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### Behavioral repertoire of Lahille's bottlenose dolphins that interact with artisanal fishers

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1 BEHAVIORAL REPERTOIRE OF LAHILLE’S BOTTLENOSE DOLPHINS THAT INTERACT WITH  
2 ARTISANAL FISHERS

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14 **ABSTRACT**

15 Many human cultures involve positive interactions with wildlife in the past and present. Lahille’s  
16 bottlenose dolphins (*Tursiops gephyreus*), for example, have developed tactics for coastal and estuarine  
17 foraging, which sustains a fishing practice known as “cooperative fishing” by traditional fishers in estuaries of  
18 southern Brazil. Here we use aerial footage to describe the behavioral repertoire of the Lahille’s bottlenose  
19 dolphins and how it relates to the frequency of net casting by fishers in the Tramandaí Inlet. From nearly eight  
20 hours of footage from June 2017 to May 2018, we mainly observed dolphins foraging in the estuary inlet when  
21 fishers were present along the shoreline. Dolphins performed at least 27 clearly distinct behaviors and three  
22 types of movement patterns. A Generalized Additive Model supported that the fishers interpret a subset of this  
23 repertoire (64%) as cues for casting their nets. The behavioral overview of the Lahille’s bottlenose dolphins  
24 presented here demonstrates not only a diverse repertoire for this population, but also its clear influence on  
25 fishers’ activities. Scientific and traditional perspectives should be integrated to better understand the ecological  
26 significance of this “cooperative fishing”, for both dolphin populations and fishers that depend on them.

27 **Keywords:** Behavioral repertoire, hunting strategy, interspecific interaction, traditional fishing, *Tursiops*  
28 *gephyreus*, Unmanned Aerial Vehicle.

## 29 **SIGNIFICANCE STATEMENT**

30 Interactions between different species can be very complex. It is a three dimensional universe that  
31 comprises the behavioral and ecological characteristics of both sides, and then the dynamic they create together.  
32 In the case of the “cooperative fishing” between fishers and dolphins in southern Brazil, we still have one  
33 dimension to disclose in detail: the dolphins behavioral repertoire. Using aerial videos from a drone we were  
34 able to shed light on how those dolphins behave and also how fishers coordinate their activity in response to  
35 the dolphins. We also showed that the dolphins’ behavioral repertoire is more diverse than assumed so far.  
36 Results suggest that the “cooperative fishing” seems to be based on the human’s perception of an extensive  
37 Lahille’s bottlenose dolphin behavioral repertoire during hunting. The knowledge provided here is essential to  
38 track the dynamic of this unique interaction in a given space and time.

## 39 **DECLARATIONS**

40 **Funding:** This study was part of the *Botos da Barra* Project (CECLIMAR/CLN/UFRGS), funded by Petrobras  
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47 **Conflicts of interest/Competing interests:** The authors declare that they have no conflict of interest.

48 **Ethics approval:** International and national guidelines for the care and use of animals were followed. Our study  
49 was entirely observational sampling dolphins in their natural habitats from a land platform. The unmanned  
50 aircraft used to capture images and fly over dolphins is registered at the Brazilian National Civil Aviation  
51 Agency (PR-437497387) and maximum care was taken to minimize any disturbance to animals during flights.  
52 Fishers were aware of them being filmed for scientific purposes and consented to participate in this study.

53 **Consent to participate:** Not applicable.

54 **Consent for publication:** All co-authors are aware of the fact and agreed to being so named.

55 **Availability of data and material:** Video footage analyzed here were logged in the databank of *Projeto Botos*  
56 *da Barra* and can be accessed upon reasonable request. The data used for statistical analysis are available as  
57 supplementary material (*Supplementary Information 2*) and in GitHub's repository ([github.com/Gui-](https://github.com/Gui-Frainer/Behavioral-repertoire-of-Lahille-s-bottlenose-dolphins)  
58 [Frainer/Behavioral-repertoire-of-Lahille-s-bottlenose-dolphins](https://github.com/Gui-Frainer/Behavioral-repertoire-of-Lahille-s-bottlenose-dolphins)).

59 **Code availability:** The R script used for statistical analysis is available as supplementary material  
60 (*Supplementary Information 3*) and in GitHub's repository ([github.com/Gui-Frainer/Behavioral-repertoire-of-](https://github.com/Gui-Frainer/Behavioral-repertoire-of-Lahille-s-bottlenose-dolphins)  
61 [Lahille-s-bottlenose-dolphins](https://github.com/Gui-Frainer/Behavioral-repertoire-of-Lahille-s-bottlenose-dolphins)).

