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13 By entering the Anthropocene, the planet Earth is becoming increasingly difficult for large

14 animal species to inhabit. Yet, these species are of major importance for the functioning of

15 the biosphere and their progressive disappearance is accompanied by profound negative

16 alterations of ecosystems [1] (Supplemental information). To implement effective

17 conservation measures, it is essential to have a detailed knowledge of the biology of these

18 species, notably regarding their social structures and the interactions between individuals.

19 Here, we show that the hippopotamus *Hippopotamus amphibius*, an iconic African

20 megaherbivore for which little is known about social communication, use vocal recognition

21 to manage relationships between territorial groups. We conducted playback experiments on

22 groups of hippos and observed their response to vocalizations from an individual of the

23 same group (familiar), a group from the same lake (neighbor), and from a distant group

24 (stranger). We found that stranger vocalizations induced a stronger behavioral reaction than

25 the other two stimuli. In addition to showing that hippos are able to identify categories of

26 conspecifics based on vocal signatures, our study demonstrates that hippo groups are

27 territorial entities that behave less aggressively toward their neighbors than toward

28 strangers. These new behavioral data suggest that habituation playbacks prior to

29 conservation translocation operations may help reduce the risk of conflict between

30 individuals that have never seen each other.

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

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

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

2

62 We worked in the *Maputo Special Reserve* (Mozambique, Austral Africa), an area

63 characterized by the presence of several lakes inhabited by hippos (Figure 1A). For each

64 group of hippos (minimum number of individuals = 3; maximum = 22), we first recorded

65 spontaneous vocalizations and then conducted playback experiments (see Supplemental

66 information for methodological details).

67 We conducted three types of playback tests on groups of hippos: one with a call from the

68 group, another with a call from a different group present on the same lake, and another with

69 a call from a distant stranger group (Figure 1B). Of the seven groups tested, five received all

70 three stimuli. Two groups received only the familiar and stranger stimuli (one group had no

71 neighbors in its lake and one has not been retested due to experimental constraints; see

72 Supplementary Table 1 for details on test design). The order of the tests was balanced

73 among the groups. The signals were played from the shore, around 70-90 meters away from

74 the group, mimicking the approach of a vocalizing individual (mean duration of a playback

75 session = 36 minutes, min-max = 15-75 min).

76 The results show that hippos respond to played back call (by calling back, approaching

77 and/or marking by defecation), but that their response depends on the category of the

78 stimulus (Figure 1C and 1D; Supplemental information). The overall intensity of the

79 behavioral response is lowest in response to a call from an individual of the same group and

80 highest in response to a call from an individual belonging to a stranger group (linear mixed

81 model, Wald X2 = 17.55, p < 0.001, see Supplemental information for detailed statistics). The

82 nature of the response also changes between stimuli. Whereas individuals responded to calls

83 from any group, marking behavior (dung spraying) is modulated by the category of the calls

84 (cumulative mixed model: Wald X2 = 11.47, p=0.003). Stranger group calls induce more

85 marking than calls from an individual of the same group (multiple comparisons tests: Z=2.41,

86 p=0.042), while there is no significant difference between reactions to the calls from the

87 same group or from a neighboring group (multiple comparisons tests: Z=0.40, p=0.915).

88 Individuals in territorial animal species often react less aggressively to a known individual

89 from a neighboring territory than to a stranger ("dear-enemy effect", see Supplemental

90 References). Sometimes, however, the opposite is observed and it is the neighbor that is

91 more strongly repelled ("nasty neighbor", see Supplemental References). Our experiments

3

92   suggest that in hippos, the arrival of a stranger individual is perceived as more threatening

93   than that of a neighbor.

94   Complementary experiments to assess sound level and sound propagation revealed that the

95   wheeze honk can propagate more than 1 km away. Although the acoustic features carrying

96   the vocal signature may be altered during long distance transmission, it is thus likely that

97   these animals can learn and recognize the voices of neighboring individuals living on the

98   same lake (Supplemental information).

99   In short, we showed that hippos use vocal recognition to manage their inter-group

100   relationships, a strategy already observed in other large mammals where competition is

101   intense and which allows to limit physical fights with often irreparable consequences [9].

