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Voice-mediated interactions in a megaherbivore

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By entering the Anthropocene, the planet Earth is becoming increasingly difficult for large animal species to inhabit. Yet, these species are of major importance for the functioning of the biosphere and their progressive disappearance is accompanied by profound negative alterations of ecosystems [1] (Supplemental information). To implement effective conservation measures, it is essential to have a detailed knowledge of the biology of these species, notably regarding their social structures and the interactions between individuals. Here, we show that the hippopotamus *Hippopotamus amphibius*, an iconic African megaherbivore for which little is known about social communication, use vocal recognition to manage relationships between territorial groups. We conducted playback experiments on groups of hippos and observed their response to vocalizations from an individual of the same group (familiar), a group from the same lake (neighbor), and from a distant group (stranger). We found that stranger vocalizations induced a stronger behavioral reaction than the other two stimuli. In addition to showing that hippos are able to identify categories of conspecifics based on vocal signatures, our study demonstrates that hippo groups are territorial entities that behave less aggressively toward their neighbors than toward strangers. These new behavioral data suggest that habituation playbacks prior to conservation translocation operations may help reduce the risk of conflict between individuals that have never seen each other.

The megaherbivores -terrestrial mammals that feed on plants and weigh over 1000 kg (elephants, hippos and rhinos)- are a major source of concern. In African savannah ecosystems, rhinos are at a survival stage -each species being present in small protected areas- and, although some populations are increasing at the cost of expensive monitoring, they remain critically endangered [2]. Elephants are much more numerous and, while they are also under pressure from human activities, our extensive knowledge of their biology allows conservationists to devise appropriate management measures, though sometimes difficult to achieve [3]. While the third type of African megaherbivore, the hippopotamus, is not yet listed as endangered, its populations have declined dramatically in recent decades. Habitat loss and unregulated hunting are of increasing concern [4]. This amphibious animal shares its life between land and water, and has a unique role in the ecosystem mainly because of its impact on the flux of energy and matter between the two environments [5]. Despite this ecological importance, the biology of the hippopotamus is still mysterious in many respects, and population management methods remain largely empirical [6].

Studying the behavioral biology of hippos in the wild is notably complicated. It is difficult-if not impossible- to identify and mark individuals, and sometimes highly challenging to locate them. Hippos are well known for their amphibious habits: while they feed on land mainly at night and are rather solitary, they gather in groups in the water during the day to avoid overheating, rest and mate. Hippo groups are socially structured around a dominant male, a variable number of females and their young, and some peripheral males [7]. However, it is unclear whether individuals in a pod form a stable group defending a territory, or it is more like a fission-fusion type organization with individuals moving rather freely from one pod to another. In any case, the hippo social system appears to rely on communication signals - hippos are very vocal- whose role and meaning remain almost unexplored [8].

In the present study, we focused on the most common hippo vocalization, the wheeze honk, a loud call heard over long distances that is assumed to be important for social cohesion and communication between groups, but whose actual function remains unknown (see Supplemental information). Based on the assumption that hippo groups are territorial entities, defended by the dominant male but also potentially by other individuals, including females, we tested the hypothesis that the wheeze honk could signal the identity of the sender and thus enable behavioral decisions by the receiver individuals.

We worked in the *Maputo Special Reserve* (Mozambique, Austral Africa), an area characterized by the presence of several lakes inhabited by hippos (Figure 1A). For each group of hippos (minimum number of individuals = 3; maximum = 22), we first recorded spontaneous vocalizations and then conducted playback experiments (see Supplemental information for methodological details).

We conducted three types of playback tests on groups of hippos: one with a call from the group, another with a call from a different group present on the same lake, and another with a call from a distant stranger group (Figure 1B). Of the seven groups tested, five received all three stimuli. Two groups received only the familiar and stranger stimuli (one group had no neighbors in its lake and one has not been retested due to experimental constraints; see Supplementary Table 1 for details on test design). The order of the tests was balanced among the groups. The signals were played from the shore, around 70-90 meters away from the group, mimicking the approach of a vocalizing individual (mean duration of a playback session = 36 minutes, min-max = 15-75 min).

