

# Apes Anonymous: western chimpanzee (*Pan troglodytes verus*) frugivory and associated ethanol ingestion



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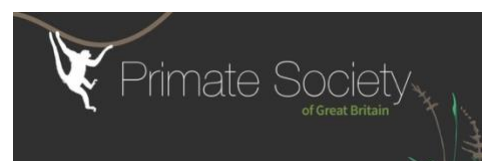
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## ABSTRACT

Ethanol (alcohol) is widely available and consumed by humans across the world, sometimes to excess. Humans' relationship with ethanol was first believed to correlate with the rise of agriculture approximately 9000 years ago, however, recently it has been suggested that ethanol's incorporation in the human diet dates back far earlier. The Drunken monkey hypothesis posits that our attraction to alcohol may derive from our frugivorous ancestors. Given yeasts ubiquity in the natural environment, foods high in sugar such as fruits and nectars, may ferment naturally. Frugivorous and nectivorous species, as such, may be regularly exposed to and ingest ethanol at least in minimal quantities. Studying ethanol exposure for wild non-human primates may provide insight into both their foraging habits and also the evolutionary origins of our own relationship with alcohol. However, there is a dearth of knowledge surrounding the alcohol content of naturally fermenting fruits and its use/ingestion by wildlife, including primates, where it is present. Here, we aim to assess the contribution of ethanol to the diet of an unhabituated community of western chimpanzees (*Pan troglodytes verus*) in Cantanhez National Park, Guinea-Bissau. Using a breathalyser to quantify ethanol values in fruits, we found ethanol to be present in 19 out of 24 fruit species within the chimpanzee community's diet. Ethanol concentrations ranged from trace quantities to as high as 2.9% (alcohol by volume- ABV). These concentrations were significantly, and positively, affected by the ripeness stage of the fruit and presence of exterior damage. In addition, using camera traps we observe chimpanzee feeding on fruits expected to contain ethanol. We provide support for increased prevalence of ethanolic fruits (*Anacardium occidentale*) on the ground and observe chimpanzees frequently selecting fruits from both the tree and ground, as well as fruits with damage, indicative of habitual ethanol intake. Furthermore, we observed fermented fruits of *Treculia africana* found to contain

ethanol up to 0.61% to be eaten and *shared* between different members of the community. Overall, our research suggests habitual ethanol exposure for one of our closest living relatives and presents novel data on ethanol abundance within the chimpanzee diet. Given our close evolutionary relationship with chimpanzees, it is likely that ethanol has long been a part of our diet.

## **INTRODUCTION**

Fruits have been incorporated in the primate diet for millions of years. Fruits and nectars, contain high concentrations of sugars and given yeasts prevalence in the environment may naturally ferment to produce ethanol (Casorso et al., 2023; Dominy, 2004; Dudley, 2002, 2000). As a result, it has been hypothesised that dietary ethanol holds an equally historic position within the diets of primates (Carrigan et al., 2015; Dudley, 2000). The Drunken monkey hypothesis suggests that ethanol within fruits may act as an olfactory guide for the location of transient, hard to obtain, ripe fruits and further may act as an appetite stimulant when consumed (Dudley, 2014, 2002, 2000). Ethanol attraction seen in modern humans, as such, may derive from this ancient association between calories and ethanol. This historic relationship has been supported by the identification of a genetic mutation that occurred in our last common ancestor ~10 million years ago which increased the rate ethanol metabolism by 40-fold (Carrigan et al., 2015). Despite this, the prevalence of ethanol in nature and its consumption has only just begun to be explored and we still know very little about its ecological and evolutionary importance.

