

1 **Repeated downsweep vocalizations of the Araguaian river**  
2 **dolphin, *Inia araguaiensis***

3

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23 **ABSTRACT**

24 Araguaian botos (*I. araguaiaensis*) are known to produce pulsed as well as tonal  
25 sounds. Here, we present the first evidence for repetitive sequences of downsweep whistles in  
26 botos that appear to be shared between individuals and we investigate the context of their  
27 occurrence. Our study was conducted along the Tocantins River located in Eastern Amazon  
28 over a period of 42 days of boat surveys between 2012-2018. We observed 82 groups of  
29 Araguaian botos and acquired 43h of sound recordings. 632 downsweep whistles were  
30 recorded in 10 encounters. Four of these encounters contained downsweep bouts (21 bouts  
31 with  $\geq 2$  whistles) with short inter-call intervals (bout criterion 50s) and up to 161 whistles.  
32 We did not find a statistical relationship between downsweep occurrence and any of the  
33 contextual parameters we investigated including socializing, travelling, feeding, group size,  
34 presence of calves and socio-sexual displays. The rarity of these signals makes them unlikely  
35 candidates for individual or group identification. It is more likely that they are associated  
36 with very specific contexts such as nursing or mating, both of which were rarely observed in  
37 our study. Further studies are required to investigate context specificity and elucidate the  
38 function of these signals.

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40

## 41 I. INTRODUCTION

42 All toothed whales (Odontoceti) produce pulsed calls for communication, with some  
43 species using these as their main social signals, e.g. orcas (*Orcinus orca*) (Ford, 1989; Deecke  
44 *et al.*, 2010), northern right whale dolphins (*Lissodelphis borealis*) (Rankin *et al.*, 2007),  
45 narwhals (*Monodon monoceros*) (Marcoux *et al.*, 2012), and pilot whales (*Globicephala* sp.)  
46 (Sayigh *et al.* 2013; Pérez *et al.* 2017). Pulsed calls are discrete signals composed of series of  
47 individual clicks (Schevill and Watkins, 1966). Such pulsed calls often encode social group  
48 identity (Deecke *et al.*, 2010; Ford, 1989) but are also used in immediate social interactions  
49 such as conflict negotiation (Overstrom, 1983). Many marine dolphins (family Delphinidae)  
50 also use whistles in their social communication (Janik 2005; May-Collado *et al.*, 2007).  
51 Whistles are defined as narrowband frequency modulated tonal sounds (Au *et al.*, 2000;  
52 Richardson *et al.*, 1995; Tyack, 2000). For most delphinids these sounds help to maintain  
53 cohesion of social groups (Janik and Slater, 1998; Janik 2005), and for some species such as  
54 the bottlenose dolphins (*Tursiops* sp.) whistles are also used to broadcast individual identity  
55 (Janik *et al.*, 2006; Sayigh *et al.* 1999).

56 River dolphins are a polyphyletic group that is particularly interesting when studying  
57 acoustic communication in cetaceans because riverine habitats are very different from marine  
58 ones and may have led to changes in communication strategies. However, comparatively few  
59 studies exist on their vocalizations. Previous studies on the susu (*Platanista gangetica*) and  
60 the baiji (*Lipotes vexillifer*) were mainly conducted in captivity and therefore focused on very  
61 few individuals (Mizue *et al.*, 1971; Wang *et al.*, 1995, 1999; 2006; Xiao and Jing, 1989).  
62 Cremer *et al.* (2017) recently described the whistles and burst pulses of wild franciscana  
63 dolphins (*Pontoporia blainvillei*) and suggested that they might be used in mother-calf  
64 communication. The most commonly studied river dolphin is the boto (genus *Inia*) (Amorin  
65 *et al.*, 2016; Caldwell *et al.*, 1966; Diazgranados and Trujillo, 2002; May-Collado and

66 Wartzok, 2007; Ding *et al.*, 1995, 2001; Kamminga *et al.*, 1993; Podos *et al.*, 2002; Penner  
67 and Murchison, 1970). Initially they were thought to lack whistles in their repertoire (Podos  
68 *et al.*, 2002) but later studies showed that whistles do occur, just not as often as pulsed sounds  
69 (May-Collado and Wartzok, 2007; Melo-Santos *et al.*, 2019). The discrepancy in these  
70 results may be partly explained by geographic and genetic differences. For example, a recent  
71 study has discovered that botos in the Tocantins-Araguaia River Basin belong to a different  
72 species, the Araguaian boto (*Inia araguaiaensis*) than those found elsewhere (Hrbek *et al.*  
73 2014).

74         Melo-Santos *et al.* (2019) described a variety of sounds produced by this new species,  
75 including whistles and pulsed calls. Araguaian boto calves were also found to produce bouts  
76 of short pulsed calls that were hypothesized to be contact calls for mother-calf  
77 communication (Melo-Santos, *et al.*, 2019). Repetition introduces redundancy into a signal  
78 and thereby increases the probability of transmitting information successfully to a receiver.