62 **Authors' contributions:** NS, GF and IBM designed the study. IBM was responsible for funding acquisition.  
63 NS, GF, BS and IBM collected the data on dolphin behavior, population composition and fishers' activities. NS  
64 examined all filming for characterizing behavioral repertoire and NS, GF and IBM interpreted the data. NS, GF  
65 and GAB statistically analyzed the data and interpreted the results. NS drafted the manuscript and GF, GAB  
66 and IBM all revised it critically. All authors gave final approval before submission.

67

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88 **INTRODUCTION**

89 Cooperation between humans and wildlife for mutual benefit has a long history. Dolphins, wolves,  
90 crows and honeyguides are known for engaging in this type of ecological interaction throughout human history  
91 (Fairholme 1856; Ridgway 1970; Busnel 1973; Pryor and Lindbergh 1990; Simões-Lopes 1991; Northridge  
92 2009; Smith et al. 2009). Site-specific behavioral specializations led some wild populations to develop ways to  
93 cooperate with other animals including humans, which have become important cultural traits of some human  
94 and non-human societies (Simões-Lopes et al. 2016; Spottiswoode et al. 2016). Current cases of human-wildlife  
95 cooperation, i.e., when both species engage in the foraging activity to achieve a mutually positive outcome,  
96 include greater honeyguides (*Indicator indicator*) in sub-Saharan Africa, Irrawaddy dolphins (*Orcaella*  
97 *brevirostris*) in Myanmar, and Lahille-bottlenose dolphin (*Tursiops gephyreus*, hereafter ‘dolphin’) in southern  
98 Brazil (Cram et al. 2022).

99 The “cooperative fishing” in southern Brazil is defined essentially based on Traditional Ecological  
100 Knowledge (TEK) (Berkes 1993). The fishing practice, involving stereotyped sequence of behaviors between  
101 dolphins and fishers (mainly targeting mullets, *Mugil* sp.), is understood especially under the fishers perception  
102 on the environment (Pryor and Lindbergh 1990; Simões-Lopes et al. 1998; Peterson et al. 2008; de Sousa et al.  
103 2022; Cantor et al. 2023). Often described as “signals” by fishers, dolphin behaviors are actually cues that help  
104 them to identify the ideal moment for net casting (Simões-Lopes et al. 1998; Lehmann et al. 2014). Dolphins,  
105 locally called as *botos*, are known to direct the fish towards the sandbank while fishers try to identify the best  
106 moment for casting their nets (Simões-Lopes et al. 1998). Learning to recognize dolphins’ stereotyped  
107 movements, and the ideal moment for net casting, is a skill passed among fishers across generations (Simões-  
108 Lopes et al. 1998; Peterson et al. 2008; da Rosa et al. 2020; Ilha et al. 2020; Valle-Pereira et al. 2022). When  
109 foraging near the shore, dolphins provide fishers with an opportunity to improve their fishing efficiency  
110 (Simões-Lopes et al. 1998; Smith et al. 2009; Kumar et al. 2012; Santos et al. 2018). It has been proposed that  
111 cast nets work as physical barriers similar to the sandbanks, disrupting fish school and facilitating fish capture  
112 by dolphins (Simões-Lopes et al. 1998; Smith et al. 2009).

113           Such dolphin-fisher interaction sustains a traditional fishing practice in Southern Brazil for decades:  
114 the oldest reported case is for Laguna, in Santa Catarina state, around 1890 (Zappes et al. 2011; van der Wal et  
115 al. 2022). This artisanal practice is known for minimal bycatch (Simões-Lopes et al. 1998; Santos et al. 2018),  
116 contributing to the conservation of the estuary fishing stocks through a sustainable practice (Simões-Lopes et  
117 al. 1998; Ilha et al. 2020). The Tramandaí Inlet is another site where the dolphin-fisher interaction happens in  
118 Brazilian waters. The presence of fishers is one of the central elements of that landscape and is strongly related  
119 to the presence of dolphins. For at least 30 years, around ten resident dolphins have been regularly observed in  
120 the small canal of the Tramandaí Inlet (Tabajara 1992; Simões-Lopes and Fabian 1999; Giacomo and Ott 2016;  
121 Silveira 2020). Due to the close relationship established for years, the fishers' perspective has driven scientific  
122 investigation on the dolphins' stereotyped behaviors. While the dynamic between dolphins and fishers is  
123 generally well studied (Tabajara 1992; Simões-Lopes et al. 1998; Simões-Lopes and Fabian 1999; Giacomo  
124 and Ott 2016; Camargo et al. 2020; Ilha et al. 2020; Silveira 2020), there is still a gap behind the behavioral  
125 repertoire on the dolphins' side.