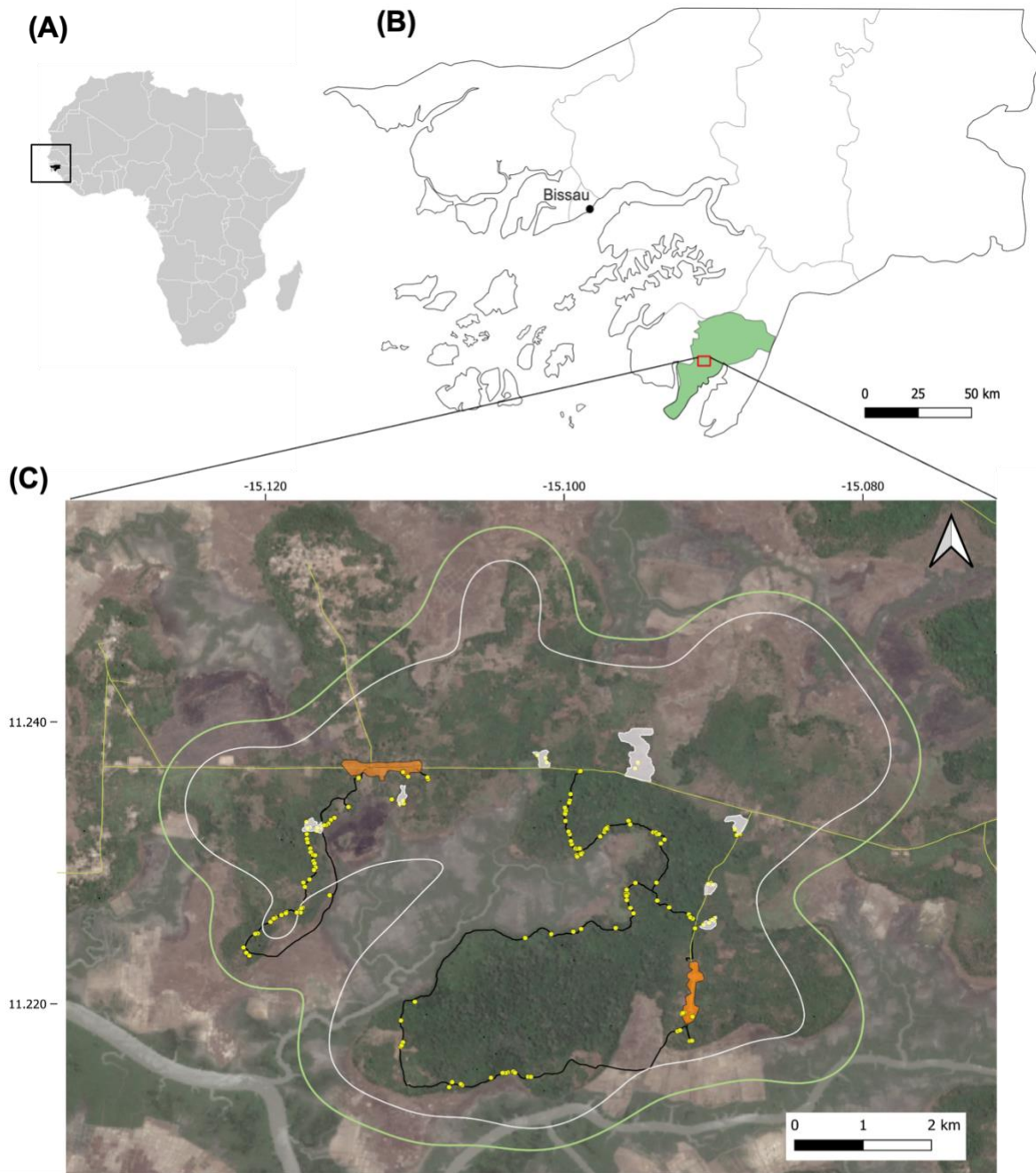
Within this study we aimed to test critical assumptions of the Drunken monkey hypothesis; that fruits ferment naturally and are not avoided when present. Specifically, we aimed to: (1)

Evaluate the ethanol content of fruit species fed on by a community of western chimpanzees (2) Assess how ethanol content varies with fruit characteristics namely ripeness stage, damage and fruit variety (cultivated or wild) (3) Assess if chimpanzees feed on a key cultivated fruit (*Anacardium occidentale*) at times when ethanol is expected, and if so (4) Determine how much ethanol chimpanzees may be ingesting.

## **METHODS**

### **Study area and chimpanzee community**

This study focuses on a community of western chimpanzees (unhabituated to researchers) located near the villages Caiquene and Cadique, in Cantanhez National Park (CNP) (CNP, N11°14.287' W15° 02.281'). CNP is located in south-west Guinea-Bissau and covers approximately 1,067km<sup>2</sup>. It consists of a mosaic of habitats including savannah, mangroves, forest, settlements, and agricultural land (Bersacola et al., 2021; Bessa et al., 2021; Hockings et al., 2020; Hockings and Sousa, 2012). The Caiquene-Cadique community is estimated to consist of 47 individuals (M.Ramon, personal correspondence) and cover a home range of 14.5km<sup>2</sup> (Bersacola et al., 2021; Hockings et al., 2020) (**Figure 1**).



