

RESEARCH ARTICLE

To drum or not to drum: Selectivity in tree buttress drumming by chimpanzees (*Pan troglodytes verus*) in the Nimba Mountains, Guinea

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Abstract

Chimpanzees live in fission-fusion social organizations, which means that party size, composition, and spatial distribution are constantly in flux. Moreover, chimpanzees use a remarkably extensive repertoire of vocal and nonvocal forms of communication, thought to help convey information in such a socially and spatially dynamic setting. One proposed form of nonvocal communication in chimpanzees is buttress drumming, in which an individual hits a tree buttress with its hands and/or feet, thereby producing a low-frequency acoustic signal. It is often presumed that this behavior functions to communicate over long distances and is, therefore, goal-oriented. If so, we would expect chimpanzees to exhibit selectivity in the choice of trees and buttresses used in buttress drumming. Selectivity is a key attribute of many other goal-directed chimpanzee behaviors, such as nut-cracking and ant dipping. Here, we investigate whether chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea, West Africa, show selectivity in their buttress drumming behavior. Our results indicate that Seringbara chimpanzees are more likely to use larger trees and select buttresses that are thinner and have a greater surface area. These findings imply that tree buttress drumming is not a random act, but rather goal-oriented and requires knowledge of suitable trees and buttresses. Our results also point to long-distance communication as a probable function of buttress drumming based on selectivity for buttress characteristics likely to impact sound propagation. This study provides a foundation for further assessing the cognitive underpinnings and functions of buttress drumming in wild chimpanzees.

KEYWORDS

behavioral selectivity, buttress drumming, long-distance communication, western chimpanzees

Abbreviations: AST, accumulative stone throwing; CI, confidence interval; DBH, diameter at breast height; GLMM, generalized linear mixed-effects model; Mt. Nimba SNR, Mount Nimba Strict Nature Reserve; p , p -value; R^2_c , conditional r^2 ; χ^2_{LRT} , χ^2 likelihood ratio test.

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1 | INTRODUCTION

Wild chimpanzees have a fission-fusion social organization (Aureli et al., 2008; Goodall, 1968; Mitani et al., 2002; Nishida, 1968), and live in social groups called “communities,” which range in membership from 7 (Bossou, Guinea; Fitzgerald et al., 2018) to approximately 200 individuals (Ngogo, Kibale, Uganda; Langergraber et al., 2017). Within communities, chimpanzees form temporary subgroups, or parties, of varying size depending on resource availability, mating opportunities, and predation pressure (Anderson et al., 2002; Boesch, 1991a; Chapman et al., 1995; Itoh & Nishida, 2007; Lehmann & Boesch, 2004; Newton-Fisher et al., 2000). Party size, composition, and spatial distribution are, thus, constantly in flux. A vast repertoire of vocal and nonvocal forms of communication, ranging from pant-hoots and grunts to body gestures (Hobaiter & Byrne, 2017; Slocombe &

Zuberbühler, 2011), allow chimpanzees to convey information in such a socially and spatially dynamic setting.

Chimpanzees drum (hit) on tree buttresses, large above-ground roots (Figure 1), with hands and/or feet (hereafter buttress drumming) to produce acoustic signals (Goodall, 1968, 1986; Reynolds & Reynolds, 1965; see <https://youtu.be/rUWncJMlaZY> and <https://youtu.be/U5BpFAL5GNo> for drumming videos). These low-frequency drum sounds, that oftentimes occur in sequence with pant hoot vocalizations, are presumed to play a role in long-distance communication between separated individuals and are often associated with travel (Arcadi et al., 1998, 2004; Arcadi & Wallauer, 2013; Babiszewska et al., 2015; Boesch, 1991b). Yet, the function of buttress drumming is not fully understood. In addition to long-distance communication, it has also been referred to as a dominant display behavior (Goodall, 1968, 1986; Nishida et al., 1999). Buttress drumming occurs in all studied wild chimpanzee populations and is