126           In this study, we present a detailed behavioral description for the dolphins in the Tramandaí Inlet using  
127 Unmanned Aerial Vehicle (UAV) video footage. We describe their repertoire when fishers were present and  
128 few occasions when fishers were absent. We therefore explored the dolphin-fisher interaction. We expected  
129 dolphins' foraging repertoire to be varied and dynamic, given the generalist diet of the genus *Tursiops* (Barros  
130 and Clarke 2009; Milmann et al. 2016; Secchi et al. 2016). The perspective adopted here provides insights on  
131 the dolphins' behavioral repertoire, on how it influences the fishers dynamics and on the nature of such complex  
132 interaction.

## 133           **MATERIAL AND METHODS**

### 134           *Study site, fishers and dolphins*

135           The Tramandaí Inlet is surrounded by an increasingly urbanized environment (da Silva et al. 2017)  
136 and it is listed as a “priority area for conservation of biodiversity” by the Brazilian Ministry of Environment  
137 (MMA 2007). It is a narrow and relatively shallow canal (average depth = 2.9 m) where the Tramandaí-  
138 Armazém lagoon system (29°58'33.7"S 50°07'10.0"W) flows into the Atlantic Ocean. This hydrographic  
139 system comprises interconnected lagoons extending for 115 km along the coastline of the Rio Grande do Sul  
140 state, southern Brazil (Viero and Silva 2010). Dolphins regularly forage in the Tramandaí Inlet (Fig.1) and

141 fishers traditionally stand on the margins of the estuary (Fig. 1C) looking for specific dolphin behaviors. At the  
142 time of data collection (2017-2018), 11 resident dolphins and a few seasonal visitors were known to the area  
143 (Simões-Lopes et al. 1998; Simões-Lopes and Fabian 1999; Giacomo and Ott 2016; Ilha et al. 2018).

#### 144 *Data collection*

145 We recorded dolphin and fisher behavior using an UAV (Dragon Fly© hexacopter, S550). The UAV  
146 was equipped with a DYS FPV Camera HDV-1 1080P video recorder, with motion stabilizer. We selected the  
147 dolphins based on our ability to observe them from land and to photo-identify individuals. When more than one  
148 individual were simultaneously present in the Inlet but clearly in different places or engaged in distinct  
149 activities, we prioritized the foraging adults. Group was defined as instantaneously spatial aggregation  
150 following Whitehead (1999).

151 We conducted UAV flights over the Tramandaí Inlet from June 2017 to May 2018, at least once a  
152 month. Exceptions were November and December 2017, due to either the absence of dolphins or unfavorable  
153 weather conditions (i.e., wind speeds > 20 km/h and/or presence of rain or fog). All UAV flights were manually  
154 operated (Verfuss et al. 2019) from land by one of us (GF), i.e., from where fishers stand for cast net fishing  
155 (Fig. 1C), and each flight duration was determined by battery life and wind conditions. Flights were stabilized  
156 and maintained at a constant safe altitude (i.e., 20–35 m above the water) before flying over the dolphins to  
157 avoid behavioral responses to the UAV presence (Ramos et al. 2018; Fettermann et al. 2019).

158 We identified dolphins individually during UAV surveys through high resolution photographs of their  
159 dorsal fins and natural marks (Würsig and Würsig 1977), taken using a Canon 7D Mark II DSLR camera with  
160 Canon EF 300mm f/2.8L IS II USM Lens. Photographs and *ad libitum* visual observations of dolphin behaviors  
161 (Altmann 1974; Mann and Smuts 1999) at surface level, were simultaneously collected to support the behavioral  
162 information from UAV video footage. Such footage were able to capture the dolphins mainly when at surface,  
163 but also underwater depending on water turbidity or the occurrence of behavioral prints on the surface (e.g.,  
164 substrate stirring up, water movements). Pictures were added and compared to *Projeto Botos da Barra* photo-  
165 ID catalogue. We logged video footage, photographs and individual information in the database of the *Projeto*  
166 *Botos da Barra* (CECLIMAR/CLN/UFRGS). Although not statistically analyzed, we took note of general



167 aspects of the dolphins' behaviors, for example the proximity to the sand bank when they occurred, and the  
168 very few occasions when dolphins were observed in the absence of fishers.

169 *Data analysis*

170 The behavior repertoire of dolphins was identified and characterized (Table 1; *Supplementary*  
171 *Information 1*) by analyzing UAV footage using BORIS (Behavioral Observation Research Interactive Software  
172 v. 7.4) (Friard and Gamba 2016). We quantified events (i.e., an instantaneous display of a non-measurable  
173 duration) and behavioral states (i.e., those that occurred for some duration: the non-mutually exclusive states  
174 defined as "activities" and "movement patterns") (Lehner 1996) for each footage and their duration were  
175 measured (Table 1; *Supplementary Information 1*). Drone footage were analyzed by a single observer because  
176 the dolphin behaviors were easily distinguishable from each other (Table 1). Net castings following dolphins'  
177 behaviors were also counted to be included in analysis.

