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Animal behaviour

Chimpanzees use tree species with a resonant timbre for accumulative stone throwing

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Animals use tools for communication relatively rarely compared to tool use for extractive foraging. We investigated the tool-use behaviour accumulative stone throwing (AST) in wild chimpanzees, who regularly throw rocks at trees, producing impact sounds and resulting in the aggregations of rocks. The function of AST remains unknown but appears to be communication-related. We conducted field experiments to test whether impact sounds produced by throwing rocks at trees varied according to the tree's properties. Specifically, we compared impact sounds of AST and non-AST tree species. We measured three acoustic descriptors related to intrinsic timbre quality, and found that AST tree species produced impact sounds that were less damped, with spectral energy concentrated at lower frequencies compared to non-AST tree species. Buttress roots in particular produced timbres with low-frequency energy (low spectral centroid) and slower signal onset (longer attack time). In summary, chimpanzees use tree species capable of producing more resonant sounds for AST compared to other tree species available.

1. Background

Many animals use specially adapted organs to effectively communicate with conspecifics, attract mates and advertise territories [1]. Additionally, some species use flexible behaviours to optimize acoustic signals relative to their environment. For example, frogs will select tree holes [2] and drainage pipes [3] that better resonate their calls. Similarly, tree crickets use leaves as acoustic baffles to increase the intensity of their sounds [4]. Among mammals, many species possess specialized vocal sacs to amplify their calls, such as those found among non-human primates (henceforth 'primates') [5]. One effective behavioural strategy for modifying communication is the use of tools, where tool use is defined as the 'external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool' [6]. Although tool-assisted animal communication is rare relative to tool use for foraging [6–8], pertinent examples include palm cockatoo drumming [9] and orang-utan 'kiss squeaking' with leaves [10].

Among animals, chimpanzees are one of the most adept tool users [7], using sticks, stones and leaves for extractive foraging and communication [7,11–13].

Recently, four wild chimpanzee communities were observed accumulative stone throwing (henceforth 'AST'; [14]) where individuals, usually adult males, habitually (i.e. occurs repeatedly in several individuals [11]) throw rocks at trees resulting in aggregations of rocks at these trees. AST was also suggested to be a cultural tradition [14]. Other examples of primate stone tool use in non-foraging contexts include throwing rocks as a threat to intruders or predators [15–18], and female capuchin monkeys throwing rocks towards males, putatively to elicit copulations [19]. However, chimpanzee AST is unique because the rock is thrown towards an external object, the tree. It has been hypothesized to be a form of communication, an enhanced male display or even for territory marking [14].

To date, all observations of chimpanzee AST have been collected via camera traps where it is difficult to hear whether the impact of the rock being thrown against trees produces a sound [14]. Moreover, in almost all cases, the chimpanzee emits a long-distance vocalization, the pant-hoot, right before throwing the rock [14]. The behaviour is thus reminiscent of the ubiquitous buttress drumming behaviour observed in all wild chimpanzees, which is often also accompanied by a pant-hoot [20]. Consequently, there are redundant auditory signals occurring during chimpanzee AST, making the potential communicative function of this behaviour difficult to disentangle. To investigate one possible function of AST, namely to produce a salient sound, we tested whether chimpanzees use tree species with particular acoustic properties.

Studies on how variation in the sound-production properties of different tree species might affect animal behaviour are lacking despite observations of chimpanzees [20] and palm cockatoos [9] drumming on trees. In comparison, humans fashion a variety of wooden musical instruments whereby the quality of sound for each instrument is dependent upon the intrinsic sound properties of the tree species used, otherwise referred to as 'timbre' [21]. In particular, it has been shown that mechanical properties of wood species such as internal friction, density and the longitudinal modulus of elasticity are important aspects that instrument makers take into account when selecting tree species. For example, the internal friction, which determines the way the sound fades out (characterized as damping factor by acousticians), seems to be the most important characteristic of wood species for constructing xylophones [22].