The results show that hippos respond to played back call (by calling back, approaching and/or marking by defecation), but that their response depends on the category of the stimulus (Figure 1C and 1D; Supplemental information). The overall intensity of the behavioral response is lowest in response to a call from an individual of the same group and highest in response to a call from an individual belonging to a stranger group (linear mixed model, Wald X2 = 17.55, p < 0.001, see Supplemental information for detailed statistics). The nature of the response also changes between stimuli. Whereas individuals responded to calls from any group, marking behavior (dung spraying) is modulated by the category of the calls (cumulative mixed model: Wald X2 = 11.47, p=0.003). Stranger group calls induce more marking than calls from an individual of the same group (multiple comparisons tests: Z=2.41, p=0.042), while there is no significant difference between reactions to the calls from the same group or from a neighboring group (multiple comparisons tests: Z=0.40, p=0.915).

Individuals in territorial animal species often react less aggressively to a known individual from a neighboring territory than to a stranger ("dear-enemy effect", see Supplemental References). Sometimes, however, the opposite is observed and it is the neighbor that is more strongly repelled ("nasty neighbor", see Supplemental References). Our experiments suggest that in hippos, the arrival of a stranger individual is perceived as more threatening than that of a neighbor.

Complementary experiments to assess sound level and sound propagation revealed that the wheeze honk can propagate more than 1 km away. Although the acoustic features carrying the vocal signature may be altered during long distance transmission, it is thus likely that these animals can learn and recognize the voices of neighboring individuals living on the same lake (Supplemental information).

In short, we showed that hippos use vocal recognition to manage their inter-group relationships, a strategy already observed in other large mammals where competition is intense and which allows to limit physical fights with often irreparable consequences [9]. While relocating endangered animals to maintain population above critical levels is increasingly common [10], our results suggest that precautions should be taken during such relocations with hippos. Before transferring a group of hippos to a new location, a potential precaution could be to broadcast their voices from a loudspeaker at a distance from the groups already present so that they get used to them and their level of aggressiveness gradually decreases. Reciprocity - getting the animals to be relocated accustomed to the voices of their new neighbors - could also be considered.

Supplemental information

Supplemental information including experimental procedures, one table, one figure and references can be found with this article online at XXX.

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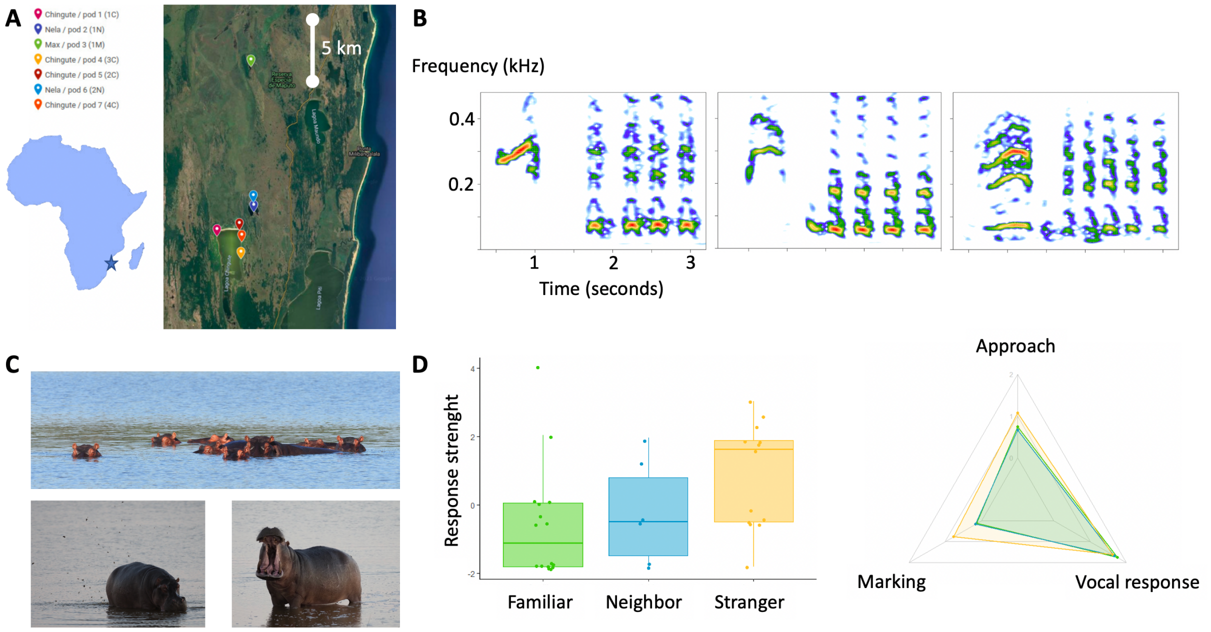


Figure 1. Playback experiments on hippos.

