International Journal of Primatology
https://doi.org/10.1007/s10764-024-00445-3

The Adaptive Role of Bark in the Diet of Budongo Chimpanzees (*Pan troglodytes schweinfurthii*)

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Received: 17 November 2023 / Accepted: 1 June 2024

Abstract

The ingestion of bark has been observed across the animal kingdom and is well documented in free-ranging chimpanzees. Thus far, the best-supported hypothesis for the adaptive function of this behavior is the fallback food hypothesis, which asserts that chimpanzees consume bark and cambium when preferred foods are scarce. However, alternative explanations exist, including the *essential nutrient and mineral hypothesis*, the *self-medication hypothesis*, and the *stressed-tree hypothesis*. We tested whether the fallback food hypothesis can explain bark-feeding across two communities of Eastern chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. We used 13 years of the site's long-term behavioral data, 5 years of food availability data, and 8 months of direct and indirect observations. We also conducted eight 400-m line transects to collect data on the distribution of tree species across community home ranges. We employed several analyses, including Pearson correlation tests, qualitative comparisons of descriptive data and heat maps, and interpretation of behavioral anecdotes. We found varying patterns of bark-feeding seasonality across tree species, with bark-feeding on several species showing no correlation with food scarcity. We also identified differences in the amounts of bark targeted between tree species and report anecdotal evidence of chimpanzees prioritizing bark over high-value foods. Lastly, we found that bark-feeding on

Badges earned for open practices: Open Data Badge. Experiment materials and data are available in the repository and supplementary materials at https://github.com/Wild-Minds/Bark-feeding.

Handling Editor: Addisu Mekonnen

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certain species disproportionally occurs far from community core areas, despite relative abundance of these species within the home range. As a result, we argue that the fallback food hypothesis cannot explain bark-feeding across all tree species. Instead, we present supporting evidence for several alternative hypotheses, including self-medication, thereby challenging the widely accepted function of this behavior.

Keywords Diet · Bark-feeding · Self-medication · Fallback food · Zoopharmacognosy

Introduction

Bark-feeding, a behavior associated with the exploitation of bark for subsequent mastication or ingestion, is a generalized term characterized by the removal and ingestion of bark and/or cambium, often through stripping or peeling (Lapuente *et al.*, 2020). Bark constitutes the outermost protective layer of a plant's stem or trunk and is generally considered to have low nutritional value (Huffman, 1997; Krief *et al.*, 2006), composed of several compounds considered indigestible for many mammals. These compounds include cellulose, lignin, and plant secondary metabolites (PSMs). Plant secondary metabolites are organic compounds that serve various ecological roles, including defense against herbivores and plant pathogens, attracting pollinators, and aiding in competition with other plants (Erb & Kliebenstein, 2020). Because these compounds can be highly toxic, ingestion of PSMs can have deleterious health costs in consumers and can be fatal when overconsumed (Forbey *et al.*, 2009).

Beneath the bark, the cambium layer, which is crucial for the secondary growth of woody plants, is not typically considered a source of high-quality nutrition and can contain high concentrations of PSMs. In some tree species, phloem sap, located in phloem tubes between the bark and cambium layers, may contain carbohydrates, vitamins, and minerals (White, 2012). However, the production, nutritional value, and palatability of both cambium and phloem sap may greatly vary between species, impacting their suitability for consumption.

Many modern human communities consume bark and cambium for both subsistence (Niklasson *et al.*, 1994; Östlund *et al.*, 2009) and medicine (Gottesfeld, 1992; Kokwaro, 1976). Evidence in the fossil record suggests that various bark removal and feeding behaviors may have been present in early hominin ancestors, including *Australopithecus sediba* (Henry *et al.*, 2012) and *Homo neanderthalensis* (Sandgathe & Hayden, 2003). If these species primarily relied on bark as a fallback food, this could have shaped their subsistence strategies and impacted their capacity to adapt to dynamic environments. Changes in dietary reliance on fallback foods, as argued by Laden and Wrangham (2005), may even have contributed to aspects of morphological divergence between our species and African great apes. The authors contend that the transition from a chimp-like diet of herbaceous leaves and piths to a reliance on fallback underground storage units led to the emergence of large jaw muscles and dental adaptations found in *Australopithecus* and *Paranthropus* (Wood & Strait, 2004). These evolutionary theories highlight the potential impact of dietary resource use and availability on hominin evolution. Investigating the adaptive function of bark ingestion throughout the history of our species as well as in our extant primate relatives may shed further light on the broader influence of bark consumption on human evolution.

Adaptive Function Hypotheses

Several hypotheses for the adaptive function of bark-feeding have been proposed across a variety of nonhuman species. For primates, the most commonly accepted of these hypotheses is the *fallback food hypothesis*, which classifies bark and cambium as fallback foods (Harrison & Marshall, 2011; Nishida, 1976). Fallback foods are subsistence resources of relatively low priority that are seasonally consumed when preferred resources are scarce or unavailable (Marshall *et al.*, 2009). Evidence to support this hypothesis in primates primarily comes from studies showing seasonal correspondence between periods of increased bark exploitation and periods of food scarcity (Lapuente *et al.*, 2020; Nishida, 1976; Pruetz, 2006).

Bark-feeding has been proposed as a fallback food behavior in several ape species, including chimpanzees (*Pan troglodytes*) (Nishida, 1976), gorillas (*Gorilla* spp.) (Rogers *et al.*, 1994), and Sumatran orangutans (*Pongo abelii*) (Campbell-Smith *et al.*, 2011), as well as in other primates including, but not limited to, Japanese macaques (*Macaca fuscata*) (Hanya *et al.*, 2006), olive baboons (*Papio anubis*) (Lapuente *et al.*, 2020), and capuchin monkeys (*Sapajus* spp and *Cebus* spp) (Falótico *et al.*, 2017). This is the most frequently cited hypothesis to explain primate bark stripping in agricultural plantations (Di Bitetti, 2019). The fallback food hypothesis has been proposed to explain bark-feeding in numerous nonprimate species as well (e.g., sika deer (*Cervus nippon*) (Jiang *et al.*, 2005)).

An alternative hypothesis is the *essential nutritional or mineral need hypothesis*, which attributes bark ingestion to the targeted acquisition of specific nutrients or minerals that are otherwise environmentally scarce (Au *et al.*, 2017; Ciani *et al.*, 2001; Nichols *et al.*, 2016). This hypothesis has been proposed for numerous primate species, including mountain gorillas (*Gorilla beringei*) (Grueter *et al.*, 2018), barbary macaques (*Macaca sylvanus*) (Ciani *et al.*, 2001), and chacma baboons (*Papio ursinus)* (Erasmus, 1993), as well as other species, including koalas (*Phascolarctos cinereus*) (Au *et al.*, 2017) and grey squirrels (*Sciurus carolinensis*) (Nichols *et al.*, 2016). Evidence supporting this hypothesis primarily comes from studies showing heightened levels of calcium, sodium, zinc, or water in the bark of the targeted species (Au *et al.*, 2017; Ciani *et al.*, 2001; Erasmus, 1993; Levia & Herwitz, 2005; Nichols *et al.*, 2016).

Bark-feeding also has been proposed as a self-medicative behavior (Huffman, 1997). The *self-medication hypothesis* posits that the bark of certain species possesses pharmacological properties that provide consumers with therapeutic benefits. Multiple lines of evidence support this hypothesis, including observations of primates consuming bark during periods of illness (Ghai *et al.*, 2015; Krief *et al.*, 2006; Ndagurwa, 2013; Pebsworth *et al.*, 2006). For example, consumption of terpene-rich pine bark amongst chacma baboons (*Papio hamadryas ursinus*) is associated with seasonal episodes of coughing and throat infections (Ndagurwa, 2013). In Kibale National Park (Uganda), wild red colobus monkeys (*Procolobus rufomitratus tephrosceles*) consume significantly more bark (from the genus *Albizia)*, when shedding whipworm eggs (*Trichuris* sp.) (Ghai *et al.*, 2015). Another line of cited evidence is that chimpanzees select bark also used in traditional human medicine (Pebsworth *et al.*, 2006). Anecdotal reports have documented parasitized Eastern chimpanzees (*Pan troglodytes schweinfurthii*) consuming bark from tree species (e.g., *Alstonia boonei* and *Albizia grandibracteata*) with documented anthelminthic ethnomedicinal uses (Pebsworth *et al.*, 2006). Finally, pharmacological assays have identified bioactive PSMs in the bark of several tree species targeted by chimpanzees (Krief, 2003). These PSMs include tannins, alkaloids, and phenolic compounds that can have antibacterial, anthelminthic, or anti-inflammatory effects. In nonprimates, this hypothesis has recently been suggested to explain bark-feeding in Asiatic black bears (*Ursus thibetanus*) (Seryodkin *et al.*, 2017).

A less well-explored hypothesis is the *stressed-tree hypothesis* (White, 2019). This hypothesis posits that trees that undergo ecological stress during development because of poor soil quality, exposure to excess sun, fire, drought, or nitrogen fertilizers, produce higher levels of nutrients, and amino acids in their phloem, making the bark nutritionally rich (Brockley & Elmes, 1987; Ciani *et al.*, 2001; Mori *et al.*, 2016; Nichols *et al.*, 2016; Pulliainen & Tunkkari, 1987; Rousi *et al.*, 1987). Stressed trees have been shown to produce higher levels of stress-associated proteins than nonstressed trees (Eberhardt, 2000; Faber, 1996; Pakkala *et al.*, 2017; Rousi *et al.*, 1987; White, 1984). Behavioral evidence for this hypothesis includes reports of Eurasian three-toed woodpeckers (*Picoides tridactylus*) and bark beetles (Curculionidae: Scolytinae) favoring stressed trees over nonstressed trees (White, 2015), and increased bark exploitation by animals during protein-scarce periods (Andreev, 1988; Beeson, 1987; White, 2019).

One of the few empirical assessments of bark-feeding's adaptive function amongst free-ranging chimpanzees came from the Mahale Mountains National Park in Tanzania (Nishida, 1976). Bark was suggested to be a fallback or "emergency" food, based primarily on evidence that the seasonal exploitation of this resource generally corresponded with periods of staple food scarcity at the site. The staple foods in this study were primarily favored fruits. However, there was no evaluation of seasonality patterns on a tree-species level, as all tree species were grouped together for this analysis. Since this study, a few anecdotal reports from Budongo and Kibale have noted free-ranging chimpanzee bark-feeding in potentially self-medicative contexts (Pebsworth *et al.*, 2006). However, few other studies have re-evaluated Nishida's hypothesis, and the dietary function of bark remains relatively unexplored in site-specific contexts. Below we discuss several of the known characteristics of bark-feeding in chimpanzees.