79         Various animal groups produce repeated call sequences including birds (Catchpole  
80 and Slater, 2008), insects (Hedrick, 1986), frogs (Fellers, 1979) and terrestrial mammals  
81 (McComb, 1991). In cetaceans, rhythmically repeated calls have been reported for a wide  
82 range of species, such as the bottlenose dolphin (Jensen *et al.*, 2012; Janik *et al.*, 2013), short  
83 and long-finned pilot whales (*Globicephala macrorhynchus* and *Globicephala melas*,  
84 respectively) (Sayigh *et al.*, 2013; Zwamborn and Whitehead, 2017); northern right whale  
85 dolphins (Rankin *et al.*, 2007), melon-headed whale (*Peponocephala electra*) (Kaplan *et al.*,  
86 2014), Guiana dolphins (Duarte de Figueiredo and Simão, 2009), humpback whales  
87 (*Megaptera novaeangliae*) (Payne and McVay, 1971), sperm whales (*Physeter*  
88 *macrocephalus*) (Watkins & Schevill 1977) and short-beaked common dolphins (*Delphinus*  
89 *delphis*) (Fearey *et al.*, 2019). Repetitive signals might work as mating calls (McComb, 1991;  
90 Smith *et al.*, 2008), individual or group identifiers (Janik *et al.*, 2013; Gero *et al.*, 2016;

91 Zwamborn and Whitehead, 2017), mother-offspring contact (Smolker *et al.*, 1993), territorial  
92 defense signals (Fellers, 1979), or even food calls (Janik, 2000). Here we present the first  
93 evidence for repetitive sequences of downsweep whistles in botos that appear to be shared  
94 between individuals and investigate the context of their occurrence.

95

## 96 II. METHODS

### 97 A. Study animals and area

98 Dolphins of the genus *Inia* are found in the Amazon, Orinoco and Tocantins river basins in  
99 South America (Best and Da Silva, 1989, 1993; Hrbek *et al.*; 2014; Santos *et al.*, 2012,  
100 2014). These dolphins prefer slow flowing, sheltered waters with large concentrations of prey  
101 (Gomez-Salazar *et al.*, 2012b; Martin *et al.*, 2004; Pavanato *et al.*, 2016). They are usually  
102 solitary or in mother-and-calf pairs. Larger aggregations are formed for mating and to feed on  
103 large schools of fish (Best and Da Silva, 1989, 1993; Gomez-Salazar *et al.*, 2012a; Martin *et*  
104 *al.*, 2008).

105 Our study was conducted along the Tocantins River located in the Eastern portion of  
106 the Amazon (Fig. 1). This river is characterized by clear waters, sandbanks, herbaceous and  
107 floating vegetation, and aquatic macrophytes in areas with light penetration (Junk *et al.*,  
108 2011). The greatest rainfall occurs from November to April, the lowest waters are in  
109 September and the highest in March (Ribeiro *et al.*, 1995). The lower Tocantins River  
110 comprises the area between the mouth of the river and the city of Tucuruí, where there is  
111 deposition of sediments and floodplains (Goulding *et al.*, 2003; Ribeiro *et al.*, 1995; Santos  
112 and Jégu, 1989). The area upstream of the Tucuruí dam is known as middle Tocantins River  
113 (Goulding *et al.*, 2003; Ribeiro *et al.*, 1995; Santos *et al.*, 1989). The Tocantins river is  
114 heavily impacted by human activities in its vicinity such as the operations of large cities and  
115 farms along the banks, fishing, the use of water for irrigation and electrical power generation,

116 the operation of vessels for transport and fishing and the refinement of ore (Goulding *et al.*,  
117 2003; Ribeiro *et al.* 1995).

118

## 119 B. **Data collection**

120 We conducted 42 days of boat surveys from June 2012 to January 2018. Surveys were  
121 conducted around the Capim Island (01°33'48.43"S 48°50'37.81"W) in the mouth of the  
122 Tocantins River and between the cities of Baião (02°38'57.26"S 49°40'44.94"W) and Marabá  
123 (05°19'21.02"S 49°7'29.02"W), including the reservoir of the Tucuruí Hydroelectric Plant  
124 (Fig. 1, Table I). Around the Capim Island we used a 7m wooden boat with a 2-stroke center  
125 engine and for the rest of surveys we used a 10m aluminum boat with 40 horsepower 4-stroke  
126 outboard engine. During surveys we maintained a boat speed between 5.4-8.1 knots in an  
127 area up to 200m from shore. *Inia* dolphins prefer these shallow areas most likely due to  
128 increased prey density (Gomez-Salazar *et al.*, 2012a; Pavanato *et al.*, 2016). When possible,  
129 we crossed the river once every 10km to include animals in the middle of the river channel in  
130 our recordings.

131 When a group of dolphins was sighted, we reduced speed, shut the engine off and  
132 began recording when we were approximately 20-50m from the animals. Recording sessions  
133 lasted between 2.53 minutes to 2.3 hours; recording time depended on our ability to track the  
134 animals. If a group avoided the boat approach three times we proceeded searching for another  
135 group. In 2012 and 2013 we used an Aquarian Hydrophone System connected to a Tascam  
136 DR-1 recorder, sampling rate 44kHz. In 2017 and 2018 we recorded dolphins using a High  
137 Frequency Soundtrap (Oceans Instruments), sampling rate 576 kHz. During recordings we  
138 took notes on group size and age composition, behavior, habitat, geographical position, and  
139 river state (0 to 3 in an increasing scale of turbulence). Behavioral sampling of aerial  
140 behavior followed the continuous *all event* method (Altman, 1974). A group was defined as

141 animals in a radius of 100m from each other; we watched continuously over group size and  
142 composition and took note on the highest number of animals for each encounter. We  
143 considered calves as those animals with less than half the size of an adult, also recognizable  
144 by their stunted rostrum. Habitat types were classified according to Gomez-Salazar *et al.*  
145 (2012a) and Pavanato *et al.* (2016) as follows: main river channel, channel, island, main river  
146 margin, lake, streams, and rocky formations. Behavioral states were categorized as: 1)  
147 travelling: unidirectional movement in any speed; 2) socializing: frequent body contact  
148 between animals and surface displays (*e.g.* leaps, object-carrying) and 3) feeding: repeated  
149 diving in the same area, surfacing in multiple directions and diving with an arched dorsum.  
150 As botos are normally slow swimmers (Best & Da Silva 1989, 1993) and the animals we  
151 observed were always in motion we did not include a resting category.