178 We modeled the relationship between dolphin behavior followed by fishers' reaction to explore and  
179 quantify the dynamics of this unique interaction at a behavioral level. The series of dolphin behaviors followed  
180 by net castings (i.e., net casting after a maximum of 5 seconds after dolphins' behavior) were first identified  
181 using software Behatrix ([boris.unito.it/pages/behatrix](http://boris.unito.it/pages/behatrix)). Although we acknowledge that important differences  
182 between the frequency of dolphins' behaviors and frequency of net castings may exist between seasons (e.g.,  
183 due to the fluctuation in fish species and availability), sample sizes were not large enough to test "season-  
184 behavior" interactions in the models.

185 To accommodate the fact that biological relationships can often be complex and poorly represented by  
186 simple linear statistical models, Generalized Additive Models (GAM; Hastie and Tibshirani 1990) were used  
187 to test the fit of either simple (e.g. linear) or more complex (e.g. nonlinear) statistical models. Each flight  
188 represented a sampling unit in the GAM analysis. The frequency observed for each behavioral event (i.e.,  
189 identified as preceding net casting) per UAV footage, divided by the duration of the footage, were used as  
190 explanatory variables (Table 1; *Supplementary Information 2*). The response variable in the models was the  
191 number of net castings divided by the number of fishers responding to dolphins' performance within an UAV  
192 footage (*Supplementary Information 2*). That ratio represents the average net casting per fisher per unit of time.  
193 The data were visually inspected, and outliers (i.e., rare extreme values) were identified and removed to improve

194 model fitting. The Gaussian distribution was assumed for the model residuals, which proved to be adequate at  
195 fitting check and diagnostics.

196 A forward covariate selection was conducted: initially, each explanatory variable was modeled  
197 independently (i.e., one variable per model) and the model presenting the lowest AIC score was selected for the  
198 following step. At each step, a set of models was created by adding, individually, non-correlated ( $r < 0.4$ )  
199 covariates to the previously selected model. Additional steps on covariate inclusion were conducted until the  
200 AIC could not be improved. Modeling analysis were performed in R statistical software (R Core Team 2020)  
201 using *mgcv* package (Wood 2001), *Hmisc* (Harrell and Dupont 2020), *tidyverse* (Wickham et al. 2019) and  
202 *rstatix* (Kassambara 2020) packages.

## 203 RESULTS

204 During this study, 78 UAV flights were performed, resulting in a total of 7h, 41min and 6s of recorded  
205 footage (average = 6.98min; minimum = 2min and 13s, maximum = 11min and 16s). A total of 11 different  
206 individual dolphins were recorded during the period of the study, including one calf. They were all known  
207 animals, being 10 residents and 1 visitor. For the 48 different dolphins' group composition observed (i.e.,  
208 individuals alone or different combinations of individuals within a group) among 20 encounters, mean group  
209 size was 2.25 dolphins (SE = 0.14, median = 2, minimum = 1, maximum = 4). Fishers were not present in the  
210 footage of only three flights and their numbers varied between 0 and 25 (mean = 6.37). Only once a dolphin  
211 appeared to react to the presence of the UAV, displaying a brief upward-directed behavior (i.e., side-roll with  
212 open mouth, Table 1), with no change in their swim direction. There was no apparent reaction to the UAV  
213 presence by fishers.

214 Dolphins were observed moving within the estuary adopting three distinct behavior patterns (Fig. 2):  
215 “milling” (n = 50, duration = 354.9min), “against-current” (n = 23, duration = 69.6min) and “prowling” (n =  
216 13, duration = 40.8min). “Prowling” is a novel behavior for genus *Tursiops* and is characterized by the smooth  
217 zigzagging swimming near of the shoreline, surrounding a specific area (Fig. 2b). Its description was based on  
218 directionality, consistency and area covered. As expected, our footage mainly recorded dolphins when in  
219 foraging state, which was evidenced by rapid and energetic surfacing, frequently with drastic changes in  
220 swimming direction, fish chases, fish fleeing and/or substrate (e.g., sand) stirred up (Table 1; *Supplementary*

221 *Information 1*). Dolphins also performed foraging behaviors (i.e., “regular dive”, “peduncle dive”, “fast swim”  
222 and “side-slap”, Table 1) during those three occasions where fishers were absent.