Bark-Feeding Behaviors in Free-Ranging Chimpanzees

In free-ranging chimpanzees, seasonal bark-feeding patterns have been reported across multiple field sites, including Mahale (Tanzania) (Nishida, 1976), Fongoli (Senegal) (Pruetz, 2006), Gombe (Tanzania) (Van Lawick-Goodall, 1968), and Comoé National Park (Côte d'Ivoire) (Lapuente *et al.*, 2020). In at least two of these field sites (Mahale and Comoé National Park), bark-feeding increased during periods of staple fruit scarcity (Lapuente *et al.*, 2020; Nishida, 1976). In Mahale, these increases took place in the mid-rainy season and at the beginning of the dry season (Nishida, 1976). In Comoé National Park, bark-feeding on the species *Ceiba pentandra* increased only during the rainy season (Lapuente *et al.*, 2020).

In Comoé National Park, bark-feeding techniques vary between primate species (Lapuente *et al.*, 2020). Chimpanzees used their fingernails or front teeth to strip and longitudinally scrape *C. pentandra* cambium, while sympatric baboons bit *C. pentandra* bark and transversely scraped the cambium with their teeth. Technical variation between these species not only looks different in practice but also leaves behind distinctive tree damage. However, variation in techniques used for bark-feeding across primate species has not yet been considered at a tree-species level.

While never systematically reviewed, chimpanzee bark-feeding techniques also appear to vary across field sites. Chimpanzees in Gombe National Park, unlike those in Comoé National Park, have been observed cutting bark with their teeth, pulling large strips of bark using their hands, and horizontally scraping bark with their teeth (Van Lawick-Goodall, 1968). It remains unclear whether variation in bark removal technique is related to morphological tree characteristics, the quantity of material targeted, cultural variation, or individual preferences.

In Comoé National Park, Lapuente *et al.* (2020) identified the presence of bark-feeding "hotspots" in the tree species *C. pentandra*. Trees were revisited yearly by members of the same community and exploited "sustainably," allowing for bark regeneration. However, as far as the authors know, there have been no further systematic comparative investigations into the spatial distribution of bark-feeding events, and none which evaluate these spatial patterns at a tree-species level.

Assessing Predictions of the Fallback Food Hypothesis

To reevaluate the adaptive function of bark-feeding in chimpanzees, we investigated whether the fallback food hypothesis can explain observations of this behavior across two neighboring chimpanzee communities, Sonso and Waibira, in Uganda's Budongo Forest. These two communities are well-suited for this study as their spatial proximity means similar exposure to seasonal and ecological conditions. In this study, we assess whether bark-feeding meets the following predictions of the fallback food hypothesis:

> ***Prediction 1****: Bark-feeding increases during periods of food scarcity and decreases during periods of ripe fruit availability.* If bark is a generalized fallback food, we predict that chimpanzees should target bark when their preferred, high-value foods are seasonally scarce, and avoid bark when their preferred foods are seasonally abundant. If seasonality is found, it is necessary to determine whether seasonality patterns apply uniformly to all targeted tree species and to consider potential ecological drivers of this seasonality.
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> ***Prediction 2:*** *The quantity of bark ingested is relatively consistent across tree species.* As bark is thought to provide little nutritional value (Krief *et al.*, 2006) and is both energetically and temporally costly to exploit compared with other foods (e.g.,

figs), we predict relatively large amounts of bark should be targeted for the benefits of exploitation to outweigh the costs. Moreover, if chimpanzees are randomly selecting species for bark-feeding to supplement their nutrition or energy needs during periods of food scarcity, we expect minimal variation in the quantities of cambium targeted across tree species, unless there is significant variation in nutritional value between species. If this variation does exist, we further predict that in the presence of significant nutritional differences, chimpanzees would prioritize high-value barks over low-value ones, assuming equal availability of the species.

***Prediction 3**: High-value foods are prioritized over bark when both are available.* The logic behind this prediction is also rooted in the assumption that bark likely provides fewer benefits and requires more energy to exploit compared to nutritionally rich, staple foods. When both high-value foods (e.g., meat) and bark are proximately available, we predict, based on the fallback food hypothesis, that chimpanzees should prioritize consuming the high-value foods to efficiently meet their dietary needs.

***Prediction 4:** If tree species are distributed throughout the home range, individuals conserve energy and minimize risk by exploiting trees for bark within or near their frequently used core areas.* If bark is a fallback food that offers minimal energetic returns, and targeted tree species are available within a community's home range, we predict that individuals should conserve energy and reduce risk by exploiting bark within, or close to, frequented core areas.

Methods

Study Site and Subjects

The Budongo Central Forest Reserve (CFR), located in the Masindi District of Western Uganda, covers a 793 km^2 area, 482 km^2 of which is made up of semi-deciduous forest (Eggeling, 1947). Historically Budongo CFR has two wet seasons, typically occurring between March–May and September–November (Reynolds *et al.*, 2005). Rainfall at Budongo ranges from 1200 to 2200 mm (average 1600 mm), and temperatures generally remain consistent throughout the year, with daytime highs ranging from 19 °C to 32 °C.

We conducted this study on the neighboring Sonso and Waibira chimpanzee communities. These communities are composed of free-ranging Eastern chimpanzees, habituated for research at the Budongo Conservation Field Station (BCFS). Sonso, which included ~ 68 individuals at the time of this study, has been continuously studied since 1990 (Reynolds *et al.*, 2005). Waibira, a larger group of at least 105 individuals, was more recently habituated, with consistent data collection beginning in 2011. The Sonso diet and surrounding flora have been intensively studied (Synnott, 1985; Tweheyo *et al.*, 2004; Villioth, 2018), whereas this information is less well-studied for Waibira (although see Villioth, 2018).

We define "home range" as the specific geographic region that a chimpanzee community uses to meet its collective needs over a defined period (Martínez-Íñigo *et al.*, 2021). This definition of home range encompasses peripheral areas the group may visit less frequently. We use "core area" to mean areas within the home range that are heavily used or visited by the community and to exclude areas that are rarely visited or which may overlap with neighboring community home ranges (Martínez-Íñigo *et al.*, 2021). In 2022, the Sonso maximum home range was 5.33 km^2, and the Waibira maximum home range was 10.28 km^2 (Badihi *et al.*, 2022).

In Budongo, a system of East–West and North–South trails delineate the main study area for each community, forming two labeled grids which cover the majority of both home ranges (Fig. 1). While parts of each home range may, in some cases, extend beyond the grid system, core areas for both communities are located within their respective grid systems. Travel outside of the grid is relatively infrequent for both communities. Sonso trails are 100 m apart forming 100 m × 100 m blocks. In the southern and eastern regions of the grid, there are several larger blocks for geographic or historical reasons. The Waibira grid system is less standardized, with some 200 m × 500 m, 200 m × 200 m, and 100 m × 200 m blocks, as trails were added over time. For this study, we standardized Waibira block sizes for easier comparison (see supplemental materials). Trails in both communities are up to 1.5 m wide. At the site, blocks are named based on which trails intersect their southwestern corner. Block names are formed from the intersecting North–South trail name, followed by the intersecting East–West trail name. Trail names consist of either numbers or letters.

Data Collection

Long-Term Site Data

We used long-term site data for Sonso between 2008–2021 and for Waibira between 2015–2021. These data, collected by trained field staff, included: **a**) bark-feeding events collected during behavioral focal follows from 75 individuals (Sonso: 41; Waibira: 44), **b**) party composition scans (15-min interval), **c**) site-specific annual

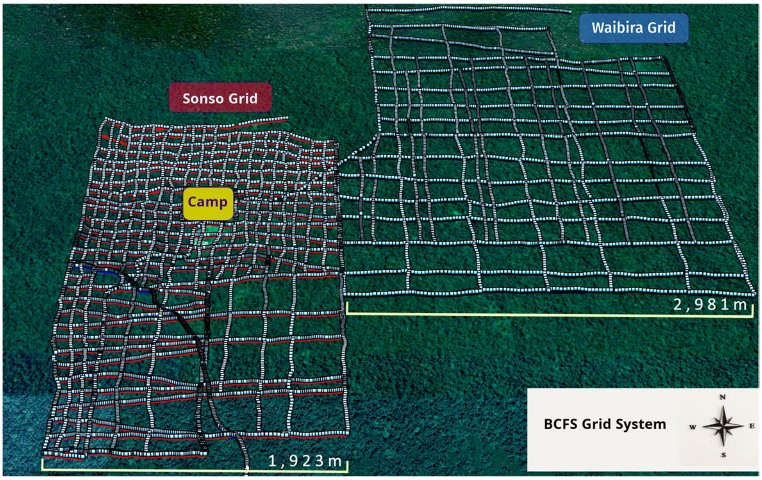

Fig. 1 Map of the Sonso and Waibira grid-systems (as of 2024) in the Budongo Forest, Western Uganda

rainfall and temperature measures, and **d**) Fruit Availability Index (FAI) data between 2013–2018. We used FAI data collected from trees that produce fruits fed on by both communities. For information on long-term data collection methods and FAI calculations, see *supplemental materials*.

Behavioral Data Collection During the Study Period

We conducted two 4-month field seasons between mid-June and mid-October (2021 and 2022). The first of these periods of direct observation was with the Sonso community, and the second was with the Waibira community. The same observer employed identical methods during both study periods to ensure data comparability. During both field seasons, we used pseudo-random focal animal selection (Hobaiter *et al.*, 2017), where parties were initially opportunistically searched for according to a random schedule, and focal animals were then selected according to prioritization criteria (see *supplementary materials*). We also collected behavioral and video data from focal individuals for this study and included direct observations of bark-feeding filmed by trained field staff or researchers within or between study periods. As these ad libitum observations were not systematically collected, we used them only to qualitatively establish bark-feeding repertoires and excluded them from quantitative analysis.

Indirect Evidence

To investigate bark-feeding techniques, we took measurements and photographs of trees with characteristic traces of bark-feeding encountered during focal follows and along transects. When possible, we took 3D tree scans on an iPad Pro using a 3D Scanner application (Laan Labs). For consistency, we only recorded traces that could be accessed from the ground and were below a max height of 2 m. While sympatric baboons may create bark-feeding traces that can be conflated with those of chimpanzees, we did not directly observe baboons bark-feeding in either field season, although past research suggests it occurs (Okecha & Newton-Fisher, 2006). Additionally, except for indirect evidence found on three tree species, all traces were documented on species already known to be used by chimpanzees for bark-feeding. Scans of indirect traces for each species were shown to trained field staff to confirm that marks matched techniques known to be used by chimpanzees from past direct observations.