102   While relocating endangered animals to maintain population above critical levels is

103   increasingly common [10], our results suggest that precautions should be taken during such

104   relocations with hippos. Before transferring a group of hippos to a new location, a potential

105   precaution could be to broadcast their voices from a loudspeaker at a distance from the

106   groups already present so that they get used to them and their level of aggressiveness

107   gradually decreases. Reciprocity - getting the animals to be relocated accustomed to the

108   voices of their new neighbors - could also be considered.

109

Supplemental information

111   Supplemental information including experimental procedures, one table, one figure and

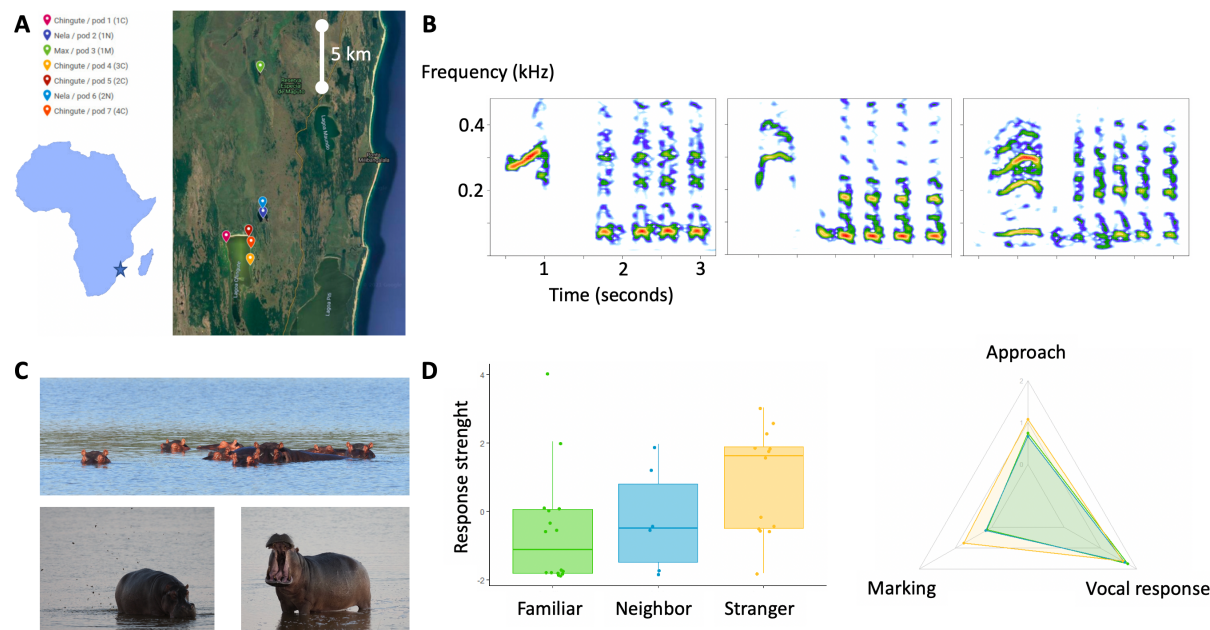112   references can be found with this article online at XXX.

113

Acknowledgements

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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).

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169   **SUPPLEMENTAL INFORMATION**

170   **The "wheeze honk".**

171   Hippos have a repertoire of calls (wheeze honk, grunts, bellows, squeals; Eltringham 1999,

172   Maust-Mohl et al 2015). The wheeze honk is emitted by both adult females and males. It is

173   an aerial, powerful signal that can be heard at long distances. It can also propagate

174   underwater (Barklow 2004). However, this underwater propagation remains to be

175   thoroughly explored as it is unlikely that sound waves propagate at long range in shallow

176   water. Although the wheeze honk is generally considered as a *contact call* that allows

177   individuals to signal their presence to one another, its social function is still unclear.