152

### 153 **C. Acoustic and statistical analyses**

154 We defined downsweeps as tonal signals with initial frequency higher than the final  
155 frequency and no inflection points. Inflection points were defined as a point where the slope  
156 of the whistle contour reverses direction (Au *et al.*, 2000). Acoustic analysis was carried out  
157 in the software Luscinia (<https://github.com/rflachlan/Luscinia/wiki>). We identified  
158 downsweeps with high signal-to-noise ratio, traced their contours and extracted the following  
159 parameters: fundamental frequency, peak frequency, duration, Wiener entropy and  
160 harmonicity. The last two parameters were added as measurements of noisiness, because  
161 sounds produced by *Inia* dolphins have, sometimes, noisy components. Then, we used a  
162 dynamic-time warping algorithm to compare the measured parameters between calls. This  
163 technique allows for extension and compression of a signal along the time axis, ensuring  
164 maximum overlapping of the frequency domain when comparing two signals (Buck and  
165 Tyack, 1993; Deecke and Janik, 2006; Sakoe and Chiba, 1978). The resulting dissimilarity

166 matrix from the time-warping analysis was converted to Euclidean distances for further  
 167 statistical analysis. We then ran a non-metric multidimensional scaling analysis (NMDS).  
 168 The dimensions of the NMDS were used in a principal component analysis (PCA) for further  
 169 data reduction. The results were plotted to visualize differences in downsweeps produced by  
 170 different groups and populations. Inter-call intervals and downsweep parameters were  
 171 measured in Raven Pro 1.5 (Cornell Laboratory of Ornithology, New York, NY, USA.  
 172 Downsweep whistle bouts with an inter-whistle interval shorter than 0.05s were excluded  
 173 from the analysis, as it appeared that they were produced by more than one individual as  
 174 indicated by occasional overlap of whistles in such bouts (112 downsweep whistles in five  
 175 bouts excluded).

176 To investigate the behavioral context of *Inia* downsweeps, we modelled the presence  
 177 and absence of downsweeps in each recording session using a generalized linear model  
 178 (GLM) (logit link, binomial family):

$$180 \quad (\overline{D}) = \frac{\exp(\beta_0 + \beta_1\phi_s + \beta_2\phi_t + \beta_3c + \beta_4g + \beta_5r)}{1 + \exp(\beta_0 + \beta_1\phi_s + \beta_2\phi_t + \beta_3c + \beta_4g + \beta_5r)} \quad D \sim \text{Binomial}(\overline{D})$$

181  
 182 where  $D$  represents the probability of one or more downsweeps being produced in a recording  
 183 session and  $\overline{D}$  represents expected probabilities. Parameters  $\beta_1$  and  $\beta_2$  represent the  
 184 difference in model intercept ( $\beta_0$ ) when dolphins were socializing ( $\phi_s$ ) or travelling ( $\phi_t$ ),  
 185 relative to feeding. The effects of the number of calves present ( $c$ ) and group size ( $g$ ) are  
 186 represented by  $\beta_3$  and  $\beta_4$ , respectively. Because our ability to record dolphin sounds varied  
 187 across behavioral state, some states were associated with longer recording durations than  
 188 others (e.g. socializing mean = 65.63 min  $\pm$  8.06 and feeding mean = 28.46 min  $\pm$  3.84).  
 189 Expecting that a call type should be more likely to be detected with longer recording samples,



190 we simultaneously estimated  $\beta_5$ , the effect of recording duration ( $r$ , mins) to avoid  
191 confounding the effects of behavior on downsweep production.

192 Next, to investigate possible relationships between downsweep production and  
193 discrete behavioral events, we fit the following GLM (logit link, binomial family):

194

$$195 \quad \overline{D} = \frac{\exp(\varepsilon_0 + \varepsilon_1\phi_b + \varepsilon_2\phi_f + \varepsilon_3\phi_l + \varepsilon_4\phi_o + \varepsilon_5\phi_p + \varepsilon_6\phi_s + \varepsilon_7\phi_t + \varepsilon_8r)}{1 + \exp(\varepsilon_0 + \varepsilon_1\phi_b + \varepsilon_2\phi_f + \varepsilon_3\phi_l + \varepsilon_4\phi_o + \varepsilon_5\phi_p + \varepsilon_6\phi_s + \varepsilon_7\phi_t + \varepsilon_8r)}$$

196

$$197 \quad D \sim \text{Binomial}(\overline{D})$$

198

199 where parameters  $\varepsilon_1, \varepsilon_2 \dots$  through  $\varepsilon_7$  represent the difference in expected probability of a  
200 downsweep being produced in a given recording session ( $\overline{D}$ ) when “body contact”, “flippers,  
201 fluke and belly exhibitions”, “leaps”, “object-carrying”, “penis exhibitions”, “synchronized  
202 leaps”, or “tail slaps” occurred, respectively, and  $\varepsilon_8$  represents the effect of recording  
203 duration ( $r$ , mins) (See Table II for descriptions of discrete behavior patterns). Both of the  
204 above models were also run as a quasi-binomial model to test for overdispersion. All  
205 statistical analyses were conducted using R 3.4.2 (R Core Team 2017).

206 In order to define downsweep bouts we used a log survivorship analysis as described  
207 by Slater and Lester (1982). We present inter-whistle intervals within bouts as well as  
208 between bouts and single downsweep emissions.