Forest Transects

To assess tree species availability in each community's home range, we conducted eight line transects between September 1 and October 10, 2022, four in each of the two community home ranges (Fig. S1). Each line transect was 400 m long and was located within the precut trail system. Four transects ran

North–South and four ran East–West (Hedges & McGrew, 2012). Transects were selected at random from samples stratified by cardinal direction in each home range. Trees > 12 cm dbh were measured on both sides of the trail within 5 m of the trail center (see supplemental materials for details).

Botanical Identification

All tree species mentioned in this study were identified by trained BCFS field staff. The most current scientific names for each species were confirmed for this paper in May 2023, according to Kew's Plants of the World Online (https://powo.science.kew.org/).

Ethical Statement

Data used in this study were collected with approval from the Uganda Wildlife Authority (permit no: COD/96/05), and the Uganda National Council for Science and Technology (permit no: NS257ES). The study was observational and adhered to the guidelines for best practice in field primatology (Riley *et al.*, 2014). All applicable international and national guidelines were followed. The authors report no conflict of interest.

Analysis

Seasonality

To determine whether bark-feeding seasonality is consistent across years, we plotted the mean number of bark-feeding events, by month, across all years in the long-term data (2008–2021), combining data from both communities. We then compared bark-feeding seasonality to rainfall and temperature patterns (1993–2022) at the site to assess climatic correlations. We used FAI data (2013–2018) as a proxy for general food abundance at the site, as ripe fruit is the most relevant high-value food in Budongo chimpanzee diets. While this index does not capture other dietary items (e.g., pith, meat, agricultural cultivars), ripe fruit abundance provides the best approximation of general food abundance and scarcity at this site. For this analysis, we compared monthly FAI data for 2013–2018 with monthly bark-feeding events for 2008–2021 using a Pearson correlation test. We used all available data for these analyses, meaning that we use different periods for different variables, based on the assumptions that annual patterns of bark-feeding, weather, and FAI are relatively consistent, and that summarizing data over as many years as possible for each variable is more representative than comparing variables for individual months where we have all variables.

To determine whether seasonal correlations differed by tree species, we created individual plots for each species with six or more associated events across both communities, scaled to show relative trends. We only plotted species with six or more associated events, as small sample sizes limited our ability to detect seasonal patterns. We then performed the Pearson correlation test on each species-level dataset, comparing mean FAI per month across all years (2013–2018) and monthly sums of bark-feeding events for each tree species across all years (2008–2021). Neither FAI nor bark-feeding datasets show any deviation from normality using the Shapiro–Wilk test as required for the Pearson correlation test (FAI: $z = 0.90$, $p = 0.18$; All Bark-Feeding Data: $z = 0.89$, $p = 0.13$). Pearson correlation coefficients (r) range from -1 to $+1$, with a value of $+1$ indicating a perfect positive linear relationship (correlated), -1 indicating a perfect negative linear relationship (anticorrelated), and 0 indicating no relationship (uncorrelated) (Schober *et al.*, 2018). Significance was set to $\alpha = 0.05$. If $p < 0.05$, we concluded that observed coefficients were generated by correlated or anticorrelated systems.

Technical Variation

We described observed variation in bark-feeding techniques from in situ photographs and 3D scans taken of exploited trees. To compare the quantity of bark/cambium targeted across different tree species, we used measurements of bark-feeding traces from the field or took post hoc measurements from our 3D tree scans when necessary. Using the longest strip on each tree, we calculated mean strip length for each tree species (all results reported in Table S1). We also calculated mean diameter at breast height (dbh) for trees targeted for bark-feeding in the long-term data (when data was available), and mean dbh for trees with bark-feeding traces reported along line transects (Table S1). We assessed and quantified the healing stage of feeding traces using a 1–4 scale established by Lapuente *et al.* (2020). While we did not classify bark type in this study, trees in the Budongo Forest have noticeable morphological differences, including bark type and hardness, which likely impact bark-feeding techniques.

Forest Transects

To calculate relative tree species abundance within each community's home range, we divided the number of trees per species by the total number of trees reported within each community's home range.

Heat Maps

Following Badihi *et al.* (2022), we used the "adehabitatHR" package (Calenge, 2020) in R (version 4.0.5) to create heat maps for bark-feeding events reported in the long-term data. Heat maps were made by using the "heatmap.2" function to map events across each community's home range using the site's current grid system (see supplementary materials for information on grid parameters). Each block was color-coded by the total number of bark-feeding events reported for that block. When events occurred outside of the grid system, denoted as "off-grid" within this paper, it was impossible to allocate them to a particular block. We consequently batched off-grid events into north, south, east, and west areas, based on where they occurred relative to the grid. Separate heat maps were produced for each community and for each targeted tree species.

To determine core areas for both communities, we created activity heat maps. These maps represented the proportional number of total scans in which group members were observed across each block in the grid system. To do this, we used party composition scans from the site's long-term data, taken every 15-min during focal follows by trained field staff. These data were extracted from Sonso between 2008–2021 and from Waibira between 2015–2021 (see supplementary materials for more information). We defined blocks as "core areas" if scans in that block were ≥ (1/3) * highest value block for each community. According to these criteria, we considered blocks core areas if they were reported in ≥ 1379 focal activity scans in Sonso, and ≥ 451 focal activity scan in Waibira. We outlined core areas for each community in blue in Figures S2–S3.

To classify distances between bark-feeding events and core areas, we measured the minimum distance between the block where the event took place and the closest core area block. If an event occurred outside grid boundaries, we measured the distance from the closest grid edge to the nearest core area block. We classified blocks or regions as "far" from a core area if they were ≥ 500 m away. Maps of community grids, with number of scans per block, can be found in Figs. S2–S3.

Results

Species Used for Bark-Feeding

In total, the long-term data included reports of 373 bark-feeding events from 27 tree species across both communities (Table I). In Sonso, these included 168 events from 24 tree species, and in Waibira 205 events from 18 tree species. Of these targeted tree species, four appear to be targeted solely for their bark (*Eucalyptus* sp., *Trichilia* sp., *Albizia glaberrima*, *Dombeya kirkii*).

During our observational study period, we directly observed and recorded 39 bark-feeding events, from 16 identified tree species (Table II). In Sonso, we recorded 13 events from 7 identified species, and in Waibira we recorded 29 events from 12 identified species. Of these species, four (*Funtumia elastica, Croton sylvaticus, Scutia myrtina, Sterculia dawei*) had never been reported as used for bark-feeding in the long-term data. We also documented indirect evidence of bark-feeding, characteristic of chimpanzees, on 65 individual trees during routine data collection, and on 27 individual trees during transects. We found traces on 18 species, three of which (*Ficus polita*, *Albizia zygia, Pseudospondias microcarpa*) had never been directly observed being used for bark-feeding in either community, across both the long-term data and our direct observational period.

Seasonality of Bark-Feeding

When we combined all bark-feeding events in the long-term data, we identified multiple seasonal peaks (Fig. 2a). Across both communities, bark-feeding peaked in October. Sonso had an additional peak in February and smaller peaks in May and July.

Table I Bark-feeding in Sonso and Waibira chimpanzee communities in Budongo, Western Uganda, 2008–2021

Species	Family	Life form	Total events		Presence in home range		Off-grid events		Other parts eaten	Months reported
			Son	Wai	Son	Wai	Son	Wai		
Broussonetia papyrifera	Moraceae	Tree	29	0	√	X	0	0	L, Fl, F	9,10
Cleistopholis patens	Annonaceae	Tree	34	9	√	√	9	0	Dw, F	all
Eucalyptus sp.	Myrtaceae	Tree	5	0	√	X	0	0		3,7,10,11
Cynometra alexandri	Fabaceae	Tree	12	72	√	√	4	0	L, Fl, S	1,4,5,6,7,8,9,10,11,12
Alstonia boonei	Apocynaceae	Tree	17	2	√	√	8	0	L	1,2,3,4,5,6,7,8,10,11
Unidentified trees	n.a	Tree	11	41	?	?	4	0	n.a	all
Ficus variifolia	Moraceae	Tree	9	0	√	√	0	0	L, F	3,5,6,7,8
Ficus sur	Moraceae	Tree	6	0	√	√	1	0	F, L	4,5,11
Syzygium guineense	Myrtaceae	Tree	6	0	√	X	0	0	F	4,6,9,10,11
Unidentified climbers	n.a	Climber	7	13	?	?	1	0	n.a	1,2,3,5,7,8,9,10,11,12
Khaya anthotheca	Meliaceae	Tree	5	0	√	√	1	0	R	3,4,9
Cordia millenii	Boraginaceae	Tree	4	4	√	√	1	1	F, Fl	6,9,10,11,12
Raphia farinifera	Arecaceae	Tree	3	0	√	√	2	0	Dw	2,4,12
Antiaris toxicaria	Moraceae	Tree	3	1	√	√	0	0	F, L	2,7
Desplatsia dewevrei	Malvaceae	Tree	3	1	√	√	1	0	F, L	5,7,11
Ficus exasperata	Moraceae	Tree	4	3	√	√	1	0	F, L, R	7,8
Lasiodiscus pervillei	Rhamnaceae	Tree	2	0	√	√	1	0	L, Fl	3,7
Ficus saussureana	Moraceae	Tree	1	3	√	√	0	1	F	5,6,10,12
Trichilia sp.	Meliaceae	Tree	1	0	√	√	0	0		2
Unidentified terrestrial herbaceous plants	n.a	Herb	1	0	?	?	0	0	n.a	3
Celtis zenkeri	Cannabaceae	Tree	1	0	√	√	0	0	F, L	11
Celtis mildbraedii	Cannabaceae	Tree	1	1	√	√	1	0	F, L	1,8

Table I (continued)

Species	Family	Life form	Total events		Presence in home range		Off-grid events		Other parts eaten	Months reported
			Son	Wai	Son	Wai	Son	Wai		
Psidium guajava	Myrtaceae	Tree	1	0	√	√	0	0	F	10
Celtis gomphophylla	Cannabaceae	Tree	0	2	√	√	0	0	F, L	9
Cola gigantea	Malvaceae	Tree	0	1	√	√	0	0	F, S, W	7
Albizia glaberrima	Fabaceae	Tree	0	1	√	√	0	0		8
Ficus natalensis	Moraceae	Tree	0	5	√	√	0	0	F	7,8,9,10
Gambeya albida	Sapotaceae	Tree	0	1	√	√	0	0	F	8
Dombeya kirkii	Malvaceae	Tree	0	44	**X**	√	0	0		1,4,5,6,9,10,11,12
Ficus mucuso	Moraceae	Tree	0	1	√	√	0	0	F, L, Fl	8
Community totals			**168**	**205**			**35**	**2**		

√ = Present in home range.