178

179   **Playback experiments.**

180   We recorded hippo vocalizations with a shotgun microphone (Sennheiser MKH8070)

181   connected to a digital audio recorder (Tascam DR-40; sampling rate = 48 kHz, 16 bit; average

182   recording distance = 80 m). To serve as stimuli during the playback tests, we selected a single

183   call per group (two calls for one of the groups), taking care that this call had an excellent

184   signal-to-noise ratio, and was not blurred by other vocalizations. Each selected call was then

185   used in playback tests as a familiar call for the group where it was recorded, as a neighbor

186   call for a group of hippos in the same lake, and as a stranger call for a distant group of hippos

187   (group of another lake). In addition, two calls recorded from captive animals were used as

188   stranger calls. Each sound stimulus was low-pass filtered (4.5 kHz) and normalized. As shown

189   by our measures of sound intensity of actual hippos vocalizing (see below), the wheeze honk

190   is emitted at 94-110 dB SPL (rel. 20 μPa, N=85 calls), at 1 meter from the animal. We thus

191   calibrated our playback loudspeaker to emit the sound stimuli at an average intensity of 100

192   dB SPL at 1 meter, and with a playback distance of 70-90 meters.

193   We observed each group of hippos during a couple of hours before and after the playback

194   experiments. Five different observers assessed the number of hippos and compared their

195   assessment. As we conducted several playback experiments over several days on each pod,

196   we re-assessed the number of hippos each time. The pods were stable in terms of the

197   number of individuals during the period we performed the study (pod 1: 7 individuals; pod 2:

7

198   10 individuals; pod 3: 3 individuals; pod 4: 11 individuals; pod 5: 8-11 individuals; pod 6: 22

199   individuals; pod 7: 7 individuals). The pods did not move much from day to day during the

200   study, remaining roughly in the same place in their lakes.

201   Before each playback test, we waited until the hippos were calm and quiet, with most

202   individuals with their head emerging out of water. We played the sound stimuli from a JBL

203   Boombox2 speaker (HARMAN International) connected via Bluetooth to a cell phone

204   (Samsung Galaxy XCover 4). If no hippo responded to the playback of the first rendition of

205   the stimulus, the same call was played again 30 seconds after (this happened in only two

206   trials: "stranger" trial n°2 of experiment 1 and "familiar" trial n°5 of experiment 6; see

207   Supplemental Table 1). A minimum delay of 15 minutes was observed between each

208   playback test. All tests were filmed and recorded.

209   Behavioral responses were scored from the videos according to the following variables, all

210   measured within 10 minutes after the onset of the stimulus playback (Supplemental Table

211   1):

212   - Approach toward the speaker (no movement = 0; movement of at least one individual less

213   than one body length = 1; movement of at least one individual more than one body length =

214   2).

215   - Marking by dung spraying (no marking = 0; one marking behavior = 1; multiple markings by

216   one or more hippos = 2).

217   - Vocal production (no vocalization = 0; one vocalizing individual = 1; multiple vocalizing

218   individuals = 2).

219   For each of these three behaviors, latencies (duration between stimulus onset and observed

220   behavior onset) were also measured. If we were to repeat the playback, the latency was

221   measured from the onset of the first stimulus.

222

223   **Statistical analysis**

224   We used principal component analysis (PCA, *FactoMineR package,* RStudio v3.6.2) with all

225   the six behavioral variables measured to create a composite behavioral score. The first

226   component explained 46.0% of the variables' variance. The approach score, the marking

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227   score and the latency to vocalize were strongly positively correlated with PC1, while the

228   vocal production, the latency to approach and the latency to mark were strongly negatively

229   correlated with PC1. Higher positive values of PC1 represented a stronger territorial

230   response, with individuals approaching and marking more, and more rapidly, and producing

231   less vocalizations. We called this PC1 the "response strength". This response strength was

232   analyzed by using a linear mixed model (*lmer* function of the *lme4 package*), with the type of

233   stimulus (i.e. familiar, neighbor, or stranger) as fixed factor, and the identity of the tested

234   pod and the sound stimulus as random factors. Post hoc multiple comparisons (Tukey

235   contrasts, *multcomp R package*) were performed to compare response strength between

236   types of stimulus. We found that the response strength was significantly higher for stranger

237   stimuli compared to familiar stimuli (Tukey comparisons: $\beta_{familiar}$ = -2.22, $SE_{familiar}$ = 0.53,

238     $Z_{familiar}$ = -4.19, $P_{familiar}$ < 0.001) and compared to neighbor stimuli (Tukey comparisons:

239     $\beta_{neighbor}$ = -1.55, $SE_{neighbor}$ =0.64, $Z_{neighbor}$ = -2.43, $P_{neighbor}$ = 0.040). Response strength was not

240   significantly different between familiar and neighbor calls (Tukey comparisons: $\beta_{neighbor}$ =

241   0.67, $SE_{neighbor}$ =0.55, $Z_{neighbor}$ = 1.20, $P_{neighbor}$ = 0.450).

