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Name: Cielo De La Rosa

Project Sponsor: Seth Philips

Faculty Sponsor: Vicky Oelze

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Abstract
Our objective is to demonstrate the link between termite-fishing behavior and the seasonal activity of termites in eastern equatorial Africa to provide evidence of chimpanzee foraging cognition and its implications for paleoanthropology. We present evidence that Issa chimpanzees have an awareness of the seasonal availability of termite (*Macrotermes subhyalinus*) activity and engage in termite-fishing behavior exclusively during the early wet season when termites are most accessible.

Investigations on chimpanzee (Pan troglodytes schweinfurthii) termite-fishing cognition: Issa, western Tanzania

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Synopsis
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Keywords
Termite-fishing, Foraging cognition, Primate cognition

Introduction

The study of tool-use in association with seasonal food resources, such as insects (Isoptera), can have implications for understanding the foraging cognition of primates. Foraging cognition refers to the behavioral adaptations that optimize foraging success (Tomasello & Call, 1997, Rosati, 2017). Specifically, foraging cognition attempts to define the ways in which primates make decisions about their feeding strategy through storing and manipulating information (Rosati, 2017). Milton (1981) describes this as a cognitive map by which primates mentally represent spatial and temporal patterns. This involves knowledge of the complex spatiotemporal distribution of foods and the use of extractive foraging techniques. Termite-fishing, a behavior exhibited by chimpanzees (*Pan troglodytes spp*), is an insightful example of how primates use this knowledge to optimize their general feeding strategy.

First described by Goodall (1963) in the Gombe stream, Tanzania, in the 1960s, termite-fishing is one of the most well-observed tool-use behaviors by chimpanzees. 'Termite-fishing' is the act of inserting a hand-made probe into a termite mound to obtain the live and highly defensive termite soldiers that occur just below the surface of the subterranean mound (Lesnik 2014). Once the termite soldiers attack the probe with their biting mandibles, the chimpanzee will remove the probe and consume them (McGrew, 2003). The probes used by chimpanzees are typically made of striped grass, bark, or modified twigs (McGrew, Tutin, & Baldwin, 1979). In addition, termites are a nutritious and high-quality food due to their high protein and fat content (McGrew et al., 1979; Rothman, Raubenheimer, Bryer, Takahashi, & Gilbert, 2014).

Seasonal variation and habitat type may play a major role in how and when chimpanzees engage in termite-fishing because of the nature of termite ecology (Van-Lawick Goodall, 1968; McGrew et al., 979). Termite colony activity has shown to be related to annual climatic cycles as colony activity and diversity increases in the wet seasons and decreases in the dry seasons (Davies, Eggleton, & Rensburg, 2015; Lesnik, 2014). Abe and colleagues (2000) discuss how the maturity of nymphal termites into swarming alates is likely held back until the first rain shower

of the season. During this time, termite workers construct flight holes from which alates exit the mound during the swarming events (Mitchell, 2007). These passageways are what make termite-fishing possible for chimpanzees. Thus, termite availability for chimpanzees may be dependent on habitat and climate. Chimpanzees in habitats with extreme seasonality in precipitation, such as in western Tanzania, may only have a short window of time during the year in which they can successfully fish for termites. If chimpanzees have an acute awareness of the termite seasonality then they should increase their investigatory behavior and fishing attempts in the rainy season when termites are most active.

We evaluate if chimpanzees in this habitat are aware of the correlation between the onset of the rainy season and termite activity in order to learn about the foraging cognition of this species. Likewise, this study attempts to reveal how Issa chimpanzees determine termite availability by identifying the investigative behaviors associated with termite-fishing. We have conducted an analysis of camera trap footage of chimpanzees exhibiting termite mound inspection and termite-fishing behavior. Specifically, we assessed different types of behaviors that indicate the investigative behavior of this chimpanzee community at termite mounds. We used ethological methods to code for the different behaviors exhibited to draw conclusions about how these chimpanzees make decisions about insect foraging and how this may relate to termite seasonality. Answering these questions will help us to further understand chimpanzee foraging cognition and can augment existing information on the termite-fishing behavior of the Issa chimpanzee community.

Materials and Methods

Study Site

The subject of this study is the savanna woodland chimpanzee community of Issa Valley, Ugalla, Tanzania. This semi-habituated community of chimpanzees is known as the Issa community. The population in the study area is comprised of 67 individuals: 31 females and 27 males (Stewart & Piel, 2013). According to a more recent publication by Vink and colleagues (2020), the main study community consists of 30 individuals.

