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Ecological Aspects of Chimpanzee Insectivory in the Budongo Forest, Uganda

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INTRODUCTION

All long-term studies of chimpanzees (*Pan troglodytes*) show that they habitually eat insects, most often social insects obtained by extractive foraging with simple tools¹. This generalisation holds across Africa from Senegal to Tanzania, but Ugandan populations are exceptional: Except for Kalinzu with ant dipping for *Dorylus*², no other Ugandan long-term study site (Budongo, Kanyawara, Ngogo, Semliki) shows regular insectivory, technically-aided or otherwise³. At Budongo, only occasional cases of eating *Cubitermes* have been recorded⁴. This dearth is puzzling, especially when these sites are compared with those (Gombe, Mahale) of neighbouring Tanzania, which have well-documented and varied elementary technology^{5,6}.

Lack of insectivory could reflect basic environmental constraints: Absence or scarcity of prey species, or absence or scarcity of raw materials for tools⁷. Less likely alternative explanations are differences between Ugandan and non-Ugandan populations in terms of genome, diet, manual dexterity, intelligence, or appetite. The presence of ant dipping at Kalinzu casts doubt on all these alternatives. Finally, such inter-population differences could result from differences in cultural knowledge, as has been found elsewhere⁸. That is, some populations of chimpanzees may not have discovered that some insects are edible or can be got with technical assistance.

Our study sought to explore the role of environmental constraints in the absence of regular insectivory in the Budongo Forest Reserve, Uganda.

METHODS

The study was done in the Sonso region Budongo from 14 July–8 September, 2011. Subjects were 80+ well-habituated chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community⁹. SH did 12 line-transects of 6 m width, each of 500 m length, along the existing grid system of trails; six ran north-south and six ran east-west. Sites of transects were balanced for the two main forest types, mixed (4,260 m) and swamp (1,740 m). Distances were measured by hip-chain, while another person scanned for evidence of social insects. Total area surveyed was 3.6 ha.

The following taxa (all known to be eaten by chimpanzees elsewhere in East Africa) were sought: *Cubitermes*, *Macrotermes*, and *Pseudacanthotermes* termites; *Dorylus* (army) and *Oecophylla* (weaver) ants; and *Apis* (honey) bees. SH checked termite mounds for activity and measured their height and circumference;

this allowed calculation of their volume, either as a cylinder or cone. Encounters with *Dorylus* ants on trails were noted by GPS data on time and place. Mounds and nests of all species were monitored weekly, after initial data-collection and surface clearing of debris. On each visit, SH checked for insect activity and signs of chimpanzee or other predator presence or exploitation. Specimens of prey species were preserved and identified later by specialists.

SH surveyed raw materials suitable for extractive foraging probes, that is, woody and non-woody vegetation with straight, elongate dimensions. Data-collection entailed marking a circle of 5 m radius around the resource and counting all plants presenting potential raw materials, in three categories: woody tree or shrub, vine, or monocotyledon (e.g. grass, sedge)¹⁰.

To measure the chimpanzees' consumption of insects, both direct and indirect data were collected. SH logged 80 hr of direct observation of opportunistically encountered parties of chimpanzees, using continuous recording of feeding or interacting with insects¹¹. For indirect data, SH collected all fresh faecal samples ($n = 26$) from chimpanzees encountered; these were sealed in ziplock bags and later sluiced in running water to detect undigested food fragments¹².

To estimate productivity, that is, amount of termites available to harvest, SH randomly sampled 10 *Cubitermes* and two *Pseudacanthotermes* mounds, removing about 150 cm³ from their tops. Once sealed in a ziplock bag, the soil was broken into chunks of less than 1 cm³; all termites, by caste, were counted in the contents⁷. Also, SH made and used flexible probes modelled on chimpanzee fishing probes, to fish termites from these mounds. To measure the payoff from termite fishing, efficiency, success rate, and error rate were calculated¹².

Because sample sizes were small and data non-normally distributed, all statistical tests were non-parametric. Alpha was set at 0.05, and all tests were two-tailed.

For specific details of methods, see Hedges¹³.