223 We documented 25 distinct behavioral events adopted during foraging from both UAV footage and  
224 direct observation (Table 1; *Supplementary Information 1*, Table S2, except “macrophyte-carrying” and “socio-  
225 sexual”; *Supplementary Information 4*). “Head behaviors” (i.e., “head slap”, n = 80; and “side slap”, n = 70),  
226 “rooster tailing” (n = 25), and “horizontal circles” (n = 9) were mostly observed when actively chasing fish.  
227 When benthic fishing, dolphins spent longer time at depth, apparently exploring the estuary bottom and causing  
228 substrate to rise towards the surface. When foraging at the surface, “side swims” and “vertical position” were  
229 mostly observed (*Supplementary Information 4*). The only calf in this study (Dolphin ID: #I26; Name:  
230 *Ligeirinho*; about 4 years old at the time) was recorded foraging in the entire extent of the water column,  
231 apparently preying on benthic to epipelagic fish. We also documented *Ligeirinho* performing “head slaps” and  
232 “side slaps” while foraging, in synchrony with its mother, which is the main matriarch inhabiting the area  
233 (*Geraldona*, #I11; Silveira 2020).

234 When dolphins displayed “head behaviors” (“head slap” and “side slap”, n=150), they were usually  
235 foraging near the sandbank (i.e., closer than ~20 m from shoreline; n=122) and, consequently, close by the  
236 fishers. We also observed individual dolphins behaving similarly while they foraged alone, i.e., in the absence  
237 of either fishers or other dolphins within 20 m (n=26). In two occasions, a group displayed those behaviors  
238 towards another dolphin. Interestingly, the only dolphin that did not perform “head slaps” was a visitor (ID:  
239 #I21). The “pinwheeling” display was observed while dolphins were foraging individually (n=7) and only once  
240 in a group (*Supplementary Information 4*). In a similar way, dolphins were observed to apparently cooperate at  
241 prey catching using “carousel” feeding on three occasions (Table S2, *Supplementary Information 1* and *4*), and  
242 only involving *Ligeirinho* (the only calf) and another resident juvenile dolphin (Dolphin ID: #I17; Name:  
243 *Esperança*). In those occasions, “carousels” were preceded and followed by “active surfacing”, “sharking” and  
244 “tail slaps”. Dolphins were also observed chasing fish in the shore break, at the estuary mouth, as well as near  
245 heavily urbanized estuary margins where permanent constructions are present in the sandbanks (Fig. 1C).

246 We identified fishers casting their nets after 16 dolphin behaviors (Table 1), i.e., the explanatory  
247 variables in the GAM. Fishers cast their nets on average of 6.14 times per footage (minimum = 0, maximum =  
248 31). The best model, as indicated by the smallest AIC score, presented an adequate fit and no autocorrelation

249 issues (Fig. S1, *Supplementary Information 5*). That model included nine behaviors as important predictors to  
250 net castings and presented 61.7% of deviance explained (Table 2; Fig. 3; Fig. S1, *Supplementary Information*  
251 5). “Head slap”, the covariate selected in the first step of the forward covariate selection, was clearly positively  
252 related to the frequency of net castings (Fig. 3). The relationship between net casting frequency and other  
253 behaviors included in the model varied in shape and precision, and they seem to be influencing the fishers  
254 perception of dolphin displays, but potentially with less importance. “Side slap” presented high correlation to  
255 “head slap” ( $r = 0.54$ ); “bubble blow” was correlated to “underwater tail-slap” ( $r = 0.43$ ) and were not  
256 considered as candidate covariates after the respective correlated covariates were selected.

## 257 **DISCUSSION**

258 Previous work on dolphin-fisher interactions have mainly investigated the interaction itself rather than  
259 the behavioral nuances in detail (Busnel 1973; Simões-Lopes 1991; Simões-Lopes et al. 1998; Smith et al.  
260 2009; Kumar et al. 2012; Simões-Lopes et al. 2016; Cantor et al. 2018; Cantor et al. 2023). Research has been  
261 focused on four stereotyped behaviors used as cues, popularly known as "signals" by fishers – i.e., “back  
262 presentation”, “head slap”, “partial emersion” and “tail slap” (*Supplementary Information 6*) (Simões-Lopes et  
263 al. 1998). Fishers’ perspective on dolphins movements is based on a broad and potentially immeasurable  
264 interpretation (Silva et al. 2021) that dialogs with Simões-Lopes et al. (1998) descriptions.

265 Here we present the most comprehensive dedicated study to characterize the foraging repertoire of  
266 Lahille’s bottlenose dolphins associated to cast net fishing in southern Brazil. Our dedicated study characterized  
267 the foraging repertoire of Lahille’s bottlenose dolphins associated to cast net fishing, revealing (i) a refined  
268 description of the behavioral repertoire of this species, and (ii) that ethological and traditional perspectives may  
269 disagree on their interpretation of this repertoire.