209

### 210 **III. RESULTS**

211 We encountered 82 groups of Araguaian botos, comprising sightings of 385  
212 individuals. Group size varied from 1 to 20 animals (mean=  $5 \pm 0.5$ ). Calves were present in  
213 28 groups. We analyzed 43 hours of sound recordings from these sightings, identifying 632  
214 downsweeps in recordings from 10 groups; calves were observed in seven of these groups.

215 The minimum number of downsweeps in an encounter was one and the maximum was 287  
216 (Table III, Fig. 2). Downsweeps were often produced in bouts with short inter-call intervals.  
217 We used 50 s as a bout inter-whistle interval criterion determined by log analysis of the  
218 distribution of inter-whistle intervals (Slater and Lester, 1982). We found 21 bouts with the  
219 shortest bout consisting of only 2 whistles and the longest of 161 whistles (median=9  
220 whistles, 25% quantile=3, 75% quantile=25). Inter-whistle intervals within bouts ranged from  
221 0.052 to 45.82 s (median=1.01, 25% quantile=0.71, 75% quantile=2.37). Intervals between  
222 bouts or single downsweep emissions varied from 51.12 to 1901.65 s (median=164.89, 25%  
223 quantile=75.51, 75% quantile=317.20) (Fig. 3, Table III). Among the 82 groups we observed  
224 in our study, three displayed social-sexual behavior (calves present in all these observations),  
225 which included object-carrying, exhibition of the penis and close body contact between  
226 individuals. Of these three groups, two emitted downsweep bouts.

227 Table III summarises downsweep whistle parameters. In the principal component  
228 analysis, the first principal component explained 68.2% of the variance in the downsweep  
229 parameters and the second principal component explained 14.9% of the variance. While there  
230 was no clear differentiation between populations (lower and middle Tocantins River), two  
231 groups, one from each population, produced very characteristic signals and formed tight  
232 clusters on the ordination analysis (Fig. 4).

233 To investigate the context of downsweep whistling, we conducted GLM analyses. We  
234 were unable to confidently identify a behavioral state for three of 82 recordings, as the  
235 animals were only observed on the surface once. These recordings were excluded from the  
236 GLMs. There was no evidence of overdispersion in either the quasi-binomial behavioral state  
237 GLM (overdispersion parameter = 0.99) or the discrete-event GLM (overdispersion  
238 parameter = 1.32). Thus, we interpreted parameter estimates from the models of the binomial  
239 family. Relative to feeding (the background behavioral state in our model), downsweeps were

240 estimated to be more likely to occur when animals were traveling or socializing, though these  
241 estimates were associated with large standard errors and were not statistically significant  
242 (Table IV). The presence of calves was also included in the analysis but again no significant  
243 relationship with downsweep production was discovered. Downsweeps were significantly  
244 more likely to be detected in long recordings, suggesting that sampling duration was more  
245 influential than the behavioral and group measures we included. Similarly, we found that  
246 none of the discrete behavioral events that we analyzed had a significant effect on the  
247 occurrence of downsweeps (Table V).

248

249

#### 250 **IV. DISCUSSION**

251 Downsweep whistles of Araguaian botos were often produced in long bouts with short  
252 inter-call intervals. All bouts occurred in social or feeding groups with the presence of calves  
253 (Table III). However, these sounds were generally rare. They were identified during only 10  
254 of 82 *Inia* encounters, which comprised over 43 hours of recordings across a wide variety of  
255 behavioral contexts and locations. Furthermore, downsweeps were not detected by Melo-  
256 Santos *et al.* (2019) in 15 hours of recordings of a socializing/feeding group of human-  
257 habituated dolphins in the lower reaches of the Tocantins River. This suggests such sounds  
258 are used in more specific behavioral contexts. Nevertheless, our GLMs do not show  
259 statistically significant relationship between the emission of downsweeps and behavioral state  
260 and/or discrete behavioral events. The occurrence of bouts was correlated with long recording  
261 sessions, which might be related to the fact that foraging and socializing groups of *Inia* were  
262 easier to track since they tended to stay in the same area for longer periods when engaged in  
263 these behaviors.

264 Downsweeps have been documented across several species of cetaceans: botos (*Inia*  
265 *geoffrensis*) (May-Collado and Wartzok, 2007); Guiana dolphins *Sotalia guianensis* and  
266 tucuxis (*Sotalia fluviatilis*) (Melo-Santos, 2018; Pivari and Rosso, 2005); pilot whales  
267 (*Globicephala macrorhynchus* and *Globicephala melas*) (Dreher and Evans, 1964; Taruski,  
268 1979); *Stenella longirostris* (Bazúa-Durán and Au; 2002); common dolphins (*Delphinus* sp.)  
269 (Dreher and Evans, 1964; Ansmann *et al.*, 2007; Petrella *et al.*, 2012); bottlenose dolphin  
270 (*Tursiops truncatus*) (Dreher and Evans, 1964; Janik *et al.* 1994; Janik and Slater, 1998);  
271 orcas (*Orcinus orca*) (Filatova *et a.*, 2012; Simonis *et al.*, 2012; Samarra *et al.*, 2015);  
272 humpback dolphins (*Sousa chinensis*) (Van Parijs and Corkeron, 2001); franciscanas  
273 (*Pontoporia blainvillei*) (Cremer *et al.*, 2017) and belugas (*Delphinapterus leucas*) (Garland  
274 *et al.*, 2015). Among these studies Garland *et al.* (2015), May-Collado and Wartzok (2007)  
275 and Petrella *et al.* (2012) and Samarra *et al.* (2015), reported downsweeps as the most  
276 common whistle type found in their samples. However, none of the above studies report  
277 downsweeps being used in a repetitive fashion or identify the contexts in which these signals  
278 were used. The exception is Dreher and Evans (1964) who reported that three juvenile  
279 bottlenose dolphins produced downsweeps in rapid repetition in situations of stress or fright.  
280 Our surface observations did not suggest that dolphins were in stress or frightful situation  
281 (e.g. aggressive behavior) when downsweep bouts were produced. However, we cannot  
282 account for behavior of dolphins whilst submerged. Simonis *et al.* (2012) also noted the  
283 repetitive use of downsweep sounds by orcas, and because of their similarities to bat  
284 echolocation calls these authors suggested that orcas might use series of downsweeps for  
285 echolocation. The downsweeps we recorded were much lower in frequency and clicks were  
286 present continuously in all of our recordings, suggesting it is unlikely downsweeps serve as  
287 echolocation sounds. Moreover, if *Inia* downsweeps were used for echolocation one would  
288 expect them to be more common, since echolocation is vital for *Inia* navigation and