X = Absent or rare in home range.

? = Unknown at a species level.

F = fruits; **L** = leaves; **Fl** = flowers; **Dw** = dead wood; **S** = seed; **Son** = sonso; **Wai** = Waibira.

NB: The barks of *Lannea welwitschia* and *Celtis gomphophylla* were reported as dietary items in Sonso by Newton-Fisher (1999), but remain unreported in the long-term data, and were thus omitted from analysis.

Table II Direct and indirect evidence of bark-feeding in Sonso and Waibira chimpanzee communities in Budongo, Western Uganda, 2021–2022

Species	Family	Life form	Direct observation events		Observation types			
					Son		Wai	
			Son	Wai	Direct	Indirect	Direct	Indirect
Eucalyptus sp.	Myrtaceae	Tree	0	0	X	√	X	X
Cynometra alexandri	Fabaceae	Tree	1	10	√	X	√	√
Alstonia boonei	Apocynaceae	Tree	4	1	√	√	√	√
Ficus variifolia	Moraceae	Tree	2	0	√	√	X	√+
Ficus sur	Moraceae	Tree	0	5	X	√	√+	√+
*Ficus polita**	Moraceae	Tree	0	0	X	X	X	√+
*Funtumia elastica**	Apocynaceae	Tree	0	1	X	X	√+	X
*Croton sylvaticus**	Euphorbiaceae	Tree	0	1	X	X	√+	√+
Syzygium guineense	Myrtaceae	Tree	2	0	√	√	X	X
Cordia millenii	Boraginaceae	Tree	0	1	X	X	√	X
Ficus exasperata	Moraceae	Tree	2	0	√	√	X	√
Lasiodiscus pervillei	Rhamnaceae	Tree	0	1	X	X	√+	X
*Scutia myrtina**	Rhamnaceae	Scandent Shrub	1	0	√+	√+	X	√+
Unidentified Climber	n.a	Climber	0	1	X	X	√	X
Ficus saussureana	Moraceae	Tree	0	4	X	X	√	√
Celtis zenkeri	Cannabaceae	Tree	0	0	X	X	X	√+
Celtis mildbraedii	Cannabaceae	Tree	0	2	X	X	√	√
Cola gigantea	Malvaceae	Tree	1	0	√+	X	X	X
Albizia glaberrima	Fabaceae	Tree	0	0	X	X	X	√
*Albizia zygia**	Fabaceae	Tree	0	0	X	√+	X	√+
Ficus natalensis	Moraceae	Tree	0	0	X	X	X	√
Dombeya kirkii	Malvaceae	Tree	0	1	X	X	√	√
Ficus mucuso	Moraceae	Tree	0	0	X	√+	X	√
*Sterculia dawei**	Malvaceae	Tree	0	1	X	X	√+	X
*Pseudospondias microcarpa**	Anacardiaceae	Tree	0	0	X	X	X	√+
Community Totals			13	29				

D = direct observation; **I** = indirect evidence.

[*] = First report of species use for bark ingestion in either community.

[+] = First report of species use for bark ingestion in indicated community.

Son = Sonso; **Wai** = Waibira.

NB: "Event" refers to a feeding bout which often included several individuals feeding at one time.

Prediction 1: *Bark-feeding increases during periods of food scarcity and decreases during periods of ripe fruit availability.*

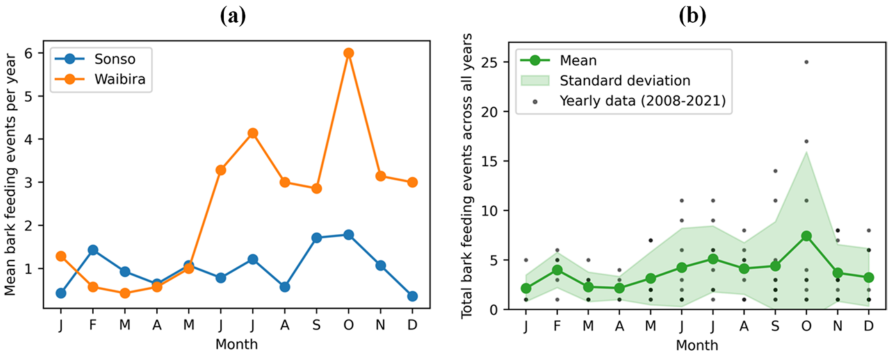

Fig. 2 Monthly bark-feeding events per year for two chimpanzee communities in the Budongo Forest, Western Uganda, 2008–2021. (**a**) By community. (**b**) Communities combined

Waibira data indicated a second bark-feeding peak in July. We also found relative seasonal consistency of bark feeding across all years present in the long-term data, with notable variability in October, due to outliers in 2012 and 2018 (Fig. 2b). When we compared bark-feeding seasonality to rainfall patterns at the site, we found that bark-feeding occurs most frequently during the month with the greatest average rainfall (October) (Fig. 3a). This relationship, however, does not apply as obviously to other months in which bark-feeding frequencies increase. While bark-feeding increased across February, May, and July, these months are historically considered drier periods or months of seasonal transition. Across years, we also noted an increase in maximum temperature and a decrease in minimum temperature in both February and December (Fig. 3b), whereas the rest of the year stays relatively consistent.

Comparing Bark-Feeding Seasonality and Ripe Fruit Abundance

Ripe fruit availability peaked in February and December in the study area, with periods of relative scarcity in July and October (Fig. 4). When we compared the

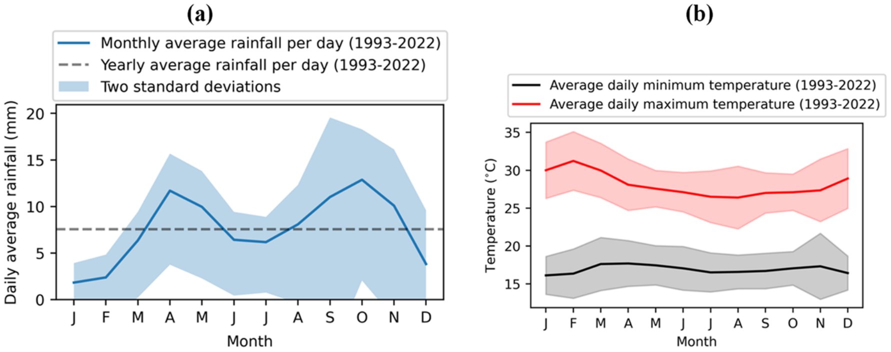

Fig. 3 Weather in the Budongo Forest, Western Uganda, 1993–2022. (**a**) Mean rainfall per day. (**b**) Mean min and max daily temperature. Shaded regions represent two standard deviations

seasonality of fruit availability to the seasonality of all bark-feeding events across both communities, without taking species-level variation into account, bark-feeding occurred most frequently during the two months when food is scarcest (July and October) (Fig. 2b). The correlation between general bark-feeding and food abundance was negative, but not significant ($n = 12$, $r = -0.557$, $p = 0.060$).

Ten tree species had six or more associated bark-feeding events across both communities (Fig. 4). The strength of the correlation between bark-feeding and fruit availability varied across these ten species, with significant negative correlations for *C. alexandri*, and no significant positive correlations (Fig. 5). We report coefficients for all species present in the long-term data in Table S1.

Several tree species appear to be targeted at increased frequencies during periods when food is scarcest (July and October). Bark-feeding on *C. alexandri,* the species

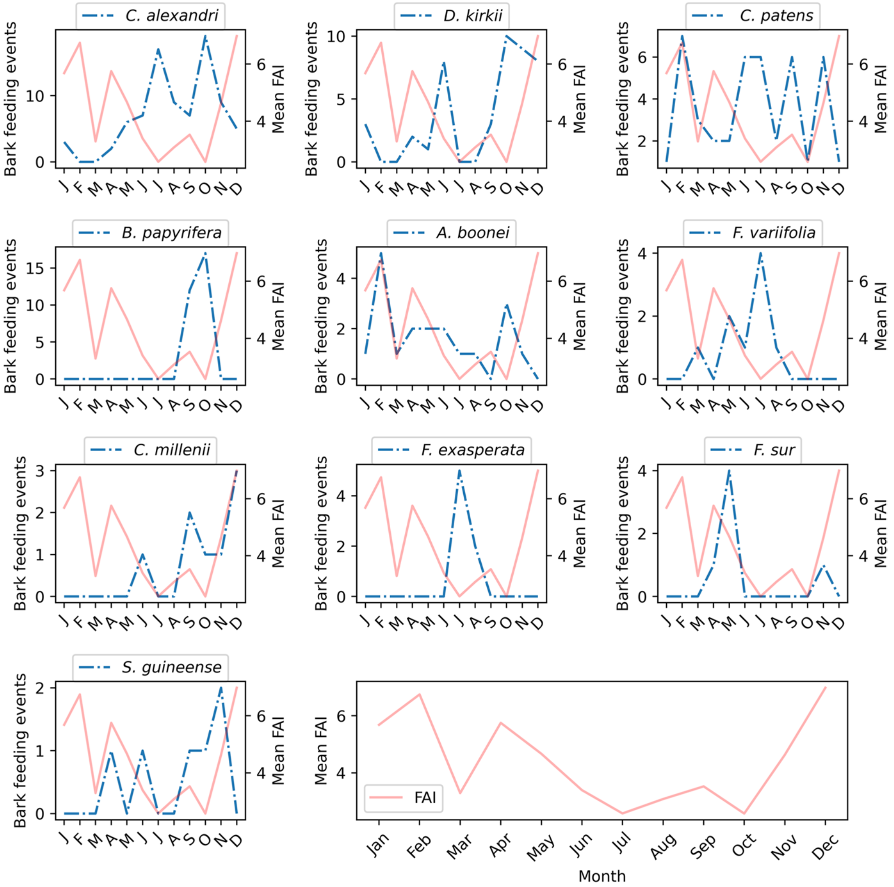

Fig. 4 Comparison of ripe fruit availability (2013–2018) (pink line) to bark-feeding seasonality across tree species in the long-term site data (2008–2021) (blue-dotted line). Species included in this plot had six or more associated bark-feeding events in the Budongo Forest, Uganda. Y-axes are scaled across plots to show relative trends

with the most reported observations (n = 84), was negatively correlated with ripe fruit availability (Fig. 5). Bark-feeding on this species peaked during months of ripe fruit scarcity (July and October) and was rarely observed during months of ripe fruit abundance (n = 0 in February, n = 5 in January). Bark-feeding on *D. kirkii*, reported 44 times, also peaked in October, with another peak in June when fruit availability rapidly declined. There are no cases reported in February for this species; however, there were several in December (n = 8). We found almost no correlation for *D. kirkii* (Fig. 5). *Broussonetia papyrifera* also was primarily targeted for bark-feeding in October (n = 17), with additional cases (n = 12) in September when ripe fruit is relatively scarce (Fig. 5).