**Figure 1: Location of research site. (A)** Map of Africa showing the location of Guinea-Bissau. **(B)** Cantanhez National Park (highlighted in green) within Guinea-Bissau and the study area within the park (red square). **(C)** Satellite image of the research site, showing the estimated home range of the Caiquene-Cadique chimpanzee community (white and green outlines). The home range was determined using kernel analysis (95% in white and 99% in green) of direct and indirect chimpanzee signs between 2013-2018 (Cantanhez Chimpanzee Project). Yellow dots denote monitored trees, along trails (black lines) and within cashew orchards (white polygons). The villages of Cadique and Caiquene are shown using orange polygons, and roads using yellow lines. Sentinel-2 imagery was obtained and modified from Sentinel Hub, Sinergise LTD (<https://www.sentinel-hub.com>) from May 5<sup>th</sup> 2022. Base maps for maps (A) and (B) were obtained and modified from Natural Earth (<https://www.naturalearthdata.com>). All maps were made using QGIS version 3.22.

## **Data collection**

### ***Fruit sample collection***

Fieldwork took place between April 2022 to mid-July 2022. Four fruit trails were set-up within the chimpanzee community's home range (**Figure 1**) for the collection of fruit samples. Each trail was walked in turn covering a total distance of 240km. Trails extended through multiple habitats including savannah, forest, agricultural land, settlements and lala (**Figure 1**). Fruit species of interest (i.e. those known to be consumed by the study community – (see Bessa et al., 2015; Catarino et al., 2020) were tagged and a GPS coordinate generated for future location. Where possible, multiple plants were tagged/sampled per species to account for intra-species differences.

### ***Ethanol measurement***

Fruit ethanol concentrations were determined using a modified portable MARK V Breathalyser (Alcovisor, Kwung Tong, Hong Kong, China), a device used to measure blood alcohol content (BAC) in humans. Fruits were sealed in a bag with at least 120ml of air, but approximately no greater than 100x the mass of the fruit. Alongside this, ethanol standards of varying concentrations (0.1%, 0.5%, 1% and 2% alcohol by volume (ABV)) were prepared, and 5 ml of each was placed in separate bags, as with the fruit samples. These standards were used to create a standard curve for each sampling period, from which all BAC values were converted to alcohol by volume (ABV%). Following equilibration time (at least one hour), 60ml of air was extracted from the bag using a 60ml syringe and inserted into the breathalyser. Prior to ethanol measurements fruit characteristics including fruit ripeness stage (unripe, mid-ripe, ripe and overripe), presence of damage and weight, were classified and noted.

### ***Behavioural data collection***

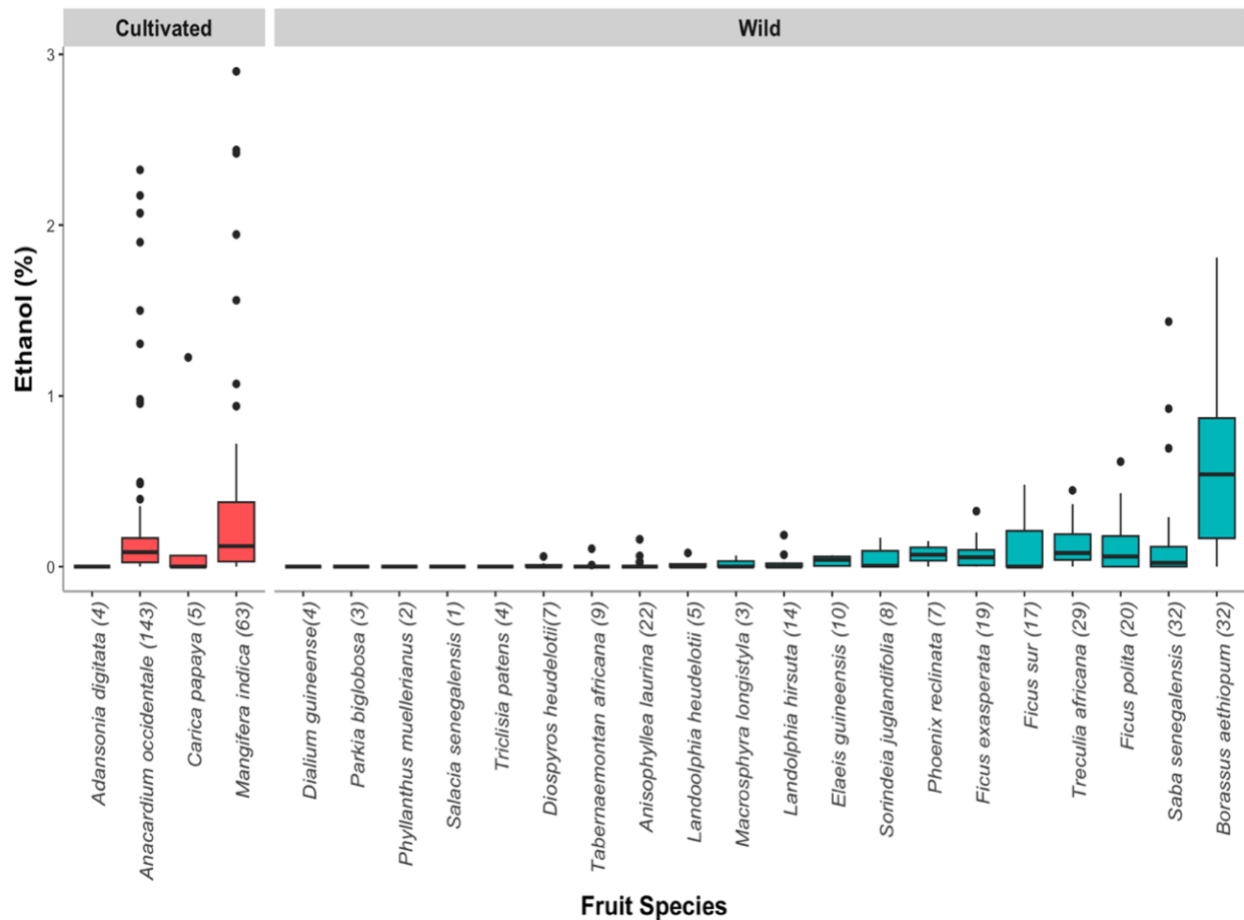
To assess chimpanzee feeding behaviour on the focal fruit species, *Anacardium occidentale* (cashew), we set-up 40 camera traps across 7 cashew orchards. Cashew orchards were selected based on the presence of fruit and knowledge of chimpanzee visitation. Cameras were placed in a paired design to increase breadth of view and set to video mode, to record for 60s with a 1-5s rest period. During the study, five camera traps were also opportunistically set to observe wild fruiting trees of a few interest species within the forest matrix.