The Issa Valley is located within Ugalla, a 3300 km^2 miombo woodland ecosystem (Stewart & Piel, 2013). Research at this site is located within an 85 km^2 study area (Fig 1.) (Stewart, 2011). There are two distinct seasons in this region: rainy and dry. The rainy, or wet, season occurs throughout the months of October and April. The dry season stretches between the months of May and September (Stewart, 2011). Due to the distinct climatic seasons, Issa is considered a site with extreme climatic seasonality. The termite species Issa chimpanzees have been known to forage are *Macrotermes subhyalinus*. This species is a fungus growing termite that builds large earthen mounds (Sanz, Deblauwe, Tagg, & Morgan, 2014; Darlington, 2011).

Data Collection

We analyzed camera trap video footage from 2016 obtained by our collaborators at GMERC (Greater Mahale Ecosystem Research and Conservation). The seven motion-triggered cameras, set up by GMERC, are located in close proximity to termite mounds where termite-fishing activity can be recorded. Camera trap placement at mounds was targeted by GMERC field personnel based on observed chimpanzee presence and presumed termite-fishing viability. All camera traps are mounted on trees and set to be active 24 hours per day recording 60-s videos at

1-s intervals (Vink, Stewart, Piel, 2020). For unknown technical reasons, some cameras recorded 15-s videos instead of 60-s. These videos were treated as normal and do not affect the overall analysis.

Using a behavior coding software, BORIS (Behavioral Observation Research Interactive Software) (Fig 2.), we coded for 13 different behaviors from an ethogram (see Table 1). We coded every video with chimpanzee presence at a mound for the entirety of 2016 (January through December). This amounted to a total of 1314 videos in which chimpanzees are present at termite mounds.

Table 1. Ethogram of chimpanzee mound inspection and termite-fishing behaviors used in this study

Behavior Type	Key	Code
point	V	Visual inspection
point	O	Olfactory inspection
point	A	Arrival on mound
point	C	Changing insertion in mound
point	P	Passing mound
state	R	Resting on mund
point	D	Successful dip
point	U	Unsuccessful dip
state	F	Fishing time
point	X	Removing soil
point	N	New tool
state	Q	Presence on mound
state	I	Investigation before fishing

The behaviors exhibited by the chimpanzees are categorized into two types: state event and point event. A *state* event categorizes behaviors in which the duration is important and must be recorded in time such as resting on the mound, or time spent actively fishing. These events are measured in seconds (s). A *point* event is defined as a behavior exhibited that occurs briefly or a number of times such as successful tool dipping or arrival at the mound. *Point* events are recorded as a discrete measurement, which can occur a number of times.

The relevant *state* events for this study include Fishing time, Presence at mound, and Investigation before fishing. *Fishing time* (F) is defined as the time during which a chimpanzee inserts the tool into the mound and then into the mouth. This action is followed by chewing and the ingestion of the termites by the chimpanzee. Next, *Presence at the mound* (Q) is defined as the time the subject is visible in the frame. Last, *Investigation before fishing* (I) is defined as the

time spent engaged in investigative techniques before fishing time. These include a visual, tactile, and/ or olfactory inspection.

The relevant *point* events for this study include Arrival on mound with tool, Visual inspection, Removing soil, and Olfactory Inspection. *Arrival on mound with tool* (A) is defined as a time when a chimpanzee enters the frame with a tool in their hand or mouth. *Visual inspection* (V) occurs when a chimpanzee visually scans the mound with intent. *Removing soil* (X) occurs when a chimpanzee uses its hands and fingers to remove soil from the mound surface. *Olfactory inspection* (O) occurs when a chimpanzee smells the mound, tool, or finger after manipulating the termite mound.

Much recent research has focused on how subadult chimpanzees acquire knowledge on termite-fishing from mature individuals (Lonsdorf, 2006; Musgrave, Morgan, Lonsdorf, Mundry & Sanz, 2016). However, for the purpose of this study, we have focused our attention exclusively on the termite-fishing behavior of adult individuals of the Issa community as they can be expected to exhibit the full spectrum of behaviors relevant for assessing termite-mound activity. Moreover, although we coded for 13 different behaviors from the ethogram, only the seven defined were relevant for this study because they are indicative of the chimpanzee interest in termite activity and presence.