289 orientation. May-Collado and Wartzok (2007) suggested that botos use whistles primarily to  
290 maintain inter-individual distance. Our observations of botos producing downsweep bouts  
291 during social and foraging activities with synchronized surface behavior suggests that this  
292 might not be the case for Araguaian botos. Further support for such a functional difference  
293 comes from the fact that downsweeps presented in May-Collado and Wartzok (2007) for  
294 botos (*I. geoffrensis*) in the Napo River (Ecuador) appeared to have different frequency  
295 contours of those recorded in our study.

296         Cetaceans often use repeated sequences of sounds to broadcast their individual or  
297 group identity (Janik *et al.*, 2013; Gero *et al.*, 2016; Sayigh *et al.*, 2013). Identity is conveyed  
298 by the patterns of frequency modulation of sounds (Janik *et al.*, 2006) or through the order in  
299 which pulses are repeated (Watkins and Schevill, 1977). As boto downsweeps have relatively  
300 simple contours (Figure 2) it is unlikely that they serve as individual identifiers in this way.  
301 However, two groups produced bouts of distinct downsweeps, suggesting possible group  
302 specificity. Nevertheless, their rare occurrence in our recordings makes it unlikely that they  
303 are required to maintain group cohesion as in delphinids (Janik, 2009). More common signals  
304 like pulsed calls (Melo Santos *et al.*, 2019) likely play a more important role in social  
305 cohesion than downsweeps.

306         Given that downsweep emissions often occurred in long bouts (Figure 3), and these  
307 bouts always occurred in the presence of calves, it is possible that they could function as  
308 begging calls (Godfray 1995a, 1995b). Animal begging calls are normally produced by  
309 infants demanding resources (often food) from their parents (Godfray 1995a, 1995b; Manser  
310 *et al.* 2008). In cetaceans, sounds occurring before suckling have been recorded for  
311 humpback whales (*Megaptera novaeangliae*), however mechanical cues are more important  
312 to initiate nursing (Videsen *et al.* 2017). Sounds associated with suckling were also reported  
313 for captive neonate bottlenose dolphins (Morisaka *et al.*, 2005). In botos, sound bouts,

314 especially whistles, might be important to start nursing. However, we did not detect a  
315 significant statistical relationship between the presence of calves and the production of  
316 downsweeps, possibly due to the small number of observations in our study.

317         In 2 out of 5 encounters with downsweep bouts, we also noticed surface displays  
318 which might indicate socio-sexual behavior such as object-carrying, exhibition of penis, and  
319 close contact between individuals. Mating calls of other animal species are also produced in  
320 bouts so as to attract the attention of possible mating partners, and this behavior is spread  
321 over a variety of taxa including insects, amphibians, birds and mammals (Catchpole and  
322 Slater, 2008; Fellers, 1979; Hedrick, 1986; Reby and Charlton, 2012). It is possible that  
323 Araguaian boto downsweeps have a similar function in the context of mating. Both  
324 downsweep production and social-sexual behavior are not observed very often which makes  
325 this a difficult relationship to study. Future studies should aim to localize sounds to  
326 individuals to help with the identification of calling contexts.

327

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335

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575

576 TABLE I. Summary of surveying effort along the Tocantins River.

Location	Month	Year	Number of surveying days
Capim Island	June	2012	1
	July	2013	3
Baião-Marabá	September	2017	20
	January	2018	18

577

578

579 TABLE II. Definition of discrete behavioral events

Behavioral event	Definition
Body contact	Animals touching each other's bodies
Flippers, fluke and belly exhibitions	Dolphins swimming sideways or belly-up so that the flippers, belly and/or fluke are shown above the water surface
Leap	Single animal jumps out of the water exhibiting most of its body
Synchronized leap	Two or more dolphins jump out of the water exhibiting most of their bodies
Object-carrying	Dolphin holding an object (e.g. pebble, vegetation) with its rostrum out of the water
Penis exhibition	Animal swimming belly-up and exhibiting its penis out of water
Tail slap	Dolphin slapping its tail fluke on the water surface one or multiple times

580

581

582 TABLE III. Characterization of all downsweep whistles. The “L” in Group ID indicates animals recorded in the Lower Tocantins River, while  
 583 the “M” stands for recordings of the Middle Tocantins River. Encounters where we detected downsweep bouts have their Group ID in bold.  
 584 Mean and standard error are presented for acoustic parameters of downsweeps.