Counter to our prediction, bark-feeding on several species peaked during months when ripe fruit was maximally abundant (February and December). The frequency of bark-feeding on most species was not significantly correlated with FAI, and some showed weakly positive, nonsignificant relationships (Fig. 5). For example, bark-feeding on *A. boonei* occured most frequently in February (5/19 observations). Bark-feeding on *C. millenii* occurred most frequently in December (3/8 observations). Bark-feeding on *C. patens* fluctuated through the year but peaked in February (7/43 observations) and was targeted least frequently in October (1/43 observations).

Prediction 2: **Quantity of bark targeted is relatively consistent across tree species.**

Bark-Removal Techniques

We recorded multiple bark removal techniques during the study in both terrestrial and arboreal contexts. During terrestrial bark-feeding events, chimpanzees removed and ingested bark while on the ground, on a tree buttress, or from the trunk (< 1 m from the ground). Removal techniques during such cases commonly involved a) peeling bark from trunk or buttresses in long strips or b) trunk/buttress biting. In most cases, following removal, individuals masticated and swallowed bark/cambium. On several occasions, we also observed individuals licking moisture or sap

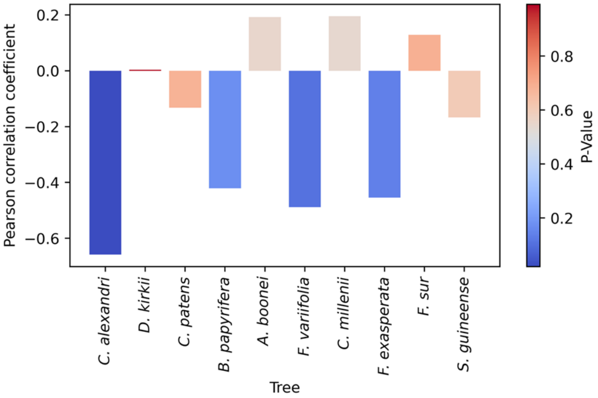

Fig. 5 Pearson correlation coefficients and *p*-values for seasonality comparison between monthly sum of bark-feeding events per species (2008–2021) and mean FAI per month across all years (2013–2018). Only tree species with six or more associated bark-feeding events are plotted

from exposed cambium on the trunk after bark removal. We never observed bark wadging (mastication and compression of bark between the lower lip and teeth or between the tongue and palate) during terrestrial bark-feeding events.

Arboreal bark-feeding occurred off the ground while individuals sat on branches or in the canopy. Removal techniques often included a) branch stripping, b) trunk stripping, or c) bark/resin scraping. After removal, individuals often scraped bark strips with their teeth and wadged the cambium. After bark/resin scraping, resin was ingested without wadging. During the study period, we observed *C. alexandri*, *F. sur, K. anthotheca*, *D. kirkii,* and *S. dawei* associated with arboreal bark exploitation. However, as indirect evidence of arboreal bark-feeding often is hard to identify and measure because of poor visibility, we excluded it from the following analyses.

Variation in Ingested Quantities of Bark

Using indirect bark-feeding traces, we identified species-level variation in quantity of bark targeted during bark-feeding. In total, we recorded 46 trees from 12 species with measurable traces considered to be characteristic of chimpanzee exploitation. The longest strip/bite lengths were for three *Ficus* species*, F. mucuso*, *F. exasperata*, and *F. sur* (Fig. 6). The smallest measurable mean strip/bite length was for *A. boonei*. Two species from the genus *Albizia, A. glaberrima* and *A. zygia,* also had single measurement lengths well under the grand mean (63.2 cm). Mean strip/bite lengths, sample size, and exploitation technique for each species are listed in Table S2.

The dbh of *A. boonei* (n = 2, μ = 89.2 cm), *A. glaberrima* (n = 1, 95.5 cm), and *A. zygia* (n = 1, 46.2 cm) trees along line transects with bark-feeding traces were all similar to, or far greater than, the mean dbh of all eligible trees targeted for bark-feeding in the long-term data (n = 200, μ dbh = 47.1 cm ± 22.0 cm). The chimpanzees, therefore, do not appear to target bite-sized quantities of bark from small trees.

The *Ficus* species were all vertically stripped along their buttresses, whereas *A. boonei* and the Albizia species were all bitten on either their buttresses or trunks (Fig. 7). *Ficus* species often had multiple strips at the same healing stage visible on the trunk. This pattern of use could imply either multiple strips per event by the same individual or multiple individuals stripping at the same time. *A. boonei* and *Albizia* species had, on average, fewer traces per tree, although sample sizes were smaller. Using strip length as a metric for quantity of targeted bark in this analysis, may therefore underestimate the total quantity ingested, particularly for *Ficus* species.

Prediction 3: High-value foods are prioritized over bark when both are available

Bark vs. Staple Food Prioritization

During our direct observations, we recorded several cases in which chimpanzees targeted bark when highly nutritious staple foods were available and nearby. We recorded one case between field seasons in March 2022 (Fig. 8; Video S1). A Sonso subadult male fed on *A. boonei* bark/cambium, following a successful blue duiker (*Philantomba monticola*) hunt. The individual's juvenile brother sat 1 m away eating

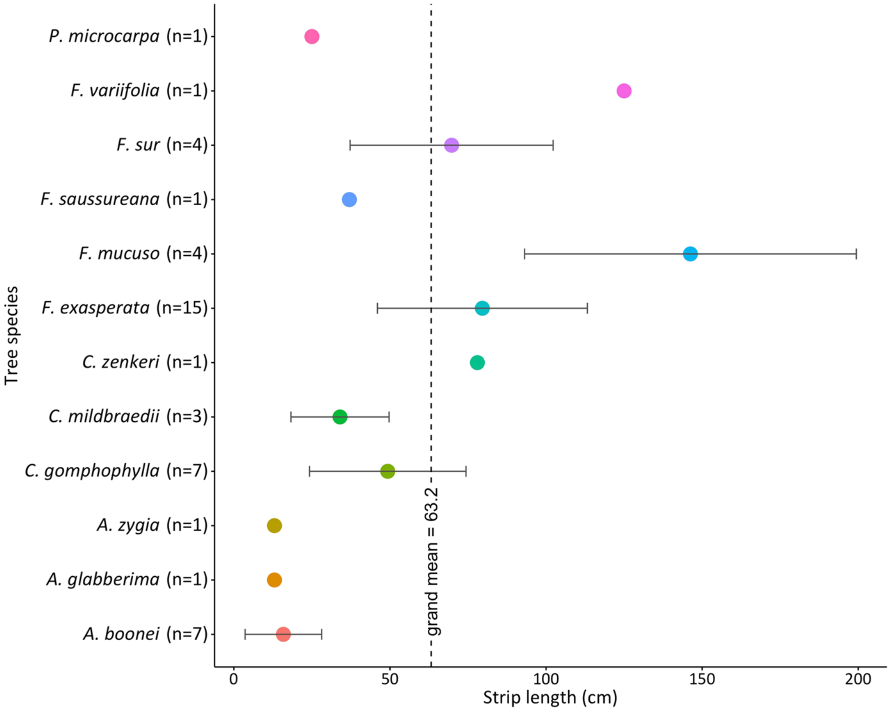

Fig. 6 Mean strip/bite of exploited bark areas across 46 trees from 12 species in the Budongo Forest, Uganda. Bars represent one standard deviation. Where we obtained only one measurement per species, it appears as a single point

meat from the carcass (Fig. 8a). After ~ 1 min, the subadult stopped bark-feeding and traveled out of sight. The juvenile dropped the carcass, checked his surroundings (Fig. 8b), and then moved toward the *A. boonei* tree to bark-feed (Fig. 8c). After feeding on the cambium for ~ 4 s (Fig. 8d), the juvenile moved away from the tree, retrieved the carcass (Fig. 8e), and followed his brother out of sight (Fig. 8f).

In a series of group feeding events during the study, we also observed groups of Waibira individuals in the canopy of an *F. sur* tree, stripping bark from the

Fig. 7 [Left] 3D scan of Ficus mucuso bark strip (110 cm). [Right] 3D scan of Alstonia boonei bark bite (8 cm). Budongo Forest, Western Uganda, September 2024

branches and trunk while others ate ripe fruits in the same tree. Over multiple days, individuals returned to this tree to eat both bark and ripe fruit. We observed high and low-ranking individuals bark-feeding during these events, as well as individuals of both sexes and all age classes. Several other staple fruit trees were bearing ripe fruit during this period.

On several other days, we observed single individuals feeding on bark, although members of the group were feeding on staple foods nearby. On one occasion, a juvenile male from Waibira fed on *C. sylvaticus* bark while other group members ate *C. millenii* fruit in a large tree within view. On another occasion, a juvenile female fed

Fig. 8 A juvenile chimpanzee from the Sonso community in Budongo Forest, Westen Uganda, leaves a blue duiker carcass unattended to bark-feed on Alstonia boonei bark (March, 2022)

on *F. elastica* bark while others in the group, including her mother, ate ripening *C. millenii* fruits in a neighboring tree. Subsequently, the juvenile joined her mother and fed on *C. millenii* fruit. In Waibira, during a group feeding event in a large *S. dawei* tree, we observed an unidentified individual wadging bark while all others fed on young leaves. In Sonso, a juvenile and sub-adult fraternal pair separated from the group after feeding on two popular food items (*F. mucuso* ripe fruits and *F. exasperata* unripe fruits), and traveled together to a *S. myrtina* scandent vine, from which they both fed on bark.