(A) Map of the *Maputo Special Reserve* (Mozambique, Austral Africa) with location of the tested hippo groups. (B) Examples of hippo vocalizations used for the playback experiments (three different individuals). (C) Top: typical hippo group. Bottom: approach toward the loudspeaker and marking (dung spraying followed by threatening display). (D) Behavioral reaction of hippos to conspecific vocalizations (familiar: call from an individual of the tested group; neighbor: call from an individual of a group from the same lake; stranger: call from an individual of a distant group). Left: Response strength represents an integrative measure of the hippo reaction to calls, calculated using a Principal Component Analysis from all behavioral variables. Right: Diagram reporting the behavioral scores for each of the three considered behaviors (approach toward the loudspeaker, number of vocalizations, and marking behavior by defecation; see Supplemental Information for details).

SUPPLEMENTAL INFORMATION

The “wheeze honk”.

Hippos have a repertoire of calls (wheeze honk, grunts, bellows, squeals; Eltringham 1999, Maust-Mohl et al 2015). The wheeze honk is emitted by both adult females and males. It is an aerial, powerful signal that can be heard at long distances. It can also propagate underwater (Barklow 2004). However, this underwater propagation remains to be thoroughly explored as it is unlikely that sound waves propagate at long range in shallow water. Although the wheeze honk is generally considered as a *contact call* that allows individuals to signal their presence to one another, its social function is still unclear.

Playback experiments.

We recorded hippo vocalizations with a shotgun microphone (Sennheiser MKH8070) connected to a digital audio recorder (Tascam DR-40; sampling rate = 48 kHz, 16 bit; average recording distance = 80 m). To serve as stimuli during the playback tests, we selected a single call per group (two calls for one of the groups), taking care that this call had an excellent signal-to-noise ratio, and was not blurred by other vocalizations. Each selected call was then used in playback tests as a familiar call for the group where it was recorded, as a neighbor call for a group of hippos in the same lake, and as a stranger call for a distant group of hippos (group of another lake). In addition, two calls recorded from captive animals were used as stranger calls. Each sound stimulus was low-pass filtered (4.5 kHz) and normalized. As shown by our measures of sound intensity of actual hippos vocalizing (see below), the wheeze honk is emitted at 94-110 dB SPL (rel. 20 µPa, N=85 calls), at 1 meter from the animal. We thus calibrated our playback loudspeaker to emit the sound stimuli at an average intensity of 100 dB SPL at 1 meter, and with a playback distance of 70-90 meters.

We observed each group of hippos during a couple of hours before and after the playback experiments. Five different observers assessed the number of hippos and compared their assessment. As we conducted several playback experiments over several days on each pod, we re-assessed the number of hippos each time. The pods were stable in terms of the number of individuals during the period we performed the study (pod 1: 7 individuals; pod 2:

10 individuals; pod 3: 3 individuals; pod 4: 11 individuals; pod 5: 8-11 individuals; pod 6: 22 individuals; pod 7: 7 individuals). The pods did not move much from day to day during the study, remaining roughly in the same place in their lakes.

Before each playback test, we waited until the hippos were calm and quiet, with most individuals with their head emerging out of water. We played the sound stimuli from a JBL Boombox2 speaker (HARMAN International) connected via Bluetooth to a cell phone (Samsung Galaxy XCover 4). If no hippo responded to the playback of the first rendition of the stimulus, the same call was played again 30 seconds after (this happened in only two trials: “stranger” trial n°2 of experiment 1 and “familiar” trial n°5 of experiment 6; see Supplemental Table 1). A minimum delay of 15 minutes was observed between each playback test. All tests were filmed and recorded.

Behavioral responses were scored from the videos according to the following variables, all measured within 10 minutes after the onset of the stimulus playback (Supplemental Table 1):

- Approach toward the speaker (no movement = 0; movement of at least one individual less than one body length = 1; movement of at least one individual more than one body length = 2).

- Marking by dung spraying (no marking = 0; one marking behavior = 1; multiple markings by one or more hippos = 2).