242   In addition, three independent statistical tests were conducted on the three principal

243   behavioral scores (approach, marking, vocal production). For each behavioral score, a

244   cumulative link mixed model was fitted (*clmm* function of *Ordinal R package*), with the type

245   of stimulus as fixed factor and the identity of the tested pod and the sound stimulus as

246   random factors. Post hoc comparisons (Tukey contrasts, *emmeans R package*) were also

247   conducted to compare the behavioral score for each type of stimulus. The results were the

248   following:

249   - Approach: no significant effect of the category of stimulus (X^2 Wald = 4.09, p =

250   0.130); no differences between groups (neighbor and stranger compared to familiar

251   group : $\beta_{neighbor}$ = 0.61, $SE_{neighbor}$ = 1.33, $Z_{neighbor}$ = 0.46, $P_{neighbor}$ = 0.891 and $\beta_{stranger}$ =

252   2.64, $SE_{stranger}$ = 1.66, $Z_{stranger}$ = 1.59, $P_{stranger}$ = 0.249; neighbor compared to stranger :

253       $\beta_{stranger}$ = 2.03, $SE_{stranger}$ = 1.51, $Z_{stranger}$ = 1.35, $P_{stranger}$ = 0.371; mean approach score =

254   0.75±0.86 and 0.67±0.52 for respectively familiar and neighbor stimuli, 1.08±0.76 for

255   stranger stimuli).

9

256   - Marking: significant effect of the category of stimulus (X^2 Wald = 11.47, p = 0.003);

257   significant difference between familiar and stranger groups ($\beta_{stranger}$ = 3.98, $SE_{stranger}$ =

258   1.65, $Z_{stranger}$ = 2.41, $P_{stranger}$ = 0.042). There is a tendency to have more marking in

259   stranger group compared to the neighbor group ($\beta_{stranger}$ = 3.37, $SE_{stranger}$ = 1.76,

260    $Z_{stranger}$ = 1.92, $P_{stranger}$ = 0.134). No significant difference between familiar and

261   neighbor ($\beta_{neighbor}$ = 0.61, $SE_{neighbor}$ = 1.51, $Z_{neighbor}$ = 0.40, $P_{neighbor}$ = 0.915). Mean

262   marking score = 0.17±0.0.41 and 0.77±0.83 for respectively neighbor and stranger

263   stimuli, compared to 0.13±0.34 for familiar stimuli.

264   - Vocal response: no significant effect of the category of stimulus (X^2 Wald = 1.65, p =

265   0.438); no differences between groups (neighbor and stranger compared to familiar

266   group : $\beta_{neighbor}$ = -1.48, $SE_{neighbor}$ = 4.08, $Z_{neighbor}$ = -0.36, $P_{neighbor}$ = 0.930 and $\beta_{stranger}$ =

267   -4.63, $SE_{stranger}$ = 6.79, $Z_{stranger}$ = -0.68, $P_{stranger}$ = 0.774; neighbor compared to stranger

268   : $\beta_{stranger}$ = -3.16, $SE_{stranger}$ = 7.05, $Z_{stranger}$ = -0.45, $P_{stranger}$ = 0.896; mean vocal

269   production score = 1.75±0.58 for familiar stimuli, 1.67±0.81 and 1.62±0.77 for

270   respectively neighbor and stranger stimuli).