270 The aerial perspective adopted here allowed a more detailed and comprehensive investigation on the  
271 dolphins’ behavioral repertoire (Table 1; *Supplementary Information 1*). Our results support the use of UAVs  
272 as a relatively inexpensive, safe and minimally invasive tool that can be an asset to behavioral science, although  
273 well-structured methods for ethological studies using UAVs are still lacking (Castro et al. 2021). The aerial  
274 perspective also allowed us to identify a novel movement pattern (“prowling”; Fig. 2B). However, most  
275 behaviors recorded here meet the definitions available in the literature for closely-related cetacean species  
276 (Shane 1990; Simões-Lopes et al. 1998; Mann and Sargeant 2003; Lusseau 2006). When chasing and catching

277 prey, dolphins in the Tramandaí Inlet use both specialized (i.e., "head slap" *sensu* Simões-Lopes et al. 1998;  
278 Simões-Lopes et al. 2016) and universal tactics (i.e., common to other coastal bottlenose dolphins around the  
279 world; e.g., "leap", "porpoise", "active surfacing" and "fish toss", Shane 1990; Mann and Sargeant 2003;  
280 Lusseau 2006).

281 Dolphins hitting the water with their throat ("head slap") is the main stereotypical behavior of this  
282 population as primarily suggested by (Simões-Lopes et al. 1998). In addition, "side slap" is also a common  
283 stereotyped foraging behavior of resident dolphins. Despite being highly correlated to each other within UAV  
284 footage, these two behaviors were seen at distinct times throughout a foraging encounter. While "side slap"  
285 seems to be displayed during prey chasing, "head slap" is apparently related to fish capture, working as the  
286 *gran finale* for the hunt. Both were originally described in a social context by Shane (1990), but here these  
287 behavioral events were often observed while resident dolphins were chasing fish against the sandbank, where  
288 normally fishers stand (Cantor et al. 2023). It is likely that these behaviors start in their early months of life, as  
289 suggested by Simões-Lopes et al. (1998), and further developed until the end of infancy.

290 Our observations of the sequential and synchronic performance of *Ligeirinho* with its mother (i.e.,  
291 *Geraldona*) illustrate one of their learning processes (i.e. vertical learning). In addition, horizontal and  
292 individual learning also plays a vital role in the development of their foraging skills (Simões-Lopes et al. 2016).  
293 Social learning plays an important role in the evolution of complex and cultural behaviors - e.g., "sponge tool  
294 use" and "beach hunting" in cetaceans (Guinet and Bouvier 1995; Patterson et al. 2015); "tool use" in primates  
295 (Whiten et al. 1999). The long-term interaction between dolphins and fishers in the Tramandaí Inlet would  
296 probably not be possible without the learning process (Cram et al. 2022). The interaction essentially depends  
297 on the fishers' ability to perceive the system and to respond appropriately to the dolphins' behavior, and this is  
298 highly dependent on learning (Simões-Lopes et al. 1998; Peterson et al. 2008; da Rosa et al. 2020; Ilha et al.  
299 2020; Valle-Pereira et al. 2022).

300 "Head slap" is known as the main trigger for net casting in the Tramandaí Inlet. Our statistical model  
301 indicated that the more the dolphins displayed "head slaps" the more fishers attempted net casting, corroborating  
302 that "head slap" is the behavior most frequently interpreted by fishers as the indication of the best time to cast  
303 their nets (Simões-Lopes et al. 1998). Additionally, eight other behaviors were important predictors for the  
304 frequency that fishers cast their nets. Six out of the nine most relevant behaviors for net casting (i.e., "head

305 slap”, “peduncle dive”, “regular dive”, “sharking”, “active surfacing” and “fast swim”) could fit in the broad  
306 descriptions of the four general categories proposed by Simões-Lopes et al. (1998) and cited previously  
307 (*Supplementary Information 6*). The other three new foraging behaviors related to fishers’ activity (i.e.,  
308 “pinwheeling”, “bubble blow” and “humping surface”) might suggest a scenario where fishers are becoming  
309 more opportunistic about the stereotyped behavioral cues of the dolphins. The regular involvement of sporadic  
310 and inexperienced fishers on the interaction with dolphins nowadays may be one of the reasons behind this  
311 opportunism (see *Local threats and future actions* section below).