- Vocal production (no vocalization = 0; one vocalizing individual = 1; multiple vocalizing individuals = 2).

For each of these three behaviors, latencies (duration between stimulus onset and observed behavior onset) were also measured. If we were to repeat the playback, the latency was measured from the onset of the first stimulus.

Statistical analysis

We used principal component analysis (PCA, *FactoMineR package,* RStudio v3.6.2) with all the six behavioral variables measured to create a composite behavioral score. The first component explained 46.0% of the variables’ variance. The approach score, the marking score and the latency to vocalize were strongly positively correlated with PC1, while the vocal production, the latency to approach and the latency to mark were strongly negatively correlated with PC1. Higher positive values of PC1 represented a stronger territorial response, with individuals approaching and marking more, and more rapidly, and producing less vocalizations. We called this PC1 the “response strength”. This response strength was analyzed by using a linear mixed model (*lmer* function of the *lme4 package*), with the type of stimulus (i.e. familiar, neighbor, or stranger) as fixed factor, and the identity of the tested pod and the sound stimulus as random factors. Post hoc multiple comparisons (Tukey contrasts, *multcomp R package*) were performed to compare response strength between types of stimulus. We found that the response strength was significantly higher for stranger stimuli compared to familiar stimuli (Tukey comparisons: $\beta_{familiar} = -2.22$, $SE_{familiar} = 0.53$, $Z_{familiar} = -4.19$, $P_{familiar} < 0.001$) and compared to neighbor stimuli (Tukey comparisons: $\beta_{neighbor} = -1.55$, $SE_{neighbor} = 0.64$, $Z_{neighbor} = -2.43$, $P_{neighbor} = 0.040$). Response strength was not significantly different between familiar and neighbor calls (Tukey comparisons: $\beta_{neighbor} = 0.67$, $SE_{neighbor} = 0.55$, $Z_{neighbor} = 1.20$, $P_{neighbor} = 0.450$).

In addition, three independent statistical tests were conducted on the three principal behavioral scores (approach, marking, vocal production). For each behavioral score, a cumulative link mixed model was fitted (*clmm* function of *Ordinal R package*), with the type of stimulus as fixed factor and the identity of the tested pod and the sound stimulus as random factors. Post hoc comparisons (Tukey contrasts, *emmeans R package*) were also conducted to compare the behavioral score for each type of stimulus. The results were the following:

- Approach: no significant effect of the category of stimulus (X^2 Wald = 4.09, p = 0.130); no differences between groups (neighbor and stranger compared to familiar group : $\beta_{neighbor} = 0.61$, $SE_{neighbor} = 1.33$, $Z_{neighbor} = 0.46$, $P_{neighbor} = 0.891$ and $\beta_{stranger} = 2.64$, $SE_{stranger} = 1.66$, $Z_{stranger} = 1.59$, $P_{stranger} = 0.249$; neighbor compared to stranger : $\beta_{stranger} = 2.03$, $SE_{stranger} = 1.51$, $Z_{stranger} = 1.35$, $P_{stranger} = 0.371$; mean approach score = 0.75±0.86 and 0.67±0.52 for respectively familiar and neighbor stimuli, 1.08±0.76 for stranger stimuli).

- Marking: significant effect of the category of stimulus (X^2 Wald = 11.47, p = 0.003); significant difference between familiar and stranger groups ($\beta_{stranger}$ = 3.98, $SE_{stranger}$ = 1.65, $Z_{stranger}$ = 2.41, $P_{stranger}$ = 0.042). There is a tendency to have more marking in stranger group compared to the neighbor group ($\beta_{stranger}$ = 3.37, $SE_{stranger}$ = 1.76, $Z_{stranger}$ = 1.92, $P_{stranger}$ = 0.134). No significant difference between familiar and neighbor ($\beta_{neighbor}$ = 0.61, $SE_{neighbor}$ = 1.51, $Z_{neighbor}$ = 0.40, $P_{neighbor}$ = 0.915). Mean marking score = 0.17±0.0.41 and 0.77±0.83 for respectively neighbor and stranger stimuli, compared to 0.13±0.34 for familiar stimuli.