FIGURE 1 Four buttressed trees in the Nimba Mountains, Guinea. The top two photos (a and b) are pictures of drum trees taken by the research team. Photo (a) is of *Terminalia superba* and photo (b) is of *Parkia bicolor*. The bottom photos (c and d) are still shots from motion-triggered camera trap videos after chimpanzees drummed. Photo (c and d) are of *Piptadenia africana*. (Photos © M. Fitzgerald). Visit <https://youtu.be/rUWncJMlaZY> and <https://youtu.be/U5BpFAL5GNo> for videos of (c and d) (respectively)

considered a chimpanzee universal (Bain et al., 2021; McGrew, 2013). As it is one of only a few forms of chimpanzee communication that depends upon a substrate to convey information (see also accumulative stone throwing [AST], Kalan et al., 2019), buttress drumming in semihabituated communities lends itself well to exploring behavioral selectivity in wild chimpanzee communication.

Selectivity is an attribute of goal-directed behavior, whereby an animal makes choices to achieve a particular outcome (Seed & Byrne, 2010). Chimpanzees are renowned for their use of tools in various contexts and have been found to select tools with functional characteristics needed for a specific task. For instance, chimpanzees prefer to use specific plant species to make dipping tools when preying on aggressive army ants (Koops et al., 2015). Selectivity for tool material and tool characteristics is common across a wide range of chimpanzee tool use behaviors (termite fishing: Almeida-Warren et al., 2017; Sanz & Morgan, 2007; nut cracking: Boesch et al., 2017; Carvalho et al., 2009; Sirianni et al., 2015; ant dipping: Koops et al., 2015; and honey extraction: Boesch et al., 2009). Tool selectivity is not limited to chimpanzees but occurs in other primate species, as well as in other taxa. Bearded capuchin monkeys (*Cebus libidinosus*) select stones of certain material and weight to crack open nuts (Schrauf et al., 2008; Visalberghi et al., 2009, 2007). New Caledonian crows (*Corvus moneduloides*) choose specific plant species from which to make hooked stick tools (Klump et al., 2019). Moreover, selectivity extends beyond tool use to other types of behaviors. Chimpanzees, along with the other nonhuman great apes, make sleeping platforms, or nests, and exhibit preferences for specific tree species, tree characteristics, and nest sites in nest building (chimpanzees: Koops et al., 2012; Sanz, Morgan, Strindberg, et al., 2007; Stanford & O'Malley, 2008; gorillas: Mehlman & Doran, 2002; and bonobos: Mulavwa et al., 2010). By investigating if, and how, selectivity exists in a certain type of behavior, researchers are better able to elucidate the function or goal of that behavior.

Compared to other chimpanzee behaviors, and particularly compared to other long-distance signals, such as the pant-hoot, buttress drumming has been relatively understudied. A handful of studies have reported the acoustic characteristics and social factors affecting drumming behavior (Arcadi et al., 1998, 2004; Arcadi & Wallauer, 2013; Babiszewska et al., 2015), but none so far have looked at the characteristics of the drumming tree itself. Related research has reported that chimpanzees at some study sites throw rocks at trees, referred to as accumulative stone-throwing, or AST (Kühl et al., 2016). Kalan et al. (2019) measured the spectral centroid, attack times, and damping coefficient of the sound produced when a rock impacts a tree. Impact sounds from AST trees were found to be more resonant than non-AST trees, a quality well-suited for propagating over long distances. Hence, trees used in stone-throwing have acoustic qualities suited for long-distance communication, one of the hypothesized functions of AST.

Here, we investigate whether chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea, West Africa, show selectivity in buttress drumming. If buttress drumming is goal-directed, namely to communicate over long distances, we predict

that chimpanzees will select trees that are larger and have more buttresses. Moreover, we hypothesize that used buttresses will have larger surface areas (i.e., more area upon which a chimpanzee can drum) and used buttresses will be thinner, as they are more pliant and conducive to producing resonant sounds that would persist in the environment longer when impacted (Kalan et al., 2019). The presence or absence of selectivity will allow us to make inferences about the function of buttress drumming.