In this study, we conducted field experiments to record impact sounds produced by throwing rocks at trees, and specifically compared impact sounds produced by tree species used for AST with non-AST tree species (those never used for AST). We predicted that chimpanzee AST tree species produce sounds that have energy concentrated at lower frequencies and a greater resonance since these impact sounds would be optimal for long-distance communication [1,23]. Accordingly, we predicted that chimpanzees use AST tree species that possess the following physical features because they may aid the production of low frequency, high resonating sounds: trees with (i) a large diameter, (ii) buttress roots, and (iii) hollow cavities, formed either by roots merged together or a hollowed out tree trunk.

2. Material and methods

Fieldwork was conducted in Boé, Guinea-Bissau, from February to June 2017 encompassing a 50 km^2 area. Data were collected via 87 km of reconnaissance transects and supplemented with infrared-sensor camera-trap recordings. In total, we found 39 AST sites, defined as a tree with visible wound marks from repeated impact by rocks and the accumulation of rocks at, or inside, the tree [14]. Of these 39 AST sites, 21 had fresh impact signs indicating recent use (figure 1). All AST trees, both with fresh and old impact signs, were only one of seven species (table 1 and *Markhamia tomentosa*). A selection of non-AST tree species were chosen based on their relative abundance as well as similar tree size and bark structure to AST species (see electronic supplementary material).

During field experiments, we aimed to control the properties of rocks (tools), as much as possible, and focused on three tree properties, namely species, size (DBH) and part of the tree impacted (buttress root, hollow cavity or trunk). However, since buttress roots and hollow cavities were only observed on AST tree species, throws targeted at these parts were only possible for AST trees. We used the same experimental design to record multiple simulated chimpanzee throws on 27 trees. An AKG C451-B microphone, used to record percussive sounds, was mounted on a stand at a height of 50 cm, covered with a windshield and connected to a Marantz PMD661 solid-state recorder. All impact sounds were recorded using a sampling rate of 48 kHz with 32 bits s^{-1}. A.K.K. was the sole thrower and impact sounds were produced using standardized rocks (SI1, SI2, SI3). The standardized rocks represented the predominant laterite and the rarer igneous type in the region. Due to SI1 breaking mid-way, SI3 was used thereafter (electronic supplementary material, table S5). We further supplemented experimental throws using presumed chimpanzee stone tools (electronic supplementary material, table S1). Importantly, the main results did not change when including these non-standardized rocks. Throwing force was standardized during experiments using a carefully controlled gesture and every throw was repeated with the same rock, once with the sound recording level set to 4 and again at 3. For details, see electronic supplementary material.

Impact sounds from throws were extracted and sent to the PRISM laboratory for acoustic analyses removing any information about the tree species. Only 125 of the 172 impact sounds recorded were free of clipping or other interference, permitting analyses (electronic supplementary material, table S5). Acoustic analyses were based on algorithms developed by the PRISM laboratory and validated in previous studies [21,22,24]. The analyses identified patterns that reveal acoustic timbre differences between signals generated by impacting one material compared to another [24]. Such patterns can be revealed through audio descriptors that characterize various sound attributes, such as timbre [21,22,25]. We investigated three timbre descriptors known to reflect intrinsic properties of a tree species: (i) the internal friction of the wood species, linked to the way the sounds fade out (*damping coefficient*), (ii) the hardness of the tree at the impact point, linked to the signal onset (*attack time*), and (iii) the modal response of the tree to the impact, linked to the centre of gravity of the frequency spectrum (*spectral centroid*; table 2; electronic supplementary material, figure S1). Note that these descriptors are not a function of the sound recording level (electronic supplementary material).

For statistical analyses, each of the three timbre descriptors served as a response variable in three linear mixed models (LMMs). All models were run in R v. 3.4.3 (R Core Team 2017) using the function 'lmer' of the package lme4 [28]. All models comprised the critical test predictors of whether the tree was an AST tree species (y/n), where on the tree the rock was thrown (trunk, buttress or hollow) and the tree's DBH. LMMs also included multiple control variables including sound recording level, weight of rock and type of rock. Random effects further accounted for repeated observations of impact sounds (i.e.