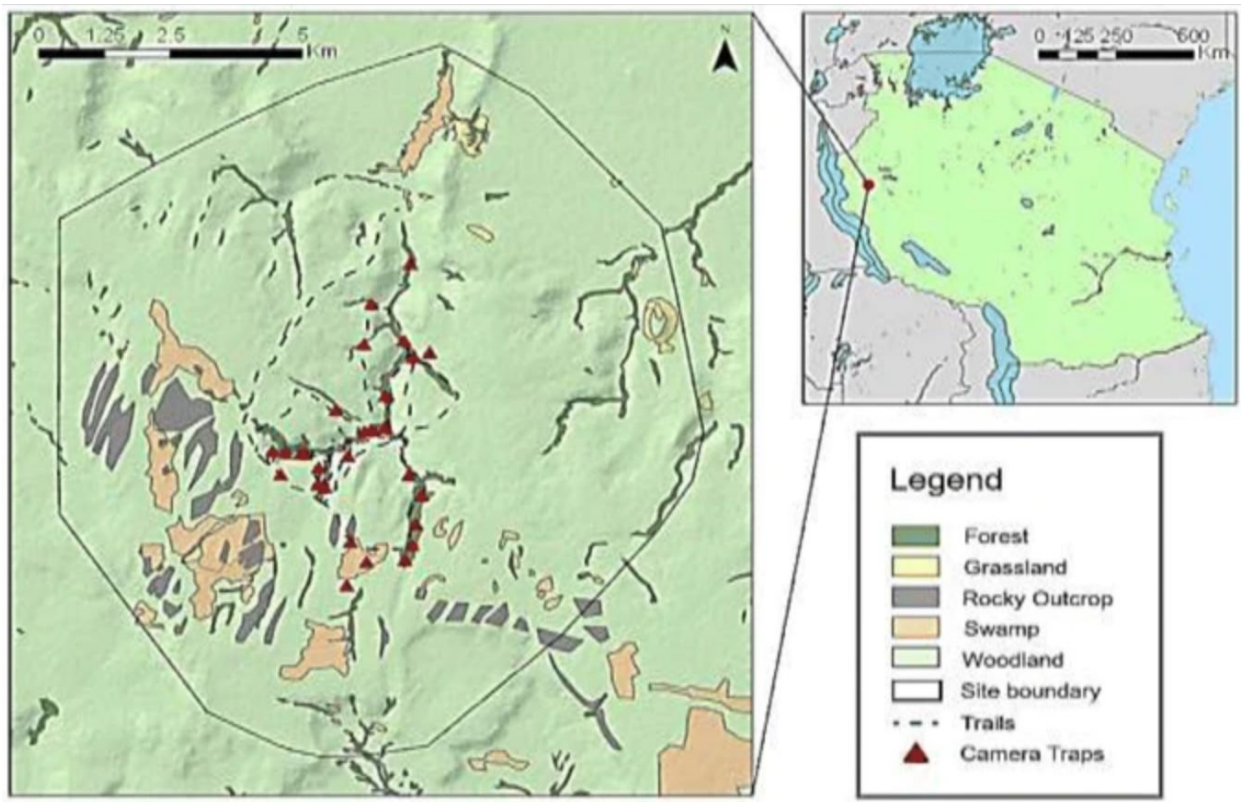

Figure 1. Map of the study site at Issa with camera trap locations (Credit: Laura. H. Jessup)