Group ID	Behavioral state	Group size	Number of calves	Recording time (min)	Number of downsweeps	Duration (sec±SE)	Minimum frequency (kHz±SE)	Maximum frequency (kHz±SE)	Frequency range (kHz±SE)	Peak frequency (kHz±SE)
<b>L1</b>	Feeding	5	1	33.48	161	0.06±0.001	5.661±0.069	16.98±0.13	11.32±0.13	7.04±0.18
L2	Traveling	2	0	4.37	1	0.04	7.27	11.24	3.97	8.58
<b>L3</b>	Socializing	6	1	52.15	44	0.04±0.005	3.52±0.15	5.45±0.16	1.93±0.12	3.97±0.16
<b>M1</b>	Socializing	18	1	138.5	131	0.042±0.002	3.83±0.08	6.09±0.16	2.64±0.12	4.63±0.09
M2	Feeding	8	2	118.15	4	0.03±0.002	3.53±0.51	5.25±1.01	1.72±0.63	3.90±0.44
<b>M3</b>	Socializing	15	1	87.36	287	0.07±0.001	9.19±0.04	13.67±0.05	4.48±0.06	9.95±0.05
M4	Feeding	2	0	18.02	1	0.07	2.66	4.80	2.13	3.37
M5	Socializing	3	0	56.26	1	0.09	8.02	20.42	12.40	8.86
M6	Feeding	8	1	56.85	1	0.02	11.65	17.13	5.48	11.95
M7	Feeding	4	1	125.9	1	0.05	9.20	14.05	4.84	13.08
Total		71	8	691.04	632	0.06±0.001	6.73±0.10	12.32±0.17	5.58±0.14	7.64±0.10

585

586 TABLE IV. Estimated parameters relating the presence of downsweep vocalizations in  
 587 recordings of *Inia* to behavioral context and group characteristics. Relationships were  
 588 estimated with a generalized linear model (binomial family, logit-link).

	Estimate	SE	z	p
Intercept	-3.737	0.875	-4.270	< 0.001
<i>Behavior: Socializing</i>	1.310	0.898	1.458	0.145
<i>Behavior: Travelling</i>	1.426	1.353	1.054	0.292
Number of calves	0.525	0.771	0.682	0.495
Group size	-0.149	0.111	-1.344	0.179
Recording duration	0.0412	0.018	2.330	0.020

589

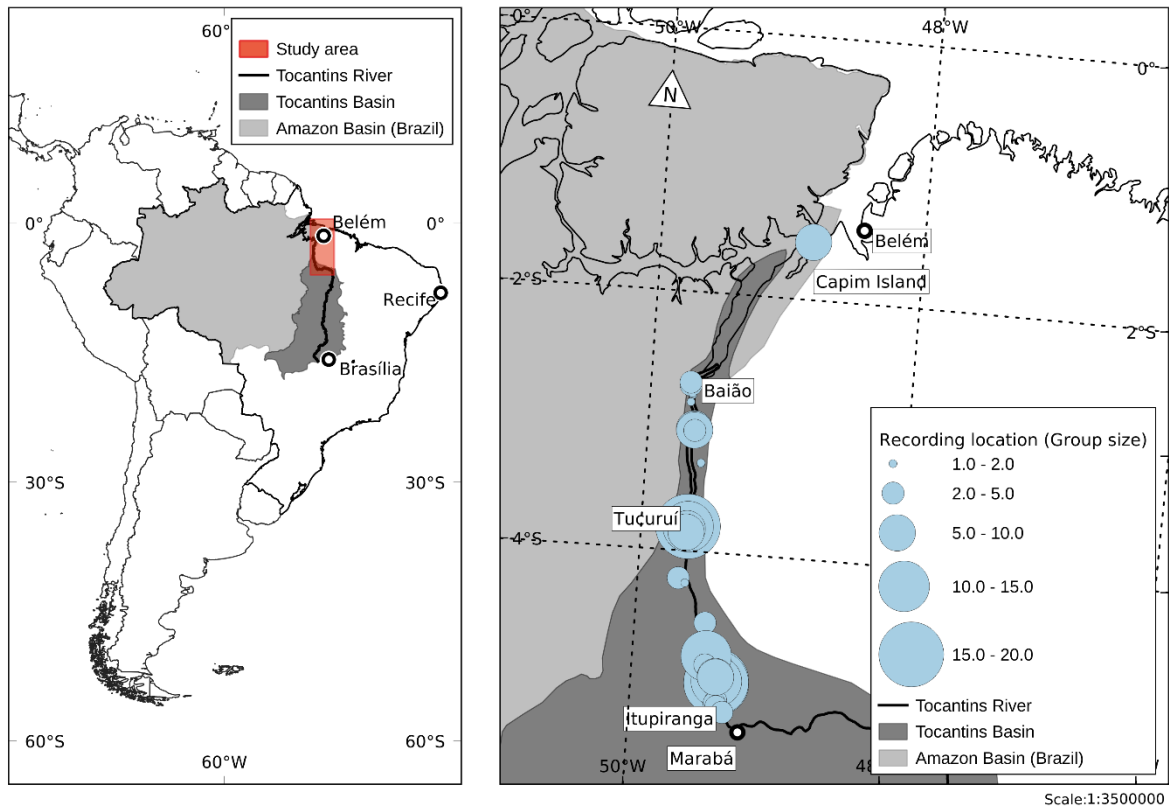
590

591 TABLE V. Estimated parameters relating the presence of downsweep vocalizations in  
 592 recordings of *Inia* to discrete behavioral events. Relationships were estimated with a  
 593 generalized linear model (binomial family, logit-link).