RESULTS

Cubitermes ugandensis mounds were found at a mean density of 34.4 mounds/ha (SEM = 8.17). Neither *Macrotermes bellicosus* nor *Pseudacanthotermes spiniger* mounds were found on transects, but two mounds of each genus were found and monitored elsewhere. Two chimpanzees were seen to eat soil from mounds, one of *Pseudacanthotermes* and one of *Cubitermes*. Two mounds (one of each genus) showed damage from chimpanzee predation, but the two *Macrotermes* mounds showed no signs of chimpanzee use.

Volume of termite mounds varied greatly but did not differ across forest types. Mean volume of *Macrotermes* mounds was almost 300 times that of the average *Cubitermes* mound, and mean volume of *Pseudacanthotermes* mounds was almost seven times as big.

Encounter rate over 6 days of *Dorylus* (*wilverthi* or *kohli*) columns on trails was 0.20 columns per km and 0.42 columns per hr. Neither *Apis mellifera* nor *Dorylus* nests were found on transects, but one of each was found and monitored elsewhere.

Raw materials for fishing probes were super-abundant. *Cubitermes* mounds afforded a mean of 580 tool sources per mound, while the numbers of sources for other insect prey species were: *Macrotermes* (155), *Pseudacanthotermes* (460), *Dorylus* (440), and *Apis* (684). Availability of raw materials did not differ across prey species, but overall, woody plants predominated over monocots or vines in abundance.

None of the 26 faecal specimens yielded insect remains.

The 12 mounds assessed for termite availability yielded an average of 104.8 termites per sample, but the range of values was huge (0–361).

SH's fishing from *Cubitermes* mounds was minimally productive, as the passageways were narrow and the soldiers passive. Fishing was a far less useful harvesting technique than detaching portions of the mound, with mean yields of 2.4 versus 123.5 termites. *Pseudacanthotermes* showed the reverse: Fishing was far more productive than detaching soil, with mean yields of 139 versus 11.5 termites. Fishing the two *Macrotermes* mound yielded almost nothing (mean of 2.5 termites).

DISCUSSION

Availability of prey or of raw materials seems not to be an obstacle to Budongo chimpanzees using tools to obtain insects. The low abundance of mounds of *Macrotermes* and *Pseudacanthotermes* is within the range of densities at other sites where these genera are fished: Bilenge (0.35/ha, *Macrotermes*; 1.03, *Pseudacanthotermes*); Campo (0.68/–); Gombe (0.40/2.04), etc. Similarly, the density of *Cubitermes* mounds at Budongo, at 34.4 mounds/ha, where the termites are eaten without tools, is intermediate in a wide range of values: 0.8/ha at Gombe at one extreme, to 233.8/ha at Lui Kotale at the other.

Similarly, encounter rates for *Dorylus* at Budongo, measured by either distance or time, are comparable to those from other sites. For distance, Budongo's encounter rate of 0.2/km is close to Gashaka's dry season rate of 0.21, where the highest rate of consumption of *Dorylus* by chimpanzees has been recorded. For time, Budongo's rate of 0.42/hr also resembles Gashaka's at 0.43¹⁴.

Too few data are available to compare abundance of *Apis* nests between Budongo and other sites. Similarly, too few data have been published or were obtained here to allow confident comparison of termite mound volumes.

Consumption of termite soil (and termites) by chimpanzees varies hugely. Budongo's rate of 0.79/100 hr of such geophagy is higher than that at Kibale (0.52) but much lower than that at Kasoje (4.07)¹⁵. This report of Sonso chimpanzees eating the soil of *Pseudacanthotermes* appears to be a first for this genus in Uganda.

Raw materials of all types for extractive probes are readily available. To take the most pertinent case, Budongo's *Macrotermes* mounds afforded 155 raw material sources on average, compared with a range from 37 at Assirik to 228 at Semliki.

Absence of termites in chimpanzee faecal samples replicates the results of an earlier study⁴, confirming that insectivory is rare.

Technical (i.e. fishing) versus non-technical (i.e. detachment) acquisition of termites seems not to have been compared systematically before this study. The closest result to ours seems to be that tools and techniques used to obtain *Dorylus* differ according to species of ant⁸. But until the chimpanzees of Budongo learn to eat *Pseudacanthotermes* and *Macrotermes*, these differences remain hypothetical.

In conclusion, the most likely explanation for the lack of extractive foraging for insects by Budongo chimpanzees is lack of cultural knowledge.

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