Prediction 4: If tree species are distributed throughout the home range, individuals conserve energy and minimize risk by exploiting trees for bark within or near their frequently used core areas

Spatial Distribution of Bark-Feeding

Our heat map analysis showed that Sonso community core areas were a minimum distance of 900 m from the eastern edge of Sonso's grid, 800 m from the western edge, 700 m from the northern edge, and 1700 m from the southern edge (Fig. S2). Core areas were thus all "far" from off-grid areas according to our operational definition. Despite this, Sonso's bark-feeding event heat map shows a strong pattern of bark-feeding events occurring outside the Sonso community grid system, "far" from their core areas. Of Sonso's 168 recorded bark-feeding events, 36 (21%) took place off-grid (Fig. 9).

Despite evidence that Sonso individuals bark-feed at high frequencies outside their core areas, our transect data suggest that this pattern is not likely to be driven by availability of targeted trees. Species targeted in off-grid Sonso bark-feeding events include *A. boonei, C. mildbraedii, C. millenii, C. patens, C. alexandri, D. dewevreii, F. exasperata, F. sur, K. anthotheca, L. pervillei,* and *R. farinifera* (Table I). We documented all these species within the Sonso grid system during transects, except for *C. patens*. Furthermore, five of these 11 species were within the top 24 most abundant species across all Sonso transects, suggesting a wide distribution within the home range (Fig. S4).

Even within the grid system across the community's territory, bark-feeding in Sonso often occurred in blocks "far" from the core areas (Fig. 10). Within the home range, but south of Sonso's central core area, bark-feeding also occurred at relatively high frequencies in two blocks (1–10 and B-11), in a swampy forest region. Neither block is in a core area, with only 102 and 192 scans per block, respectively, and both are at least 600 m from any other core area block. Bark was ingested in 1–10 and B-11 from *A. boonei* (n = 4 events), *C. patens* (n = 2), *F. exasperata* (n = 1), *R. farinifera* (n = 1), as well as from unidentified terrestrial herbaceous species (n = 1), unidentified tree species (n = 3), and unidentified climber species (n = 2).

Waibira core area blocks were a minimum of 500 m from the eastern edge of the grid system and 600 m from the grid's northern and southern edges (Fig. S3). Only one core area block was within 500 m (10-N) of the western edge. All but the western off-grid events, therefore, were "far" from core areas. Waibira's bark-feeding

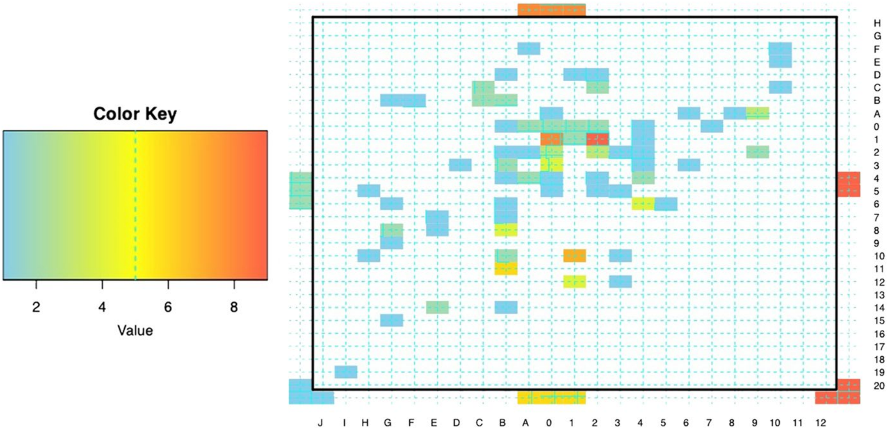

Fig. 9 Heat map of bark-feeding events by the Sonso chimpanzee community in the Budongo Forest, Western Uganda, 2008–2021. Area within the black lines represents the Sonso community grid-system. Colored blocks outside the black lines represent off-grid events. White blocks are regions where we reported no bark-feeding events

heat map did not show the same pattern of frequent off-grid events but did show some bark-feeding outside of core areas. Of Waibira's 205 bark ingestion events, only two (1%) took place off-grid (Fig. 11).

Transect and feeding data from the study period also suggest that the occasional off-grid bark-feeding in Waibira was not driven by availability of targeted species. Of the two off-grid Waibira bark-feeding events, one targeted a *C. millenii* tree off-grid to the north, and the other an *F. saussureana* tree off-grid to the west. While we did not identify *C. millenii* along Waibira transects, suggesting relative scarcity, it is present across the territory and *C. millenii* fruit is considered a staple food for both communities. During the direct observation period, we regularly observed Waibira individuals feeding on *C. millenii* fruit from several different trees in their home range, including trees within core areas. We assume, therefore, that Waibira

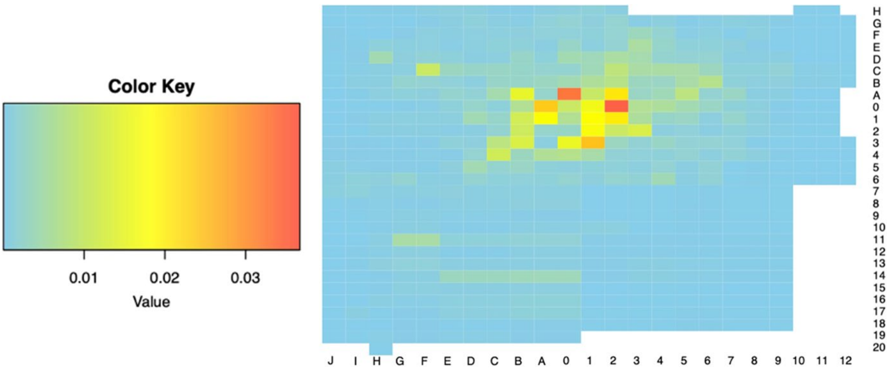

Fig. 10 Heat map of Sonso community focal activity scans in the Budongo Forest, Western Uganda, 2008–2021. White blocks are regions where the group was never reported

chimpanzees know the location of accessible *C. millenii* trees in their territory. We recorded *F. saussureana* along one transect in Waibira and the fruits of this species are also a staple food. We recorded several on-grid *F. saussureana* fruit feeding events during the direct observational period, again suggesting group members' knowledge of *F. saussureana* tree locations. Despite this, the off-grid bark-feeding event occurred within the neighboring Sonso community home range (block 5–4), 1000 m west and 400 m south of the closest Waibira core area block (20–0).

In Waibira, unlike in Sonso, bark-feeding appears to occur most frequently in core area blocks. Waibira's bark-feeding event heat map shows the most events in block 30-R, where the core group spent the highest proportion of their time (n = 1353 scans) (Fig. 12). Tree species targeted in this block included *C. alexandri* (n = 12 events), *D. kirkii* (n = 3), *C. millenii* (n = 1), unidentified tree species (n = 4), and *G. albida* (n = 1).

Species-Level Heat Maps

In Sonso, some species were disproportionately represented in off-grid bark-feeding events. These included *C. patens* (n = 9) and *A. boonei* (n = 8). In Sonso's long-term data, *C. patens* was the most commonly targeted tree species for bark-feeding. Of all recorded *C. patens* bark-feeding events (n = 34), nine (26%) took place outside the grid system (Fig. 13). Of all *A. boonei* Sonso bark ingestion events (n = 17), eight (47%) took place off-grid (Fig. 14). Within the grid system, a relatively high concentration of events involving both *C. patens* and *A. boonei* occurred in block B-11, toward the south of the grid, far from any core areas. Our transect data further suggest that the long distances traveled by Sonso

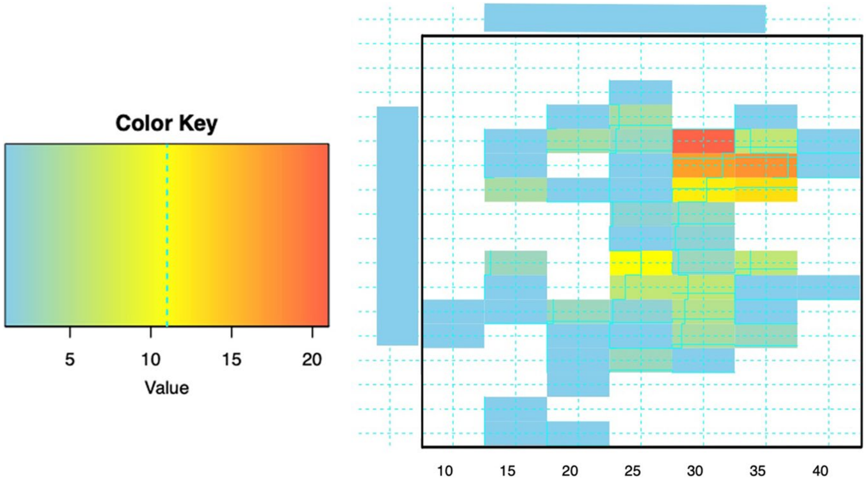

Fig. 11 Heat map of bark-feeding events by chimpanzees in Waibira community in the Budongo Forest, Western Uganda, 2015–2021. Area within the black lines represents the Waibira community grid-system. Colored blocks outside of the black lines represent off-grid events. White blocks are regions where we reported no bark-feeding events

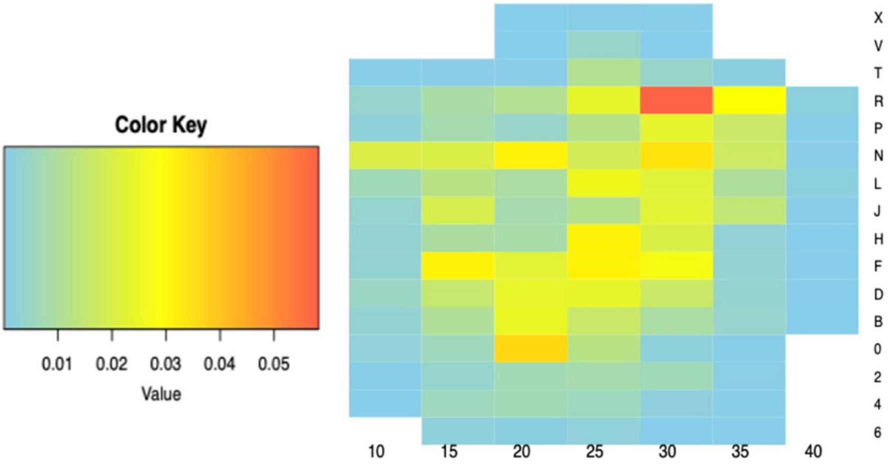

Fig. 12 Heat map of focal activity scans for the Waibira community of chimpanzees in the Budongo Forest, Western Uganda, 2015–2021. White blocks are regions where the group was never reported

individuals to access *A. boonei* bark cannot easily be explained by availability of this species, as *A. boonei* occurred along all transects in both the Sonso and Waibira home ranges (Fig. S6). Overall, *A. boonei* comprised 1% of the total forest composition in both communities. This availability, however, may not be true for *C. patens,* which was absent from Sonso transects, suggesting relative scarcity in at least some regions of the home range.