All videos where chimpanzees were observed to be feeding, interacting, or handling fruits of interest were coded using Behavioural Observation Interactive Software (BORIS v7.13.9; Friard and Gamba, 2016) to obtain more detailed information.

## **RESULTS**

### **Ethanol content within fruits**

A total of 463 fruits, across 24 species, were successfully tested for ethanol content. Of these 19 species (79%) were found to contain ethanol across at least one ripeness stage. Ethanol concentrations ranged from trace quantities to as high as 2.9% (ABV-alcohol by volume) (**Figure 2**). Ethanol was detected in unripe fruits of four species (Cultivated: *Anacardium occidentale*, *Mangifera indica*; Wild: *Landolphia hirsuta*, *Treculia africana*) only when damage was present.



**Figure 2: Ethanol concentrations (%ABV) for cultivated (n=4) and wild fruit species (n=20) (all ripeness and damage categories combined). Numbers in brackets following species name indicates sample size.**

**Factors affecting ethanol content.**

Ripeness stage had a significant effect on both ethanol presence (LRT:  $\chi^2 = 44.83$ ,  $df = 3$ ,  $p < 0.001$ ) and ethanol concentrations within fruits (LRT:  $\chi^2 = 93.418$ ,  $df = 3$ ,  $p < 0.001$ ); with the probability of observing no ethanol being significantly lower for ripe and overripe fruits. Damaged fruits were more likely to contain ethanol (LRT:  $\chi^2 = 20.749$ ,  $df = 1$ ,  $p < 0.001$ ) and where ethanol was present possess higher ethanol concentrations (LRT:  $\chi^2 = 9.885$ ,  $df = 1$ ,  $p = 0.002$ ). Overall, fruit variety (cultivated or wild) had no significant effect on ethanol

concentrations (LRT: $\chi^2= 1.0772$ ,  $df=1$ ,  $p= 0.2993$  ) but did implicate ethanol presence, with cultivated fruit species demonstrating a higher likelihood of ethanol presence.

### **Chimpanzee ingestion of Cashew fruits**

Ethanol content of cashew fruits (*Anacardium occidentale*) ranged from 0.00- 2.32% (ABV). Ethanol presence and concentrations were significantly affected by location (tree vs ground), damage presence and ripeness stage. With a higher likelihood of ethanol presence observed for ripe fruits, damaged fruits and fruits collected from the ground. When ethanol was present concentrations were higher in overripe fruits, damaged fruits and fruits from the ground.