2 | METHODS

2.1 | Ethics statement

All research adhered to the American Society of Primatologists' principles for the ethical treatment of nonhuman primates. The Direction Nationale de la Recherche Scientifique in Guinea permitted data collection on the Seringbara chimpanzees in the Nimba Mountains and research adhered to all legal requirements in Guinea.

2.2 | Study site

The Mount Nimba Strict Nature Reserve (Mt. Nimba SNR) is classified as a UNESCO World Heritage Site in Danger (World Heritage Committee, 2017). It encompasses most of the Nimba Mountain range in Guinea and much of the range in Côte d'Ivoire. The range, in its entirety, forms a natural border between Guinea, Côte d'Ivoire, and Liberia. Covering approximately 175 km², the reserve is dominated by wet, montane forests with diverse topographical features including rocky peaks, rough cliffs, steep river valleys, and high-altitude savannahs (Koops, 2011a). It is home to a variety of flora and fauna, including the Critically Endangered western chimpanzee (*Pan troglodytes verus*) (World Heritage Committee, 2017).

The Seringbara study site (N07.634°, W08.425°), spanning about 30 km², is located on the Guinean side of the Mt. Nimba SNR (Figure 2). The site is largely composed of dense, primary tropical forests, with elevations ranging from 595 to 1511 m. The climate is characterized by a rainy season from February to October and a dry season (i.e., monthly rainfall <70 mm) lasting from November to February (Koops et al., 2012).

We studied two communities of chimpanzees (i.e., Gahtoy and Tongbongbon), known as the Seringbara communities (Fitzgerald et al., 2018; Koops, 2011b; van Leeuwen et al., 2020). The Seringbara communities have been the focus of research and conservation efforts since 2003 (Koops, 2011b) with intermittent ecological studies and surveys reaching back to 1996 (Humble & Matsuzawa, 2001, 2004; Matsuzawa & Yamakoshi, 1996). Despite many years of study, the chimpanzees remain mostly unhabituated to humans as a result of the extremely rugged and mountainous terrain (Koops, 2011b; Koops & Matsuzawa, 2006).

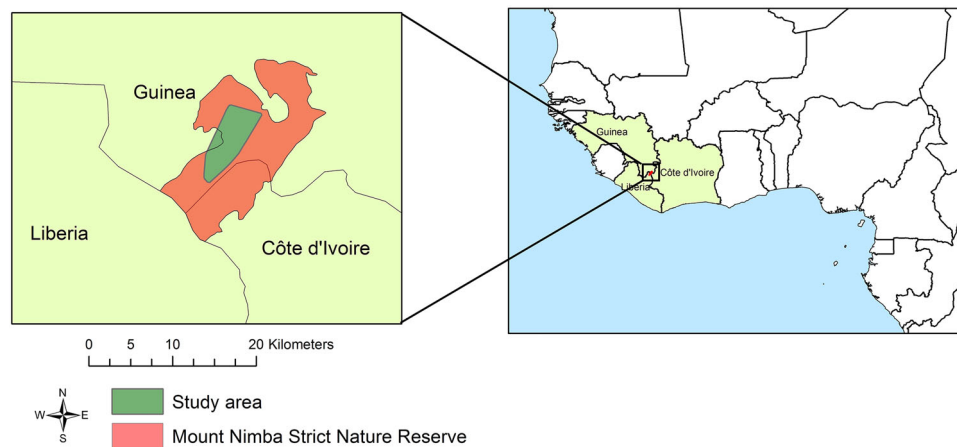


FIGURE 2 Location of the study area



FIGURE 3 Drumming traces (dirt residue and noticeable wearing of buttress surfaces) are present on two drum trees.