312           The final model showed a range of different relationships between the relative frequency of net casting  
313 and of dolphin behaviors (Fig. 3). Most of them could not be precisely estimated, denoted by large p-values  
314 (i.e., non-significant at  $\alpha = 0.05$ , Table 2). That is likely a consequence of the sample size for net casting and,  
315 in some cases, small frequencies of some behaviors within UAV footage. Most of the covariates selected seem  
316 to show a positive relation to the response, indicating they are part of the complexity of displays interpreted  
317 popularly as “signals”. Clear exceptions are “Sharking” and “Fast swim”, that possibly are part of the common  
318 behavioral repertoire. Here, traditional fishers were not differentiated from amateurs or tourists (Zappes et al.  
319 2011; Silva et al. 2021), neither during fieldwork or footage analyses, however individual factors for both  
320 dolphins and fishers may be relevant to the interaction and it should be take into account in future  
321 studies. Including fishers’ identification as a random effect in the models would not be possible since the casting  
322 net frequencies (i.e., the response variable) are not fisher-specific, but an average of net castings of multiple  
323 fishers within a footage. Thus, we suggest that further studies investigate fisher-specific response to the  
324 dolphins, addressing on a finer scale the difference that experience might express on the way they respond. In  
325 conclusion, our modeling results successfully reflect how strongly some dolphin behaviors influence the  
326 decision of net casting by the traditional fishers in the Tramandaí Inlet.

327           The "signals" interpreted by the fishers are part of an extensive foraging repertoire displayed by the  
328 Lahille's bottlenose dolphins in the Tramandaí Inlet. Dolphin behaviors are in fact cues rather than signals at  
329 that interspecific interaction (Ruxton and Schaefer 2011). This perspective opens the possibility to see the  
330 phenomenon popularly known as “cooperative fishing” as a more dynamic and flexible interaction. It is known  
331 that fish can be “stolen” from inside cast nets by dolphins (Ilha et al. 2020) and teeth marks on mullets captured  
332 by fishers are not rare (Simões-Lopes 1991). Thus, considering the non-fixed nature of any ecological

333 interaction, this relationship may fall within a flexible continuum around the cooperation depending on the  
334 individual's engagement and environmental factors, such as kleptoparasitism and commensalism (Dounias  
335 2018; Moran et al. 2022; Cantor et al. 2023). The elements of this continuum are not only possible evolutionary  
336 precursors of wildlife-human cooperations (Cram et al. 2022), but can also have a narrower, more precise,  
337 meaning for the interacting dolphins currently. Further investigation should address the benefits from such  
338 interaction for individual dolphins, and for those populations, to clarify such questions in different temporal  
339 scales (i.e., along day, seasons and years) (Cram et al. 2022), and how dolphins behave when fishers are absent.

340 Our results demonstrate that dolphins of Tramandaí Inlet have a diversified foraging repertoire that are  
341 used as cues by fishers during fishing activities. It is clear that dolphin behaviors are essential for this socio-  
342 cultural heritage known as “cooperative fishing” (Simões-Lopes 1991; Stépanoff and Vigne 2019): the  
343 performance of “head slap” is the hallmark of these coastal-estuarine dolphins living in the Tramandaí Inlet,  
344 but other behaviors also play an important role on their dynamics as well as on the ecological interactions. This  
345 flexible and peculiar interspecific interaction is a vivid example of how wildlife and humans can influence and  
346 harmonically interact to each other in the contemporary world.

#### 347 *Local threats and future actions*

348 Understanding animal behavior and culture are important for effectively conserving the populations  
349 as well as their ecological interactions (Brakes et al. 2019). The human-wildlife cooperation has been affected  
350 negatively by environmental changes (van der Wal et al. 2022; Cantor et al. 2023). In addition to the ongoing  
351 risks that contributed for Tramandaí Inlet dolphins to be locally, nationally and globally vulnerable to extinction  
352 (FZB 2014; Vermeulen et al. 2019; MMA 2022), current local infrastructural projects (e.g., new bridge and  
353 port construction, offshore and inshore wind farm) maximize the threats not only for this population but also  
354 for the people who participate in such interactions (Camargo et al. 2020). New generations of fishers, who act  
355 as knowledge repositories, are not encouraged to follow that activity anymore, which is attributed to public  
356 policy negligence, lack of interest from stakeholders and decrease of fish stocks targeted by the “cooperative  
357 fishing” (i.e., mullets) (Ilha et al. 2020; Silva et al. 2021; Cantor et al. 2023). Protective actions against  
358 overexploitation by non-professional fishers should be created for at least the mullet season since it affects the  
359 prey availability for professional fishers’ and disturb their traditional fishing practice (Smith et al. 2009; Kumar  
360 et al. 2012; Santos et al. 2018). Our study framework may help assist in finding processes potentially influencing

361 changes in the behavioral repertoire of Lahlille bottlenose dolphins, as well as the fishers' interpretation upon  
362 dolphin behaviors that could identify potential disturbance in this interaction. Conservation measures have to  
363 be taken if we are to ensure a favorable landscape for the future of this remarkable interaction, such as defining  
364 priority areas for conservation and sustainable use of local natural resources, to prevent future urban  
365 development and consequent habitat loss.