Figure 1. AST sites and a non-AST tree used in this study: (*a*) screenshot from a camera-trap video of a *C. febrifuga* AST site, (*b*) an *Erythrophleum guineense* non-AST tree species, (*c*) a *Treculia africana* AST site from a camera-trap video, and (*d*) close-up of a *Bombax costatum* AST site where fresh impact points on the rock and tree are visible (circled in yellow). (Online version in colour.)

Table 1. Summary of experiments comparing impact sounds of tree species used for AST and a selection of tree species not used by chimpanzees for AST (non-AST).

	tree species	tree density (trees/km^2)[a]	no. of trees	mean tree size (DBH) ± s.d.[b]	no. of impact sounds analysed
AST tree species	*Bombax costatum*	417	3	68 ± 30 cm	15
	Ceiba pentandra	8.62	2	340 ± 28	8
	Pterocarpus erinaceous	1640	3	66 ± 13	16
	Crossopteryx febrifuga	80.5	3	35 ± 6	31
	Cola cordifolia	167	2	105 ± 24	6
	Treculia africana	0.00	1	60	9
non-AST tree species	*Cordyla pinnata*	621	2	55 ± 7 cm	5
	Erythrophleum guineense	532	2	83 ± 25	8
	Detarium senegalensis	77.6	2	105 ± 35	6
	Parinari excelsa	17.2	1	155	3
	Parkia biglobosa	767	2	72 ± 9	7
	Daniellia oliveri	175	2	100 ± 7	5
	Khaya senegalensis	144	2	95 ± 21	6
overall	13 species	357	27	97 ± 76 cm	125

[a]Calculated from reconnaissance transects totalling 87 km.
[b]DBH is the diameter of the experiment tree(s) measured at breast height (1.2 m high); s.d. is standard deviation.

throws) using the same rock, tree species or same individual tree (details in electronic supplementary material, file S2).

3. Results

The acoustic features of impact sound timbres exhibited significant variation with respect to whether or not the tree was an AST species and the part of the tree impacted by the rock. The other predictor, tree DBH, had no effect on any of the timbre features (electronic supplementary material, tables S2–S4). The absolute damping coefficient was significantly smaller for AST tree species compared to non-AST tree species ($\chi^2 = 13.27$, d.f. = 1, $p < 0.001$, $N = 125$; figure 2*a*), meaning that impact sounds were more resonant for AST tree species

Table 2. Description of the three timbre descriptors used in this study (cf. electronic supplementary material, figure S1) and their relation to the perceived sound or timbre produced and how they reflect intrinsic properties of tree species.

acoustic descriptors	definition	calculation	relation to timbre (sound) properties	relation to wood (tree) species properties
attack time (ms)	characterizes the global onset of the temporal signal, i.e. the increase in the sound energy to its maximum amplitude.	the rising time of the signal envelope (onset portion of the signal) to deploy its energy from 20 to 90% of the maximum amplitude is estimated	correlates with the percussiveness of a sound. Main auditory cue for the distinction between hard and soft impacts [22,24,25]	linked to the nature of the surface of the excitation point, and to the wood density [26]
spectral centroid (Hz)	corresponds to the centre of gravity of the frequency spectrum	$SC = \frac{\sum_k f(k)\lvert\hat{s}(k)\rvert}{\sum_k \lvert\hat{s}(k)\rvert}$, where $\lvert\hat{s}(k)\rvert$ is the modulus of the discrete Fourier transform of the signal and *f(k)* the frequency [25]	correlates with the perceived brightness of the sounds [27]	both linked to the size of the tree and to its modal response to the excitation [22]
damping coefficient	describes the global decay of the temporal signal, i.e. the decrease in the sound energy as a function of time	the temporal envelope of the signal is fitted from its maximum amplitude to the end with an exponential function: $s(t) = Ae^{\alpha t}$ where A is the amplitude. The damping coefficient α is estimated from this function	an essential cue to distinguish one material from another [21,24]	strongly linked to the internal friction of the impacted tree [21,22]

