Goualougo Triangle is located within the southern sector of the Nouabalé-Ndoki National Park, which is located in the Republic of Congo (Fig. 1). The study area covers 380 km^2 of evergreen and semideciduous lowland forest, with altitudes ranging between 330 and 600 m. The climate can be described as transitional between the Congo-equatorial and subequatorial climatic zones. Rainfall is bimodal, with a main rainy season from August through November and a short rainy season in May.

Between February 1999 and April 2006, we spent a total of 80 months in the Goualougo Triangle habituating and studying wild chimpanzees. We conducted reconnaissance surveys in