- Vocal response: no significant effect of the category of stimulus (X^2 Wald = 1.65, p = 0.438); no differences between groups (neighbor and stranger compared to familiar group : $\beta_{neighbor}$ = -1.48, $SE_{neighbor}$ = 4.08, $Z_{neighbor}$ = -0.36, $P_{neighbor}$ = 0.930 and $\beta_{stranger}$ = -4.63, $SE_{stranger}$ = 6.79, $Z_{stranger}$ = -0.68, $P_{stranger}$ = 0.774; neighbor compared to stranger : $\beta_{stranger}$ = -3.16, $SE_{stranger}$ = 7.05, $Z_{stranger}$ = -0.45, $P_{stranger}$ = 0.896; mean vocal production score = 1.75±0.58 for familiar stimuli, 1.67±0.81 and 1.62±0.77 for respectively neighbor and stranger stimuli).

Measures of sound intensity and estimation of call range.

We used recordings made at distances of 70-150 m from the animals to estimate the sound pressure level (SPL) of hippo vocalizations (N = 85) at 1 m (calibrated audio chain composed by a Sennheiser shotgun microphone connected to a TASCAM DR-40 recorder). Sound pressure level estimates averaged 102 ± 3.6 dB re. 20 µPa (min = 94, max = 110 dB). The measured ambient noise amplitude was 43 dB SPL, corresponding to 50% SPL percentiles, i.e. 50 % of the time the noise amplitude was below 43 dB SPL considering all the recordings from the several lakes (measured from the calibrated recordings considering 1 s segments and the 0-3 kHz bandwidth; noise SPL ranged 39 to 51 dB with exceptionally quiet moments as low as 34 dB SPL; notice that recordings were made with a shotgun Sennheiser microphone, which might lead to underestimate the level of the background noise due to its anisotropy. However, we assume that our measurements are representative because 1) the average level of background noise remains approximate due to variations during the day and with weather conditions, 2) it is not clear which microphone, shotgun or omnidirectional, is closer to the directivity of the hippo's auditory system). As a result, the distance at which the sound level of the hippo wheeze honk no longer exceeds that of the background noise according to spherical spreading should be at least 1 km (see black curve in Supplemental Figure 1A).

This estimation was firstly corroborated by recordings of spontaneously emitted hippo vocalizations along a lake shore (blue curve in Supplemental Figure 1A). The recorders (Audiomoth v1.2.0 loggers) were placed along the shore near the water of Chingute lake, at different distances from a hippo pod. The distance from the first recorder to the hippo pod was estimated at 80 m. The following recorders were placed at 50, 100, 200, 400, 800, 1700 meters from the first recorder. As it was not possible to place the recorders in a straight line relative to the hippo pod, these distances must be considered as approximative. Hippo calls appear to attenuate according to the spherical model and were no more detected from recordings at a distance of 1700 m from the vocalizing animals (which explains why there is no point at this distance on the figure).

This estimation was also corroborated by another analysis integrating signal and noise levels within standard mammalian auditory bands (1/3rd octave bands; Dooling and Blumenrath, 2014; Erbe et al., 2016; Putland et al., 2017). To do so, we averaged the frequency spectrum of all hippo calls including spontaneous vocalizations and calls recorded during playback experiments (normalizing for recording distance) and further calculated spectra at different distances using the spherical propagation model and adding a frequency-dependent excess attenuation component. To measure the excess attenuation, we did a propagation experiment using white noise (sequences of 20 seconds of white noise; bandwidth 0-20 kHz; propagation at 1, 5, 10, 15, 20, 25, 30 and 61 m over an open and flat savannah; sounds played back from a JBL BoomBox2 loudspeaker and recorded with a Sennheiser MKH8070 microphone and Tascam DR-40 recorder). Besides, we computed the average background noise spectrum (1/3rd octave bands) using 20 files with sound recordings obtained just before or after the hippo calls considered for this analysis. We chose to consider the percentiles 5, 20 and 50 since they indicate that the background noise spectrum is respectively 5%, 20% and 50% of the time below the measured value. The data are displayed in Supplemental Figure 1B. Considering the frequency bandwidth where the hippo call exhibits the more energy (40-500 Hz), this call is likely to be above the background noise till