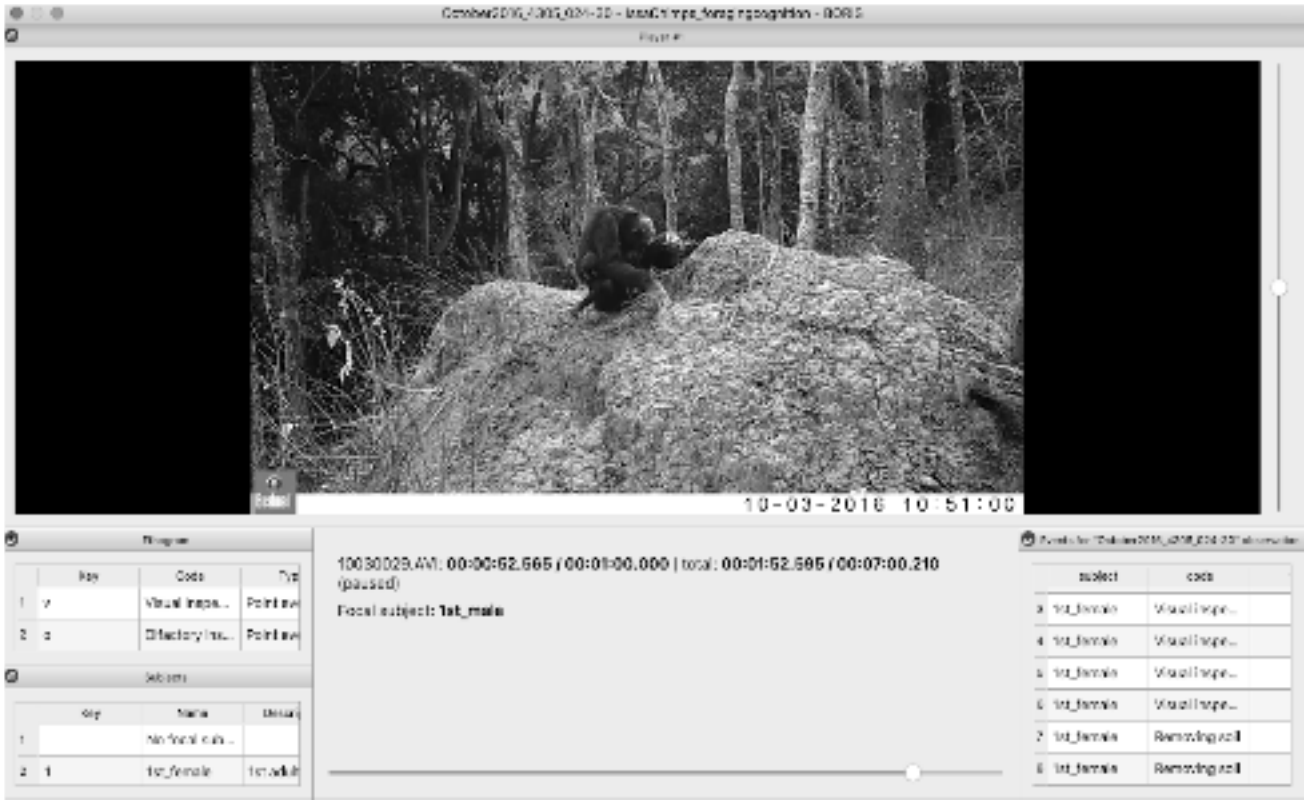

Figure 2. Screenshot during coding in the software BORIS

Results

Our observations show that Issa chimpanzees only engaged in mound inspection and termite-fishing behavior in the early wet season months of October, November, December, and January (Fig 3.). Of these months, chimpanzees spent the most time fishing in November (~6.37 hours). This time accounts for 65% of the total time spent fishing in 2016. Moreover, chimpanzees were most present at the mounds during the months of November (~8.5 hours), October (~4.5 hours), and September (~23 min). The occurrence of *Presence at mound* increased between the months of July (~1 min) and November (~8.5 hours) and then dropped suddenly in December (~18 min). Overall, 96% of *presence on the mound* occurred during the wet season.

Investigatory behavior also increased during the wet season (October–April). *Arrival on mound with tool* occurred in the months of January (3), August (1), September (1), October (39), November (54), and December (9); with the most instances coinciding with the onset of the rainy season. Also, instances of investigatory behaviors (point events) peaked in November at 301 total events (Table 2). Of the point events, *Visual inspection* occurred the most throughout the 12 months (240 times); 53% of those occurring in November and 89% occurring in the wet season.