2.3 | Data collection

From January 2012 to April 2014 (27 months total), research teams surveyed the study area, collecting ecological and behavioral data on the Seringbara chimpanzee communities. Researchers maintained a nearly constant presence in the forest during this period, missing data collection for only 1–2 days a month. Data collection included tracking and observing chimpanzees, as well as monitoring a grid of motion-triggered camera traps. Although direct observations of drumming bouts were extremely rare, we were able to identify trees that were drummed on (hereafter drum trees) by the traces left on the buttresses, namely dirt residue and the noticeable wearing of the buttress surface (Figure 3). We are not aware of any other species that would leave similar traces on tree buttresses. We validated our use of these traces to identify drum trees by placing motion-triggered camera traps (Bushnell Trophy Cam) at four suspected drum trees. At these trees, the place of drumming on the buttress was confirmed using motion-triggered camera videos. We also confirmed that similar traces were left on drum tree buttresses by fully habituated chimpanzees in Bossou, Guinea (approximately 6 km from the Seringbara study site). We, therefore, consider the occurrence of use traces on buttresses to be an accurate indication that chimpanzees drummed on a given tree and buttress.

We collected the following data for each drum tree ($N = 19$):

1. Diameter at breast height, DBH (cm), measured around the trunk above buttresses with a DBH tape measure (in some instances this was above breast height).
2. The number of individual buttresses per tree.

For each tree buttress, we collected the following data ($N = 348$):

1. Surface area (m^2), measurements of the height, and base length of a buttress were taken to calculate the surface area of one buttress side. Measured with a tape measure. Although this measurement is not exact, it was standardized and provides an estimate of buttress surface area. In some cases, a buttress may have a smaller buttress protruding from it. If so, the smaller buttress was measured as a separate buttress and its height was measured from the ground to the point of entry into the larger buttress. Additionally, buttresses that were too small to allow researchers to hit with an open palm (approximately 20 cm^2) were deemed unusable and neither measured nor recorded as buttress.
2. Thickness (cm), three measurements were taken with a tape measure along the ridge of the buttress (near the top, middle, and bottom of the buttress) and then averaged. This was consistent across all measured trees.
3. Used for drumming or not (0/1). Hereafter referred to as used or unused buttresses.

For each drum tree ($N = 19$), we set up a 20 m \times 20 m vegetation plot with the drum tree at the center of the plot. Within these plots, we recorded the DBH for all trees with a DBH ≥ 10 cm. If any of these trees had buttresses, but lacked evidence of drumming, they were measured as “potential drum trees” and used as control trees ($N = 51$). For the data analysis, we used only those plots in which we measured at least two buttressed trees. Thus, although we initially located 24 drum trees, we ended up including only 19 drum trees across 18 plots. We compared measurements of “drum trees” to “control trees” and “used buttresses” to “unused buttresses,” as discussed below.

2.4 | Data analysis

To investigate whether the probability of a tree being selected for drumming (yes/no) can be understood in terms of its DBH and number of buttresses, we fitted a binomial generalized linear mixed-effects model (GLMM) with a logit link function. To account for potential dependencies in these data (due to incorporating observations on multiple trees within the same plot), we included plot ID as a random effect.

Second, we fitted another binomial GLMM to evaluate whether a buttress was used for drumming or not and considered the potential effects of thickness and surface area. Tree ID nested within plot ID was included as the random term in this model to control for the dependent data structure.

All analyses were conducted in R 4.0.3 (R Core Team, 2020) using the R “lme4,” “car,” and “MuMIn” packages (Barton, 2020; Bates et al., 2015; Fox & Weisberg, 2019). Overall model significance for both GLMMs was calculated by means of a likelihood-ratio test comparing the two full models to their respective null models, consisting of fixed and random intercepts only. Moreover, models incorporating interaction terms were considered as well, but since these did not result in an appreciably improved model performance ($\Delta AICc = -2.034$, and $\Delta AICc = 1.900$, respectively), we report findings from the “main effects only” models below. See Supporting Information for the R script and data.

3 | RESULTS

Our first binomial GLMM ($N_{\text{observations}} = 70$ from 18 plots; χ^2 likelihood ratio test [$\chi^2_{\text{LRT}} = 26.105$, p -value [$p] < 0.001$, conditional R^2 [$R^2_c] = 0.595$) revealed that the odds of a tree being selected for drumming increased with both its DBH (odds ratio = 1.019, 95% confidence interval [CI] = 0.993–1.045, $p = 0.155$), and its number of buttresses (odds ratio = 1.677, 95% CI = 1.127–2.496, $p = 0.011$), although the former failed to achieve statistical significance (Figure 4). Thus, we can say that, on average, the odds of a tree being selected for drumming increased about 68% with every additional buttress it had.