(electronic supplementary material, figure S1). Damping did not differ depending on the part of the tree impacted ($\chi^2 = 2.94$, d.f. = 2, $p = 0.23$, $N = 125$; electronic supplementary material, table S4). For attack time, impacts on buttress roots had longer attack times relative to the trunk or hollow cavities ($\chi^2 = 10.86$, d.f. = 2, $p = 0.004$, $N = 125$; figure 2*c*). However, attack time did not differ significantly between AST tree species and non-AST tree species ($\chi^2 = 2.86$, d.f. = 1, $p = 0.09$, $N = 125$; electronic supplementary material, table S2). The spectral centroid was significantly lower in AST tree species ($\chi^2 = 5.85$, d.f. = 1, $p = 0.02$, $N = 125$; electronic supplementary material, figure S1) and in buttress roots, while hollow cavities and trunks did not differ from one another ($\chi^2 = 9.13$, d.f. = 2, $p = 0.01$, $N = 125$; figure 2*b*,*d*).

4. Discussion

These results show that chimpanzees use AST tree species that produce resonating impact sounds with spectral energy concentrated in the lower frequencies. Buttress roots are also an important AST tree feature because they emit low-frequency impact sounds and have longer attack times, meaning a longer sound duration. However, buttress roots cannot account for all the variation observed since two AST tree species never develop buttresses but instead form hollow cavities (*Crossopteryx febrifuga* and *Markhamia tomentosa*). Moreover, tree species, target of throw and DBH were all tested simultaneously, thereby accounting for the average effect of one while testing the significance of the other.

The longer attack time suggests that buttress roots are softer or more pliant than trunks or hollow cavities. This seems counterintuitive since buttress roots function as mechanical supports or tension elements [29]. However, the function of buttress roots is not well understood, and a single explanation is unlikely to apply to all species since their anatomy demonstrates a large degree of variability due to the trade-off between structural integrity and vascularization [29,30]. The latter predicts roots that should be more pliant, whereas the former suggests a reduction in elasticity. These factors, including age and bark composition, may affect how hard or soft the root or tree is when impacted by a rock. Variation in throw force may also influence attack time despite standardization of the throw gesture and experimenter. However, attack time was not a distinguishing feature of AST tree species (electronic supplementary material, table S2); therefore, a systematic experimental bias in throw force variation is unlikely (see also electronic supplementary material).

Overall, this study suggests that at least one function of AST behaviour is sound production. Low-frequency sounds travel further in the environment and are better suited for long-distance communication [23]. A sound that is more resonant will also persist in the environment for longer which is characteristic of AST tree species. However, with respect to sound transmission, a single throw would be less effective than the multiple beats characteristic of chimpanzee buttress drumming [20]. Moreover, AST is almost always accompanied by a pant-hoot vocalization [14] which is far more conspicuous than the impact sound. Therefore, despite our evidence for one functional explanation for AST, there must be additional explanations to account for the persistence of this behaviour in some chimpanzee communities.

Only 39 individual trees had any signs of use by chimpanzees out of the potentially hundreds of AST trees available (table 1). Future research should focus on testing the factors influencing individual tree and tool selection, including testing more tree species, and more trees