271

272 **Measures of sound intensity and estimation of call range.**

273 We used recordings made at distances of 70-150 m from the animals to estimate the sound

274 pressure level (SPL) of hippo vocalizations (N = 85) at 1 m (calibrated audio chain composed

275 by a Sennheiser shotgun microphone connected to a TASCAM DR-40 recorder). Sound

276 pressure level estimates averaged 102 ± 3.6 dB re. 20 µPa (min = 94, max = 110 dB). The

277 measured ambient noise amplitude was 43 dB SPL, corresponding to 50% SPL percentiles,

278 i.e. 50 % of the time the noise amplitude was below 43 dB SPL considering all the recordings

279 from the several lakes (measured from the calibrated recordings considering 1 s segments

280 and the 0-3 kHz bandwidth; noise SPL ranged 39 to 51 dB with exceptionally quiet moments

281 as low as 34 dB SPL; notice that recordings were made with a shotgun Sennheiser

282 microphone, which might lead to underestimate the level of the background noise due to its

283 anisotropy. However, we assume that our measurements are representative because 1) the

284 average level of background noise remains approximate due to variations during the day and

285 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

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317 1 to 2 km. Since this estimation is based on an average call, louder calls (the loudest being

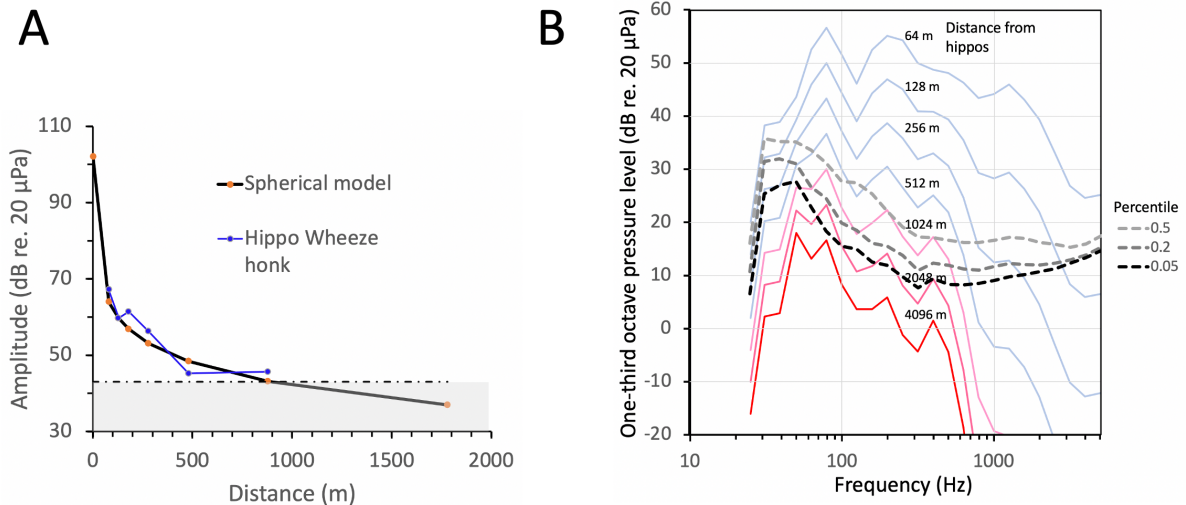318 almost 10 dB above average) may be perceived at longer distances.

319

320 **Discussion: The impact of megafauna on ecosystems**

321 This topic was recently highlighted in a paper that demonstrates that megafauna are

322 disproportionately important for the functioning of the biosphere (Enquist BJ et al, 2020.

323 Nature Communications, 11, 699). Large herbivorous mammals thus have a major role in the

324 flux of nutrients and energy in the biosphere through their feces, urine and flesh. The

325 redistribution of nutrients and the fertilization of ecosystems are highly dependent on them,

326 and there is evidence that a biosphere without the largest animals is less productive,

327 contains less biomass, is less fertile. On the other hand, the introduction of a large mammal

328 as an alien species in an ecosystem where it was not initially present can profoundly alter

329 the ecosystem. This is what is currently happening with the emerging population of hippos in

330 Colombia. This population originated from a few animals in captivity, and has been growing

331 steadily over the last three decades. Their presence is causing eutrophication of the lakes

332 where they live and may pose a threat to the original ecosystems as well as to human

333 populations (for the full story, see these two recent papers: Shurin JB et al, 2020. Ecosystem

334 effects of the world's largest invasive animal. Ecology, 101, e02991; Castelblanco-Martinez

335 DN et al, 2021. A hippo room: Predicting the persistence and dispersion of an invasive mega-

336 vertebrate in Colombia, South America).

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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)

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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).

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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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Cover picture