The second GLMM ($N_{\text{observations}} = 348$, stemming from 70 trees within 18 plots; $\chi^2_{\text{LRT}} = 15.243$, $p < 0.001$, $R^2_c = 0.371$), showed that the odds of a buttress being used for drumming decreased with its

thickness (odds ratio = 0.835, 95% CI = 0.709–0.982, $p = 0.030$), yet increased with its surface area (odds ratio = 1.177, 95% CI = 1.053–1.315, $p = 0.004$; Figure 4). In other words, on average, an increase in thickness by 1 cm was associated with a 17% decrease, while an increase in surface area of 1 m² was associated with an 18% increase in the odds of a buttress being selected for drumming.

4 | DISCUSSION

Our findings indicate that chimpanzees show selectivity in buttress drumming. This implies that drumming is not a random act, but rather is goal-oriented and requires knowledge of suitable trees and buttresses. In particular, the Seringbara chimpanzees are selective for tree and buttress characteristics. Drum trees were found to have a larger DBH compared to nearby control trees (i.e., trees with buttresses not used for drumming). Likewise, drum trees had more buttresses than control trees. From these characteristics, we can generalize to say that chimpanzees prefer to use larger trees for drumming. This makes intuitive sense given that buttressed trees generally are larger than many non-buttressed trees and given that having more buttresses to choose from may increase the likelihood that a tree is drummed upon.

Additionally, Seringbara chimpanzees preferred tree buttresses with larger surface areas and thinner width. Although we did not measure acoustic properties of each buttress, such as stiffness or dampening capacity (Roohnia, 2016), we predict that surface area and thickness are important factors influencing a buttress' acoustic (mechanical) properties and the sound signals it is capable of producing when struck. These two measures are further predicted to impact the propagation of the drum sound across a landscape and the extent to which information is communicated. This is analogous to how properties of the batter head and the shape of the shell determine the volume and therefore the sound produced by a snare or bass drum (Yamaha Corporation, 2020). Future research will address exactly how tree and buttress characteristics impact the tree's acoustics and thereby sound propagation. A study on AST by chimpanzees showed that AST trees appear to have acoustic properties that produce sounds better suited for long-distance communication, one of the suspected functions of AST (Kalan et al., 2019). A similar experimental approach could be taken for buttress drumming, although accurately reproducing a chimpanzee drum may be challenging. Nevertheless, chimpanzee selectivity for buttress surface area and thickness indicates that chimpanzees are selecting buttresses with certain qualities that impact long-distance sound propagation, which suggests that long-distance communication is indeed one function of this behavior.

Drumming has long been suggested to be a form of long-distance communication and to play a role in information exchange between spatially separated individuals (Arcadi et al., 1998, 2004; Arcadi & Wallauer, 2013; Babiszewska et al., 2015; Boesch, 1991b). Yet, much of this is anecdotal and based on drums being low-frequency sounds, similar to bass drums. No studies to date have quantitatively shown