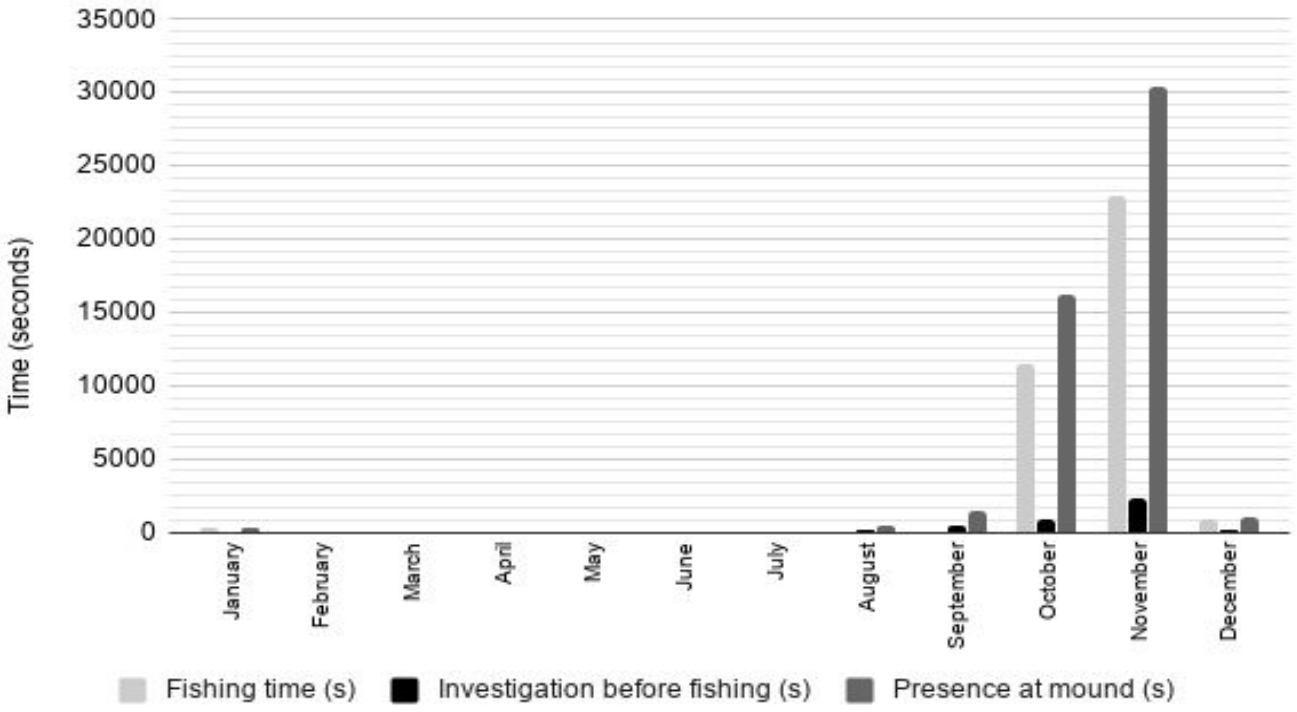

Figure 3. State Events: Time spent on mounds record in seconds for 2016

Table 2. Annual distribution of termite mound investigation events recorded for the Issa chimpanzees

Month	Arrival with tool	Olfactory inspection	Removing soil	Visual inspection	Total
January	3	1	1	2	7
February	0	0	0	0	0
March	0	0	0	0	0
April	0	0	0	0	0
May	0	0	0	1	1
June	0	0	0	0	0
July	0	0	1	2	3
August	1	3	3	7	14
September	1	7	10	16	34
October	39	13	43	72	167
November	54	7	113	127	301
December	9	0	10	13	32

Discussion

Our observations and analysis suggest that Issa chimpanzees are aware of the seasonality of termite availability due to the extremely low occurrence of mound inspection behaviors and the absence of termite-fishing behavior in the dry season (May– September). A temporal pattern in fishing activity emerges, as illustrated in figure 3, of termite-fishing occurring exclusively in the months of October, November, and December. The pattern follows a wider trajectory for the presence at mound occurring in the months of August, September, October, November, December, and January. Moreover, our data shows chimpanzees are not visiting mounds or engaging in any investigative or fishing behavior during the months of February, March, and April (Table 2). This time falls directly between the end of the wet season and the beginning of the dry season. These factors of our data reflect a pattern that suggests that Issa chimpanzees are cognizant of termite availability increasing in the early wet season. The sudden and dramatic drop in fishing time and presence at mounds between November and December may be correlated to climatic changes, however, the true reason for this sudden decline is unknown to us. Climatic data from the field may elucidate an answer.

As predicted, observations of investigatory behavior and fishing attempts increased considerably with the early onset of the wet season. Chimpanzees appear to only anticipate that termite-fishing is feasible in October through January, as only then they arrive at termite mounds with a fishing tool. *Arrival on mound* with tool specifically shows us that Issa chimpanzees are anticipating the availability of termites at this given time. Likewise, it can give us insight into what the chimpanzees are thinking as they are preparing for the ability to successfully fish for termites. The few inspection behaviors occurring in the dry season, (May and July), and the steady increase of these through the very early wet season indicate the anticipation of termite activity at the mounds by chimpanzees (Table 2). This finding is important because it demonstrates the cognition taking place among the chimpanzees that allows complex knowledge of the temporal distribution of the termites and the ability to foresee an outcome.