	Estimate	SE	z	p
Intercept	-3.746	0.817	-4.585	< 0.001
Body contact	0.014	1.257	0.011	0.991
Flippers on belly	0.761	1.255	0.606	0.544
Leap	0.950	1.043	0.911	0.362
Object carrying	-0.249	1.799	-0.138	0.890
Penis exhibition	17.529	2399.545	0.007	0.994
Synchronized leap	-0.225	1.367	-0.165	0.869
Tail slap	-0.427	1.412	-0.302	0.763
Recording duration	0.025	0.014	1.801	0.072

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595

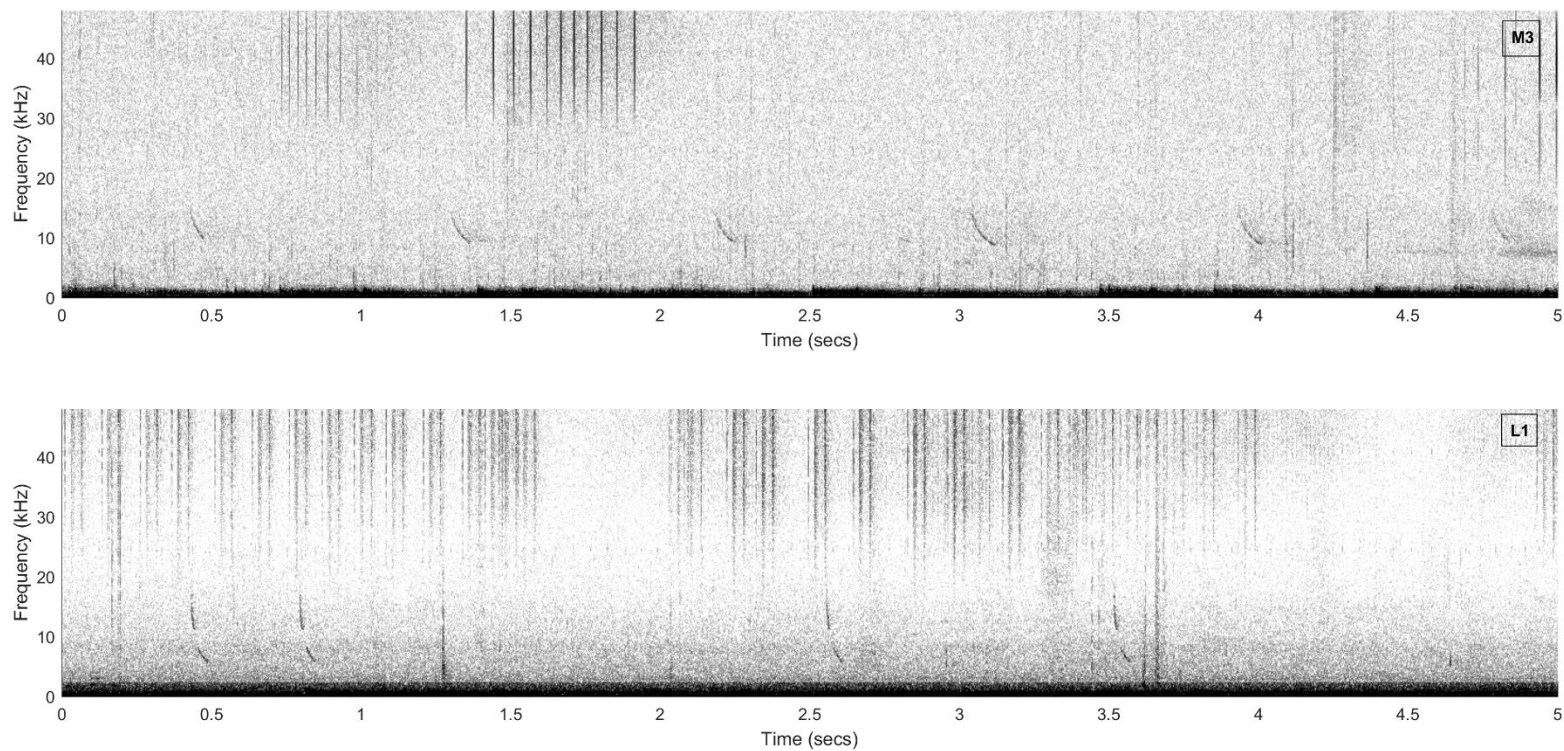


598 FIG. 1. Location of study area and of sound recordings of Araguaian botos, *Inia*  
599 *araguaiaensis*, in the Tocantins River.

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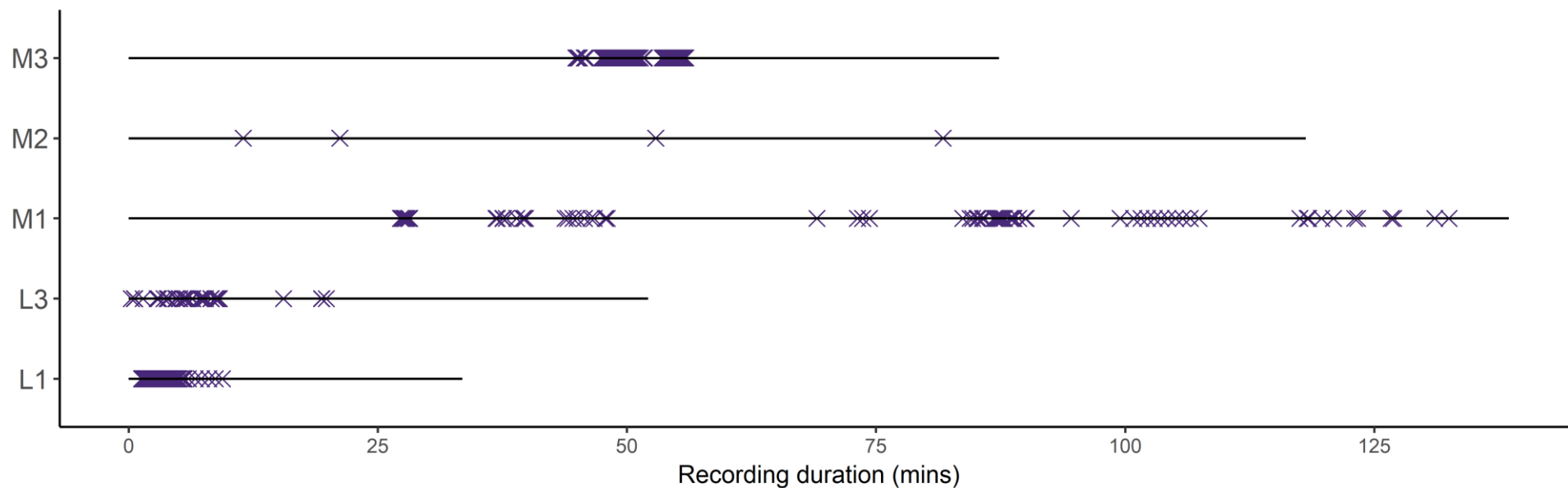