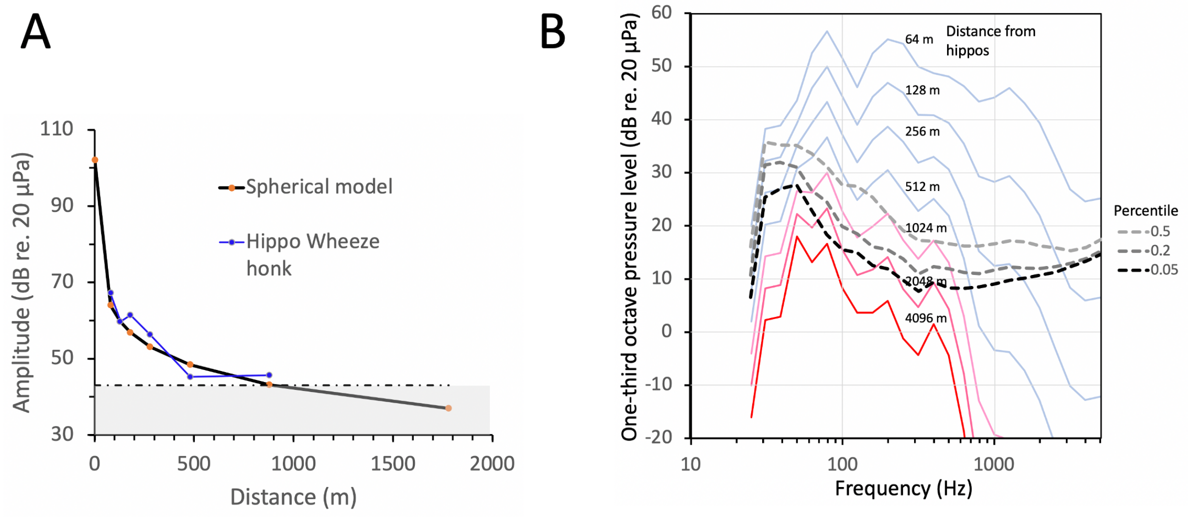
1 to 2 km. Since this estimation is based on an average call, louder calls (the loudest being almost 10 dB above average) may be perceived at longer distances.

Discussion: The impact of megafauna on ecosystems

This topic was recently highlighted in a paper that demonstrates that megafauna are disproportionately important for the functioning of the biosphere (Enquist BJ et al, 2020. Nature Communications, 11, 699). Large herbivorous mammals thus have a major role in the flux of nutrients and energy in the biosphere through their feces, urine and flesh. The redistribution of nutrients and the fertilization of ecosystems are highly dependent on them, and there is evidence that a biosphere without the largest animals is less productive, contains less biomass, is less fertile. On the other hand, the introduction of a large mammal as an alien species in an ecosystem where it was not initially present can profoundly alter the ecosystem. This is what is currently happening with the emerging population of hippos in Colombia. This population originated from a few animals in captivity, and has been growing steadily over the last three decades. Their presence is causing eutrophication of the lakes where they live and may pose a threat to the original ecosystems as well as to human populations (for the full story, see these two recent papers: Shurin JB et al, 2020. Ecosystem effects of the world's largest invasive animal. Ecology, 101, e02991; Castelblanco-Martinez DN et al, 2021. A hippo room: Predicting the persistence and dispersion of an invasive mega-vertebrate in Colombia, South America).