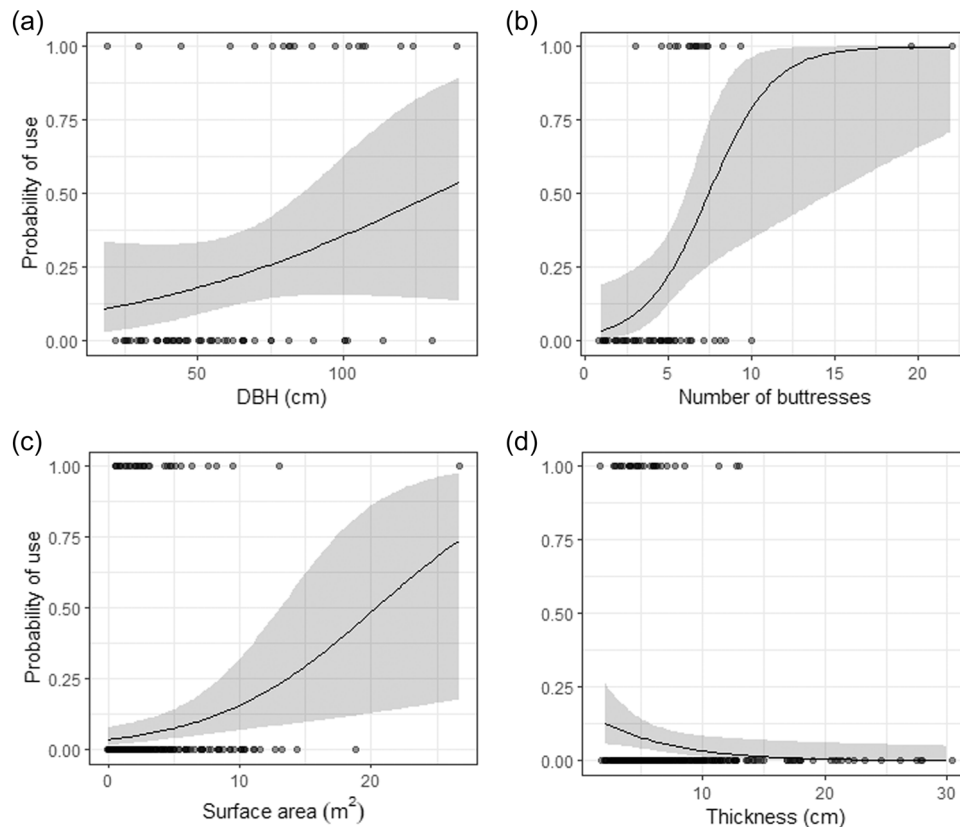


FIGURE 4 Model prediction plots showing the relationship between tree (plots a and b) and buttress level (plots c and d) variables and the probability of a buttressed tree being used for drumming. DBH, diameter at breast height

the extent to which chimpanzee drums propagate in a given landscape. The propagation of sound is dependent on many factors, such as ambient noise, atmospheric conditions, attenuation based on habitat or landscape characteristics, and the sound source (Brown & Waser, 2017; Farina, 2019; Richards & Wiley, 1980; Waser & Brown, 1986; Waser & Waser, 1977). In this study, we focused on understanding aspects of the sound source and the behavioral selectivity exhibited in drumming. Our study provides a foundation for future research assessing the propagation of chimpanzee drum sounds across the landscape and thereby quantitatively addressing whether drumming is an effective long-distance communication modality relative to other forms of chimpanzee communication. Such research could start by investigating the potential selectivity of drumming sites and how location in a rugged, mountainous environment, like the Nimba Mountains, impacts sound propagation. For example, future research could assess whether selected drumming sites are located along ridges, valleys, or slopes, as this would alter the potential propagation of a drum across the landscape.

Studying the complex behavioral repertoire of chimpanzees provides insight into the chimpanzee mind. Selectivity in buttress drumming suggests this behavior is goal-directed and, in particular, our results indicate that one such goal is long-distance communication. Along with the previous studies on buttress drumming (Arcadi et al., 1998, 2004; Arcadi & Wallauer, 2013; Babiszewska et al., 2015; Boesch, 1991b), our

research provides a foundation for further assessing the cognitive underpinnings and functions of buttress drumming.

AUTHOR CONTRIBUTIONS

Maegan Fitzgerald: Conceptualization (equal); formal analysis (lead); investigation (lead); methodology (equal); writing – original draft (lead); and writing – review and editing (lead). **Erik P. Willems:** Formal analysis (supporting); visualization (supporting); and writing – review and editing (supporting). **Aly Gaspard Soumah:** Supervision (supporting) and writing – review and editing (supporting). **Tetsuro Matsuzawa:** Funding acquisition (supporting) and writing – review and editing (supporting). **Kathelijne Koops:** Conceptualization (equal); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (equal); writing – original draft (supporting); and writing – review and editing (supporting).

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information for this article.

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SUPPORTING INFORMATION

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