Additionally, our findings demonstrate that Issa chimpanzees exhibit various behaviors when inspecting a mound. These include tactile, olfactory, and visual inspections. Chimpanzees were observed to use their sense of smell to detect termites by smelling their fingers, or a tool after using them for probing, or by sniffing the mound directly. Chimpanzees were also observed using their fingers and hands to remove soil from mounds in an attempt to reveal termite passageways. Lastly, chimpanzees were observed visually scanning the area of the mound. These investigatory techniques, which increased with the onset of the rainy season suggest that Issa chimpanzees are aware, to some extent, of termite activity patterns. If these behaviors were observed throughout the year, we would be unable to discern whether these are indicative of anticipation or just a normal behavior at mounds year-round. However, our data show that these behaviors only occurred with the onset of the wet season, therefore, we can firmly say that Issa chimpanzees are cognizant of termite-activity patterns.

Here we provide an ethological study of the distinct termite-fishing behaviors of the Issa chimpanzee community of the Issa Valley, Tanzania. Using Stewart and Piel (2013) and Sanz and Morgan (2009) as references, this study augments the already existing information on chimpanzee termite-fishing behavior. Moreover, few primate cognition studies use behavioral analysis from camera trap footage in the wild. Our study of chimpanzee termite-fishing behavior is unique because it is done in a remote way that allows for an in-depth investigation of primate behavior in relation to seasonality. Due to time restrictions, this study has been limited to only

one year of data analysis from which we could draw conclusions. Although it was beyond the scope of this particular study, it would be important to include data from several years in order to make even firmer conclusions about this chimpanzee community. Similarly, gathering data on termite-availability and climatic conditions from the field would benefit the temporal analysis of this behavior and provide a broader context.

The study of primates has long aided in the understanding of the social and ecological behaviors of our hominid ancestors. By using living great apes as models, paleoanthropologists have made compelling inferences about the socioecology of extinct species that could not be made through the fossil record alone (Willems & Schaik, 2017; Parker & Gibson, 1979; B.J. King, 1986). Principally, wild chimpanzees (*Pan troglodytes*) have been used as living models for understanding the evolution of primitive tool technology due to the genetic similarity between them and humans (Sanz et al., 2014). Thus, studying the cognitive and technological skills of living chimpanzees can have implications for understanding the behavioral ecology and tool-use emergence within extinct hominid species.

Our conclusion that Issa chimpanzees have some awareness of termite activity patterns in relation to extractive tool-use can have implications for the ecological intelligence hypothesis. Zuberbühler and Janmaat (2010) define the ecological intelligence hypothesis as the theory that large brains in primates are a product of extensive mental mapping requirements faced by frugivorous species. The ability to retain information about the spatial and temporal distribution of foods allowed effective feeding and thus improved nutrition (Zuberbühler & Janmaat, 2010). While the cognitive process of primates can only be inferred, foraging cognition among primates can demonstrate how cognition is shaped by ecology (Rosati, 2017). Our findings exemplify this as they demonstrate that wild chimpanzees exhibit evidence for the anticipation of future ecological events and thus must have a cognitive awareness of the temporal distribution of a food source. Moreover, chimpanzee tool-use has been thought to resemble that of australopithecines and early *Homo* species (Sanz et al., 2014). Further studies on seasonal insectivory of great ape communities could shed light on the foraging cognition of our archaic ancestors.

Conclusion

This study deepens concepts of chimpanzee behavioral ecology and their interspecific interactions with termites. By expanding our knowledge of how and why chimpanzees exhibit termite-fishing behavior, primatologists can have a broader understanding of the intimate relationship between chimpanzees and their environment.

Due to species decline, it has become increasingly important to study the unique behavior of our primate cousins in order to obtain a deeper understanding of the complexities of chimpanzee society before these cultural traits are ultimately lost. Doing so will spread awareness of their advanced cognitive abilities and provide incentives for stricter conservation. Additionally, studies like this expand the field of primatology and enable us to draw comparisons between ourselves and other primate species who serve as templates for our early ancestors.

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