Experience	Trial	Location	Pod	Pod size	Playback	Stimulus	Approach (lat)	Marking (lat)	Vocalization (lat)
1	1	Chingute	1	7	familiar	pod 1	1 (7)	0 (inf)	1 (5.9)
1	2	Chingute	1	7	stranger	captivity	0 (inf)	2 (48)	0 (83.9)
1	3	Chingute	1	7	familiar	pod 1	1 (4)	0 (inf)	2 (7.5)
2	1	Nela	2	10	stranger	captivity	1 (3)	0 (inf)	2 (8.3)
2	2	Nela	2	10	familiar	pod 2	2 (1)	0 (inf)	2 (6.2)
2	3	Nela	2	10	stranger	captivity	1 (2)	0 (inf)	2 (8.2)
2	4	Nela	2	10	familiar	pod 2	0 (inf)	0 (inf)	2 (10.8)
2	5	Nela	2	10	stranger	captivity	0 (inf)	1 (54)	2 (11.2)
3	1	Max	3	3	stranger	captivity	1 (1)	0 (inf)	2 (15.7)
3	2	Max	3	3	familiar	pod 3	1 (1)	0 (inf)	2 (6.7)
3	3	Max	3	3	stranger	captivity	1 (1)	0 (inf)	2 (8.2)
3	4	Max	3	3	familiar	pod 3	2 (1)	0 (inf)	2 (7.5)
4	1	Chingute	4	11	familiar	pod 4	0 (inf)	0 (inf)	2 (0)
4	2	Chingute	4	11	stranger	pod 3	2 (1)	1 (211)	1 (45)
4	3	Chingute	4	11	familiar	pod 4	0 (inf)	0 (inf)	2 (7.1)
4	4	Chingute	4	11	stranger	pod 2	2 (1)	0 (inf)	0 (inf)
4	5	Chingute	4	11	neighbor	pod 1	1 (1)	0 (inf)	0 (inf)
5	1	Chingute	5	11	familiar	pod 5	0 (inf)	0 (inf)	2 (6.7)
5	2	Chingute	5	11	stranger	pod 2	1 (1)	2 (84)	2 (8.2)
5	3	Chingute	5	11	familiar	pod 5	0 (inf)	0 (inf)	2 (7)
5	4	Chingute	5	11	neighbor	pod 4	0 (inf)	0 (inf)	2 (8.6)
6	1	Nela	6	22	neighbor	pod 2	1 (2)	0 (inf)	2 (8.3)
6	2	Nela	6	22	stranger	pod 5	1 (1)	2 (42)	2 (5.2)
6	3	Nela	6	22	familiar	pod 6	0 (inf)	0 (inf)	2 (5.3)
6	4	Nela	6	22	neighbor	pod 2	1 (1)	0 (inf)	2 (6.3)
6	5	Nela	6	22	familiar	pod 6	0 (inf)	0 (inf)	2 (54.7)
7	1	Chingute	1	7	familiar	pod 1	2 (7)	1 (288)	0 (inf)
7	2	Chingute	1	7	familiar	pod 1	2 (2)	1 (382)	1 (7.5)
7	3	Chingute	1	7	stranger	pod 3	2 (8)	1 (168)	2 (10)
8	1	Chingute	5	8	stranger	pod 3	2 (2)	1 (40)	2 (13.7)
9	1	Chingute	7	7	neighbor	pod 5	0 (inf)	0 (inf)	2 (4.5)
9	2	Chingute	7	7	familiar	pod 7	0 (inf)	0 (inf)	2 (4.2)
9	3	Chingute	7	7	stranger	captivity	0 (inf)	0 (inf)	2 (7.5)
10	1	Chingute	1	7	neighbor	pod 5	1 (1)	1 (24)	2 (10.3)
10	2	Chingute	1	7	familiar	pod 1	1 (1)	0 (inf)	2 (66.2)

Supplemental Table 1. Playback experiments.
The score (0, 1, 2) and the latency (between brackets, in seconds; Inf = “infinite” latency) are indicated for each of the three considered behaviors (Approach, Marking, Vocalization). (Location = name of the lake; pod = hippo group).



Supplemental Figure 1. Propagation range of the hippopotamus wheeze honk. A. Propagation of hippo vocalizations along the Lake Chingute shore close to the water. The shaded area in grey indicates the background noise (below 43 dB SPL during 50% of the time; min = 34 dB SPL, max = 51 dB). Black curve: amplitude of a hippo call as a function of distance calculated using the spherical propagation model (call amplitude at 1 meter = 102 dB). Blue curve: amplitude of hippo calls recorded at different distances from the vocalizing individuals. In these recordings, hippo vocalizations were detected up to 880 m but not at 1700 m. **B.** Propagation range of wheeze-honk calls comparing one-third octave spectra of averaged hippo calls and background sound level. Solid lines represent the frequency spectra of an averaged hippo call for different propagation distances (values are represented at the centre frequency of each one-third octave band; the spectrum at 64 meters was obtained based on recordings from different individuals on several lakes; spectra at other distances were calculated using the spherical propagation model and adding the excess attenuation measured in white noise propagation experiments). The dashed lines represent the background noise spectrum (one-third octave spectrum; averaged over 20 files with sound recordings obtained in different locations; the three curves represent the 5%, 20% and 50% percentiles of the distribution of background noise measurements, respectively - which means that the background noise was below the 0.05 curve during 5% of the total time of our recordings, below the 0.2 curve during 20% of the total time, and below the 0.5 curve during 50% of the total time). These calculations confirm that the transmission range of the hippo call can reach more than 1 km.

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