Behavioural analysis revealed chimpanzees regularly select fruits from both the tree and ground and even those with clear exterior damage (as confirmed in 12% of feeding events where the exterior could clearly be seen). Ripe fruits were the most common selected comprising 87% (145/173) of total feeding events. Using behavioural observations of chimpanzee cashew feeding and selection from the tree and ground, in combination with data on ethanol content of cashew fruits collected from the tree and ground, we were able to provide estimates of ethanol intake. Bootstrap analysis revealed an average ethanol ingestion of between 0.075- 0.25ml within a single feeding event, although when considering among-individual variation these levels could reach >2ml on occasion.

### **Opportunistic observation: sharing of fermented fruits**

During the study period we opportunistically observed the sharing of *T.africana* fruits on 10 separate occasions, with ethanol confirmed in 9 of these and levels reaching as high as

0.61%(ABV). Fruits were shared across all sex and age classes and sharing took place even when other non-monopolised fruits were available.

## **DISCUSSION**

Overall, we find ethanol to be a common constituent of fruits within the western chimpanzee (*Pan troglodytes verus*) diet in Cantanhez National Park (CNP), Guinea-Bissau and provide evidence that ethanol is a regular dietary component.

Across ripeness stages, we found ethanol to be most common in ripe and overripe fruits. This corresponds to the observed increase in sugar concentrations and yeast colonisation as fruits ripen (Vadkertiová et al., 2012). Given the low sugar levels and high carbohydrate content of most unripe fruits, they as expected, contained minimal ethanol. These findings are consistent with the hypothesis that odour plumes associated with fermenting fruits (including ethanol, acids, CO<sub>2</sub> - (Nevo and Valenta, 2018; Zhu et al., 2003) may act as a 'true' signal of nutrient and caloric reward, for foraging species (Dudley, 2004, 2002).

Despite expectations, cultivated fruits (those which generally possess higher sugar contents (McLennan and Ganzhorn, 2017)), did not contain higher ethanol concentrations, though ethanol presence was more common. This may be driven by species-specific variation. Though most wild fruits species contained relatively low ethanol levels, the ripe fruits of the palm *Borassus aethiopum* consistently possessed high ethanol which may have elevated the expected values for this category. While the dry fruit of cultivated species *Adansonia digitata*, possessed no ethanol which may have lowered values. This highlights the variation that can

be seen amongst plants and emphasises the importance of monitoring the ethanol levels of fruits from individual species.

When examining the feeding behaviour of wild chimpanzees on cultivated cashew fruits, fruits were regularly selected from both the tree and ground and despite the expectation that apes rarely feed on fleshy fruits once they have fallen (Fleagle, 2013; Hockings et al., 2015), chimpanzees appeared to show no such aversion to these fruits. Our simulations show low but habitual ethanol intake by chimpanzees, with preliminary evidence of variation amongst sex classes. As chimpanzees at this site are unhabituated and we were unable to conduct focal follows, our estimates are based on events where chimpanzees can be seen to fully ingest cashews. As such the estimates provided are certainly an underestimate and represent a minimum likely intake by the Caiquene-Cadique chimpanzee community. The lack of aversion to feeding on fermented fruits was further corroborated via the opportunistic observation of chimpanzees feeding and sharing fruits of *Treculia africana*, with known ethanol presence. These results contribute an important addition to the study of ethanol in animal nutrition and indicate ethanol's commonality within the diet of one of our closest living relatives.

Though we have expanded upon previous research, there are still gaps in our knowledge. To fully understand the extent of ethanol exposure and the drivers of ethanol ingestion by chimpanzees at CNP in response to changing ecological and environmental conditions necessitates year-round data on the ethanol content of fruits consumed coupled with data on feeding behaviour. Furthermore, if ethanol concentrations are in fact sufficient to effect physiology there may be behavioural implications to its ingestion. The behavioural effects, if any, of ethanol ingestion in natural contexts has scarcely been explored.

Our findings constitute the most in depth study of chimpanzee ethanol exposure via frugivory to date. We join and extend previous research (Dudley and Maro, 2021; Hockings et al., 2015) in showing that non-human primates, including one of our closest living relatives, are not averse to ethanol and likely consume it in non-trivial quantities. Importantly this research indicates consumption under natural contexts and begins to explore factors shaping ethanol concentrations in fruits to help provide more robust estimates of ethanol intake. We encourage further research to better understand animal-ethanol interactions, as well as the frequency and drivers of fermented food use. Findings of which may have ultimate implications for the understanding of our own relationship with the molecule.

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### **Breakdown of Grant spendings**

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