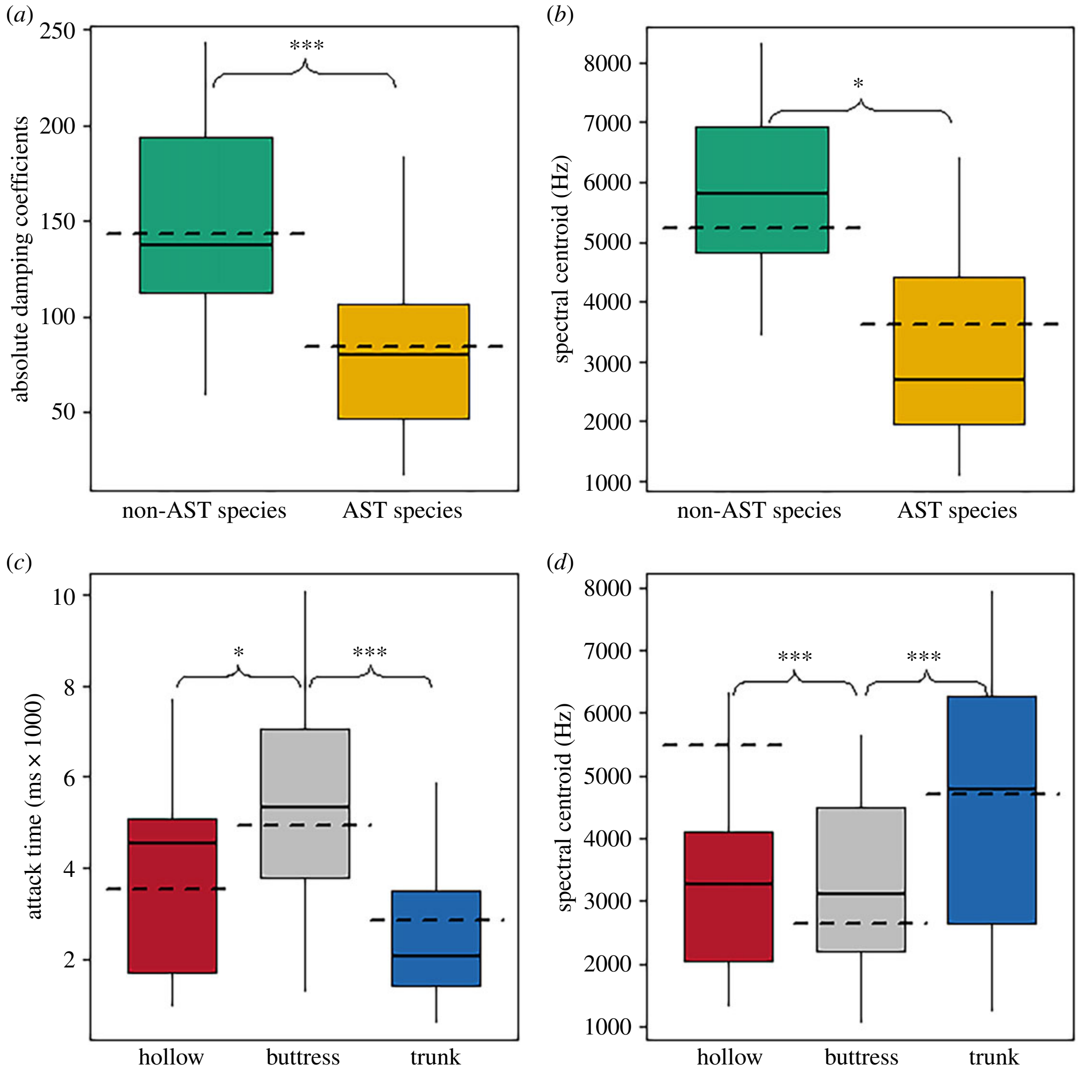

Figure 2. AST tree species relative to non-AST tree species had (*a*) lower absolute damping coefficients and (*b*) a spectral centroid concentrated at lower frequencies. The physical characteristics of where a tree was impacted also affected acoustic properties, namely buttresses had (*c*) a longer attack time and (*d*) a lower spectral centroid. Medians of all impact sounds (i.e. throws) per category are represented by solid horizontal lines and model estimates by dashed horizontal lines when all other variables are at their average value. Coloured boxes represent quartiles and vertical lines show 2.5 and 97.5% of the data. Asterisks indicate significance levels (*$p < 0.05$; ***$p < 0.001$) or otherwise non-significant. Sample size is 125 impact sounds for all models. (Online version in colour.)

per species. Additional studies investigating putative cultural aspects of AST would also be important for their potential to assist chimpanzee conservation efforts in the wild [13,31].

Ethics. Permissions to conduct non-invasive fieldwork were granted by Instituto da Biodiversidade e das Áreas Protegidas via the Chimbo Foundation and adhered to the rules and regulations governing Boé National Park in Guinea-Bissau.

Data accessibility. The data supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. A.K.K., R.K.-M., S.Y., J.C. and M.A. designed the study and analysed data; A.K.K. and E.C. conducted field experiments; A.K.K. drafted the manuscript with feedback from all co-authors. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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