In Waibira, *C. alexandri* bark-feeding events represented 35% (n = 72) of all bark-feeding events in the long-term data. Most of these events occurred in block 30-R, the most frequented block in the home range (Fig. S5). Our transects suggest that this species-level pattern may be explained by availability, as *C. alexandri* is

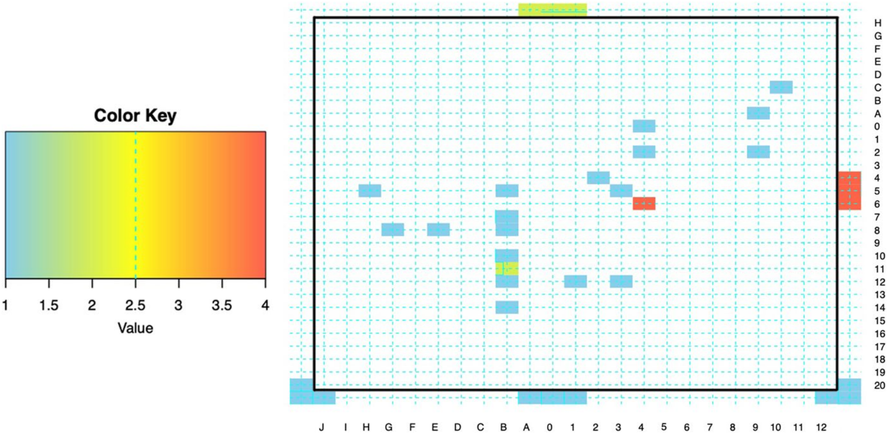

Fig. 13 Cleistopholis patens bark-feeding events by chimpanzees of the Sonso community in the Budongo Forest, Western Uganda, 2008–2021. Area within the black lines represents the Sonso community grid-system. Colored blocks outside of the black lines represent off-grid events

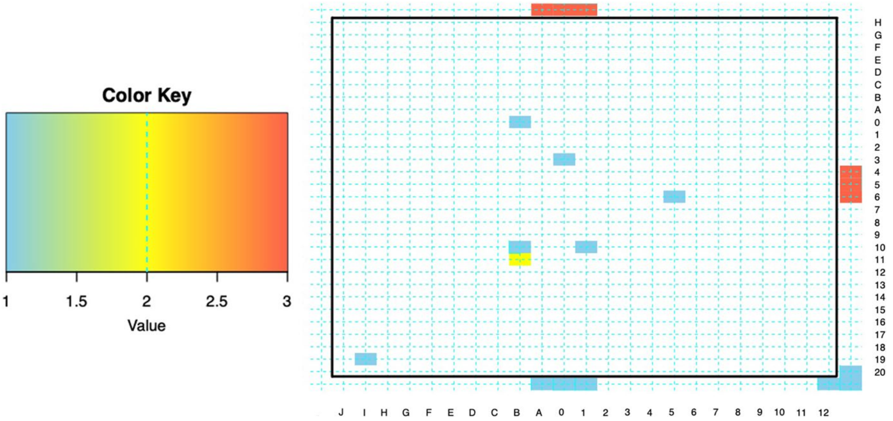

Fig. 14 Alstonia boonei bark-feeding events by chimpanzees of the Sonso community in the Budongo Forest, Western Uganda, 2008–2021. Area within the black lines represents the Sonso community grid-system. Colored blocks outside of the black lines represent off-grid events

the fourth most abundant species within Waibira's grid system, comprising ~ 6% of the community's forest composition. The generalizability of this pattern is, however, challenged by the finding that *C. alexandri* also comprises ~ 5% of the forest composition in Sonso's grid-system, despite only being targeted in 7% of Sonso bark-feeding events.

Direct Observations of Bark Ingestion Events Outside the Core Area

During the study, we directly observed individuals bark-feeding far from core area blocks, both at the edge of the grid system and in other community home ranges. In Sonso, we observed three individuals ingesting bark of *F. exasperata* at the eastern Sonso-Waibira border (block 9–4) while on a group-wide patrol, before immediately traveling into Waibira with the rest of the group. In a previously described bark-feeding event, two Sonso males traveled to the periphery of Sonso's grid (block 9-A), to exploit the bark of *S. myrtina,* despite nearby calls from Waibira. We also observed a subadult male in Waibira feed on bark from a *C. millenii* buttress in block 30-F, immediately before traveling off-grid east with his group.

Discussion

Using data from two communities of Eastern chimpanzees, we found that several tree species targeted for bark-feeding fail to meet one or more of the predictions of the fallback food hypothesis. This pattern suggests the presence of multiple, non-mutually exclusive adaptive functions for this behavior. In contrast to Nishida's findings from Mahale (Nishida, 1976), bark-feeding in Budongo does not universally increase during periods of food scarcity across all tree species, failing to support **Prediction 1** of the fallback food hypothesis. While bark-feeding on certain species (*C. alexandri, D. kirkii,* and *B. papyrifera)* peaked during periods of staple fruit scarcity, bark-feeding on others (*A. boonei, C. patens, C. millenii*) peaked instead during periods of staple fruit abundance. For most tree species, bark-feeding seasonality was not significantly correlated with the seasonality of food scarcity. Only *C. alexandri* bark-feeding showed a significant negative correlation with ripe fruit availability, making it a possible fallback food. Given that *C. alexandri* was the most frequently targeted species for bark-feeding in Budongo, its prevalence may have distorted the seasonality pattern exhibited when all bark-feeding events were combined, highlighting the importance of species-specific investigations. A similar bias may have impacted seasonal patterns of bark-feeding detected at other sites (Nishida, 1976). In this study, as the paired data points in our correlation analysis were collected over different sample periods, we operate under the assumption that seasonal food abundance is relatively consistent across years in the bark-feeding dataset. This may mean that shifts in fruit availability for years when FAI data is unavailable might not be fully captured in this study.

Why do chimpanzees consume the bark of certain tree species during periods of staple fruit abundance? The heightened frequency of bark-feeding on certain species during periods of relative fruit abundance in both wet and dry seasons implies that rainfall or temperature may not be the primary drivers of this behavior. Furthermore, if chimpanzees preferentially target the barks of individual trees which have been nutritionally enhanced by developmental stress, as predicted by the stressed-tree hypothesis, bark-feeding would still likely increase during periods of staple fruit scarcity—when nutritionally-rich resources are required. Alternatively, if these barks were of high enough quality, we would expect to see individuals feeding on the bark of stressed trees consistently throughout the year.

Our seasonal patterns of bark-feeding at the species level may be compatible with the essential nutrient and mineral hypothesis, as some barks could seasonally provide nutrients and minerals that are difficult to access during periods of the year, regardless of staple fruit abundance. To test this, nutritional and mineral analyses should be conducted on the bark of each targeted tree species, using standardized methods across the year. While we did not assess water content of bark for each tree species (Klich, 2017), bark-feeding most commonly occurred in October, the month with the highest average rainfall. Water acquisition, therefore, is unlikely to drive this behavior.

The seasonality of bark-feeding on several tree species in this study does align with the self-medication hypothesis. Bark-feeding is most frequent during the wet season, or periods of seasonal transition, which correspond with increases in internal parasite load associated with wet or low-temperature conditions (Huffman, 1997; Kaur *et al.*, 2008). Of these species, *C. patens* and *A. boonei* warrant particular attention, as chimpanzees targeted their barks most in February, when ripe fruit was most abundant. In the last few years, severe respiratory infections have repeatedly occurred in February–March at Budongo (C. Hobaiter, personal communication), suggesting a possible relationship between bark-feeding on these species and the presence of seasonal viral infections. The ingestion of these barks could, therefore, be an adaptive self-medicative behavior for therapeutically or prophylactically combatting illness during periods of increased susceptibility.

Our findings also failed to support **Prediction 2** of the fallback food hypothesis, which stated that the quantity of bark targeted for bark-feeding should be relatively consistent across tree species. When we compared quantities of bark targeted across tree species, we identified differences on a tree-species level, not only in quantities targeted but also in the techniques used for exploitation. In addition to the use of stripping and peeling techniques (Lapuente *et al.*, 2020), we identified the presence of trunk/buttress biting amongst the Budongo chimpanzees. Specifically, we found that these communities both exploit several tree species in quantities likely too small to justify the energetic and temporal costs of exploitation.

Why do chimpanzees expend energy ingesting bark in small quantities? Species-level nutritional or mineralogical differences may affect the quantity of bark targeted by consumers, supporting the essential nutrient and mineral hypothesis. If this were the sole driver, we would expect to find bark removal in small quantities only if the species possessed high concentrations of the targeted compound, or if these compounds were able to fulfill dietary requirements in small amounts. Further research to assess the nutritional and mineral content of bark across all targeted species will refine our understanding of these findings.

In accordance with the self-medication hypothesis, chimpanzees may also selectively target bark quantities based on the presence and density of medicinal PSMs. While PSMs can negatively impact the wellbeing of healthy individuals if ingested in large amounts (Forbey *et al.*, 2009), in appropriate quantities, some species may provide medicinal benefits to the consumer. If so, individuals targeting bioactive bark material must do so at just the right dose—a Goldilocks context in which they need sufficient material to attain pharmacological benefits while avoiding toxic side effects. The bark of several species ingested by chimpanzees (e.g., *A. boonei* and *A. toxicaria*) are traditionally considered toxic by people living in villages surrounding Budongo but are also commonly used in small doses as medicine (E. Freymann, unpublished data). Further support for the self-medication hypothesis comes from taste tests conducted on barks mentioned in this study. Species with the largest quantities of targeted bark (*F. mucuso, F. exasperata, F. variifolia*) had a sweet or neutral flavor, while species with the lowest quantities of targeted bark (*A. boonei, A. zygia, A. glaberrima)* were bitter in taste. Bitterness is a commonly cited proxy for PSM density and pharmacological activity (Behrens *et al.*, 2018; Dragoș *et al.*, 2022; Ntie-Kang, 2019). To further investigate the self-medication hypothesis, systematic bioactivity testing should be conducted on selected species to determine the pharmacological properties and toxicity levels at targeted quantities.