603

604 FIG. 2. Examples of downsweeps produced by Araguaian botos in the Tocantins River. Labels in the spectrograms indicate the group of botos  
605 from which the sound recording is represented. The “L” in Group ID indicates animals recorded in the Lower Tocantins River, while the  
606 “M” stands for recordings of the Middle Tocantins River.

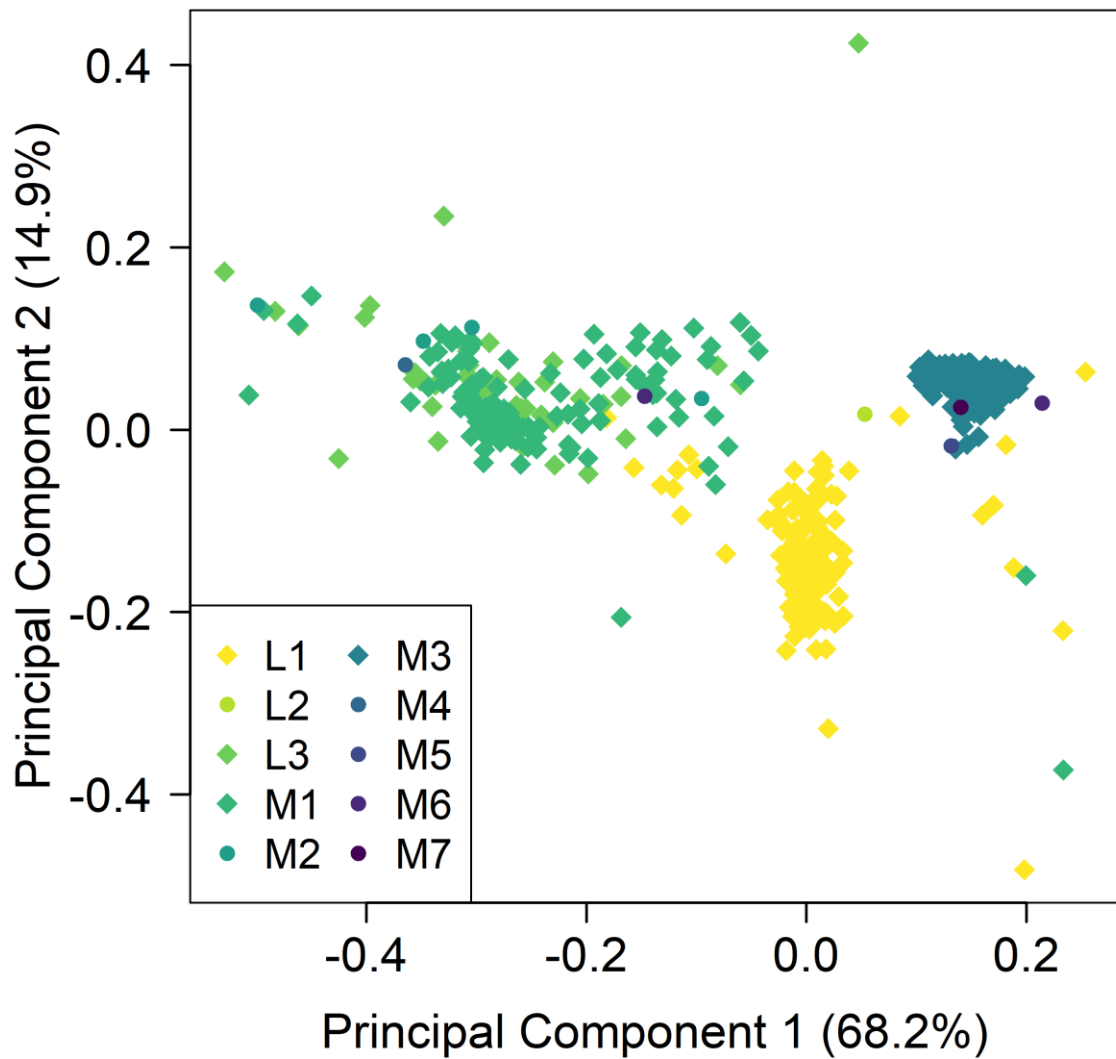


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608

609 FIG. 3. Distribution of downsweeps within each recording session. Purple X's represent downsweep emissions and the continuous lines  
610 represent the recording time for each group of Araguaian botos.



611

612 FIG. 4. Visualization of downsweep characteristics in multivariate space according to two  
 613 components in a PCA. Colours and shades indicate recording sessions. The “L” in  
 614 Group ID indicates animals recorded in the Lower Tocantins River, while the “M”  
 615 stands for recordings of the Middle Tocantins River.