There are limitations to our use of bark strip/bite size as a measure of material ingested. Most obviously, morphological factors such as bark type, thickness, or propensity to tear in intact strips, may influence techniques needed to exploit the bark, affecting targeted quantities. However, if morphological characteristics alone determine the quantities of bark exploited across tree species, assuming equal nutritional, mineral, and medicinal benefits, we might expect bark types that are harder to strip to be avoided in favor of those that are easier to exploit. This pattern would be especially pronounced if the easier-to-exploit bark types are abundant in the home range. As the Budongo chimpanzees appear to target hard-to-strip barks such as *A. boonei*, we suggest that differences in targeted compounds across tree species must be an underlying reason for species-level variation. Further investigation, however, is needed to assess how accurately bark strip/bite size reflects the actual quantity of consumed compounds. We also encourage field studies on the technical characteristics of chimpanzee bark removal and on indirect traces left after use of different techniques. Such data will be important for ensuring cross-site replicability.

Contrary to **Prediction 3**, direct observations of bark-feeding reveal that some tree barks are prioritized over high-quality resources. Our observations of individuals prioritizing certain barks over staple fruits are noteworthy given the relatively energy-intensive processing techniques required for consuming bark as compared to fruit. The case of a Sonso juvenile favoring *A. boonei* bark over a protein and fat rich resource like meat is also notable. These observations collectively suggests that bark is likely not targeted solely for calories or proteins, challenging assumptions underlying both the fallback food hypothesis and the stressed-tree hypothesis.

Why do chimpanzees occasionally prioritize bark over other valuable resources? Our observations suggest the adaptive function of bark-feeding is not always nutritionally related. Rather, selected barks likely provide chimpanzees with other essential mineral or medicinal benefits that cannot be found in meat or fruits.

Contrary to **Prediction 4**, Sonso individuals frequently ventured far beyond their core area to ingest bark. 21% of all Sonso bark ingestion events occurred off-grid, despite the availability of targeted species within the community's wider home range and core area. This pattern was particularly pronounced for specific species like *C. patens* and *A. boonei*. The significance of this finding is heightened when considering the small quantities of *A. boonei* exploited per bout (µ15.8 cm). It seems implausible that the nutritional benefits of ingesting bite-sized quantities of *A. boonei* bark outweigh associated travel costs or justify the risk of intergroup encounters, especially when staple fruits are seasonally abundant within the safety of the core area. This finding further challenges the generalizability of the fallback food hypothesis in explaining bark-feeding across all tree species, underscoring the need for a species-by-species exploration of alternative hypotheses.

In Waibira, bark-feeding events did not follow the same spatial pattern, with most events occurring in frequently visited core-area blocks. While our initial results suggest that Waibira group members opportunistically target tree species (e.g., *C. alexandri*) based on species abundance in frequented blocks, we cannot exclude the possibility that the group frequents these blocks *because* of the abundance of preferred bark species. Another possibility is that off-grid bark-feeding events may be underreported in Waibira as dense thickets and valleys along grid boundary areas make focal follows more difficult.

Habitat types may also impact tree species availability and growth. For example, *A. boonei* and *C. patens* both prefer wet tropical biomes typically found along rivers or in swamps (POWO, 2023). While this might suggest that Sonso individuals travel to specific habitats in search of these species, transect data revealed that *A. boonei* trees are consistently distributed throughout Sonso's core area, spanning multiple habitat types and elevations. Despite *A. boonei* potentially growing at higher densities in wet forest regions, accessibility extends to dry and central regions within the community's home range, and near to core areas. The distribution of *C. patens* is less established as it was unreported along Sonso transects. Nevertheless, it remains to be established whether chimpanzees show a preference within tree species for specific trees, or trees that grow in specific habitats.

Why do Sonso chimpanzees exhibit a disproportionate tendency to bark-feed on certain species far from their core areas? The essential nutrient and mineral hypothesis may explain bark-feeding spatial patterns for some tree species. Specific landscapes or substrates may yield plants with increased concentrations of certain minerals (Reynolds *et al.*, 2009), impacting primate ranging patterns. For example, mountain gorillas (*gorilla beringei*) in Rwanda, travel to far subalpine and alpine zones to access two plant species with sodium-rich piths (Grueter *et al.*, 2018). The same study found that neighboring gorilla communities risk ranging in human-populated areas to access sodium-rich eucalyptus bark (*Eucalyptus* sp.).

According to the stressed-tree hypothesis, a tree's life-history, including habitat type and the substrate in which it grows, may alter the chemical composition of its bark (White, 2019). Sonso chimpanzees, therefore, may also travel extended distances to selectively feed on individual trees which have been subjected to certain environmental conditions that are rare or absent in their core areas. For example, in the Sonso community, on-grid bark-feeding events involving *A. boonei* and *C. patens* were highly concentrated in block B-11, designated as a swamp region. Clay soil, characteristic of swamp habitats, is relatively rare in Sonso's home range. While the stressed-tree hypothesis specifically contends that ecological stress, such as substrate increases trees' protein production (White, 2019), it is possible that it also promotes increased production of medicinal PSMs (e.g., Ramakrishna & Ravishankar, 2011; Selmar, 2008; Selmar & Kleinwächter, 2013) enhancing the bark's medicinal value. If this is the case, the spatial pattern of bark-feeding could also be explained by the self-medication hypothesis.

To further investigate the spatial patterns of bark-feeding, it is essential to compare the nutritional, mineralogical, and pharmacological composition of samples collected from diverse habitat-types. Future studies should also seek to determine whether forays off-grid are specifically undertaken for bark-feeding or if this behavior aligns opportunistically with other activities (e.g., boundary patrols or exploitation of other resources).

Overall, our study identified several tree species which fail to meet one or more of the above predictions of the fallback food hypothesis. These include *A. glaberrima*, *A. zygia*, *C. millenii*, *F. saussureana, F. sur*, *S. myrtina*, *C. sylvaticus*, *C. patens*, and *A. boonei*. We propose that bark-feeding on *A. boonei*, which fails to meet all predictions of the fallback food hypothesis, can be best explained by the self-medication hypothesis. This proposition is supported by several in vitro and in vivo studies, reviewed by Adotey *et al.*, (2012), who reported strong pharmacological activity in *A. boonei* bark. This species is also known to have widespread ethnomedicinal uses across East Africa, traditionally taken to treat bacterial infections, gastro-intestinal issues, malaria, snake bites, asthma, and dizziness (Adotey *et al.*, 2012; Burkill *et* *al.*, 1995; Kokwaro, 2009). However, identifying the specific pathogens or ailments driving the ingestion of this species by Budongo chimpanzees requires further study.

Chimpanzee bark-feeding behaviors may offer valuable insight into the role bark and cambium played in early hominin diets. With rapid advancements in zooarchaeological, paleoanthropological, and palaeobotanical methods, we can now identify bark removal traces as far back as the early Holocene (Edvardsson *et al.*, 2021). Advancements in morphometric and machine learning methodologies, as highlighted by Luncz *et al.*, (2022), also could enable the identification of specific bark exploitation techniques in the fossil record. Further investigation into the pharmacological properties of barks consumed by present-day chimpanzees may also provide insights into the potential use of medicinal plants by our hominin ancestors. However, our discoveries underscore the need to exercise caution when interpreting early-hominin bark-feeding behaviors in the fossil record. Based on our results from two chimpanzee communities—and reports from across other primate sites and species—it is likely that our ancestors relied on bark for a variety of reasons, targeting certain barks in specific seasons, quantities, and locations.

Conclusions

We conducted a comprehensive examination of bark and cambium's role in the chimpanzee diet in Uganda's Budongo Forest. Our findings challenge the hypothesis that tree bark, irrespective of species, is a generalized fallback food for free-ranging chimpanzees. Instead, we advocate for a species-specific approach when evaluating the adaptive function of bark-feeding and suggest that this could be further enhanced by investigating differences in bark-feeding between individual trees or across different habitats. More generally we propose a shift in how primatologists assess the adaptive function of certain dietary behaviors. Rather than grouping food items based on plant part or processing technique, we stress the importance of investigating these behaviors at a species level, considering taxonomic, morphologic, pharmacologic, and life-history characteristics of the species consumed. Further exploring the adaptive function of bark-feeding will be crucial for the survival of our primate relatives. As the climate warms and once-common trees grow scarce or are put under ecological stress, a better understanding of how and why chimpanzees exploit the trees in their habitats could inform conservation strategies. We, therefore, strongly encourage collaborations with conservation and government agencies to ensure tree species used for bark-feeding are protected and remain available in chimpanzee home ranges.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10764-024-00445-3.

Acknowledgements We are grateful to all the field colleagues and staff working with the Sonso and Waibira communities, including Chandia Bosco, Monday Mbotella Gideon, Adue Sam, Asua Jackson, Steven Mugisha, Atayo Gideon, and Kizza Vincent who provided invaluable instruction and guidance in the field. We would also like to thank Moses Businge, leader of the phenology team at BCFS, for assisting with forest transects and tree identification. We are also thankful to the BCFS management and the other researchers working at the site for their support, including David Eryenyu who facilitated the collection of FAI data, and Vernon Reynolds who founded the field station. We would also like to thank the Royal Zoological Society of Scotland which provides core funding that keeps the station operational, and Uganda Wildlife Authority and Uganda National Council for Science and Technology for granting permission to work in the country. Lastly, we would like to thank Arran Davis and Sophie Berdugo for their assistance with data visualization, Derry Taylor for his support during data collection, and the reviewers and editors from IJP who offered important insight and feedback on the manuscript. EF was funded by Keble College, Oxford, the Clarendon Fund, the British Institute of Eastern Africa, and the Explorers Club. CH and GB received funding from the European Union's 8th Framework Programme, Horizon 2020, under grant agreement no. 802719.

Author's contribution The study was conceptualized, developed, designed, and instituted by EF. Data were collected during the study period by EF with support from GM, ERY, and DS. Long-term site data were collected by field staff at the research station between 2008–2021. Data analysis was conducted by EF, with assistance on spatial analysis from GB, and on the Pearson correlation test from SO. The writing and preparation of the original draft was done by EF. The manuscript was reviewed and edited by EF, SC, MAH, CH, GB, and KZ. Funding through research grants was acquired by EF. EF was supervised by SC, MAH, and CH. All authors read and approved the final manuscript.

Data Availability Bark-feeding data used in this study are available on GitHub (https://github.com/Wild-Minds/Bark-feeding). Further video data are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

Inclusion and Diversity Statement Several authors of this study are from the geographical location where the research was undertaken and were actively involved in the study's conception, design, data collection, analysis, and/or interpretation of the findings.

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