366         These ongoing pressures make this harmonic system vulnerable to disappear before this century ends  
367 (Cantor et al. 2023). The three pillars of dolphin-fisher interaction (i.e., mullet availability, dolphins'  
368 interaction, and fisher experience) are under threat and each of them have to be investigated both as single and  
369 combined elements. Our study provided a detailed characterization on dolphins' behavioral repertoire in the  
370 Tramandaí Inlet and its context within the so-called "cooperative fishing" with artisanal fishers in southern  
371 Brazil. It may be a useful starting point to quantitatively monitor not only the dynamicity of this unique  
372 interaction, but also the health of this population by assessing their ethological information in long-term studies.  
373 The historical record of behavioral and cultural traits depends directly on these studies (Laland et al. 2015) since  
374 they are volatile evolutionary features that strongly drive how species adapt under the environmental conditions.

## 375                 **LITERATURE CITED**

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541

542 **Tables**

543 **Table 1** Description and observed quantity of behavioral events performed by dolphins which were followed  
544 by cast net throws (i.e., explanatory variables for statistical modeling). Behaviors are listed in decreasing order  
545 according to the total number observed from UAV footage. Complete ethogram is present as *Supplementary*  
546 *Information 1*.

Behavioral event	Description	Source of description	Number observed
Regular dive *	Only the blowhole, part of the back, and the dorsal fin are exposed. Dolphin leaves surface by sinking at end of a breathing series without arching peduncle or raising flukes out of water.	Shane (1990); Mann and Sargeant (2003)	702
Peduncle dive *	The dolphin arches its back and exposes its peduncle arched at dive but not its flukes as it submerges after breathing (or becomes partially submerged).	Shane (1990), as tail-stock dive; Mann and Sargeant (2003); Lusseau (2006), as tail-stock dive	99
Head slap *	Dolphin exposes its head and hits the surface with its throat.	Würsig and Würsig (1979); Shane (1990), as forward slap; Simões-Lopes et al. (1991), as head knock; Simões-Lopes	80

		et al. (1998); Lusseau (2006), as head flop	
Side slap	Dolphin exposes its head and hits the surface with the lateral of the head.	Shane (1990)	70
Fast swim *	A dolphin rapidly accelerates and/or swims fast along or below the water surface.	Mann and Sargeant (2003)	65
Sharking *	Dolphin swims horizontally at the water surface with its dorsal fin visible above water	Lusseau (2006)	63
Active surfacing *	Rapid surfacing with spray (horizontal posture), the dolphin's <i>ventrum</i> does not clear the water surface.	Shane (1990), as racing dive; Mann and Sargeant (2003), as rapid surface; Lusseau (2006)	62
Humping surface *	A normal speed surface in which the dolphin "humps up" its posterior half to break its forward motion as it descends. Often seen when dolphins are driving and pursuing the prey in shallow waters.	Mann and Sargeant (2003)	29
Underwater tail-slap	A dolphin slaps with their flukes underwater.	Smolker and Richards (1988)	27
Bubble-blow *	Exhaling underwater, producing a stream of bubbles	Lusseau (2006)	22
Porpoise	Rapid surfacing whereby dolphin almost clears surface in horizontal position but <i>ventrum</i> remains on surface. The dolphin's entire body does leave the water surface in the course of the dive.	Mann and Sargeant (2003)	18
Side-roll	Head and body slightly turned to one side.	Shane (1990); Ramos et al. (2018)	17
Horizontal circle	Dolphin swims rapidly in a circle on its side with body bent forward, much like a cat chasing its tail.	Shane (1990)	9
Pinwheeling *	Dolphin increases its speed suddenly (often with its fin constantly exposed) for 10-20m toward shoreline. Just before it reaches the shore, the dolphin leans on its side and spins in a circle or makes a hairpin turn.	Leatherwood (1975); Smolker and Richards (1988); Shane (1990)	8
Tail-out dive	The dolphin arches its back and exposes its flukes as it dives. Usually used for deep dives.	Shane (1990), as flukes-up dive; Mann and Sargeant (2003); Lusseau (2006)	7
Leap	Dolphin jumps out of the water with entire body clears (any height).	Würsig and Würsig (1979); Shane (1990); Mann and Sargeant (2003)	5

547 \* Behavioral events included in the final model as predictors for net casting.

548



549 **Table 2** Explanatory variables (behaviors) included in the final model for fishers response facing dolphins  
 550 behaviors in order of inclusion during covariate selection (edf = effective degrees of freedom; i.e., reflects the  
 551 degree of non-linearity of a curve).

Order	Behavior	edf	p-value	F-test
1	Head slap	1.817	0.0661	2.581
2	Peduncle dive	3.173	0.0596	2.236
3	Regular dive	4.697	0.3071	1.098
4	Sharking	4.421	0.0356	2.299
5	Active surfacing	1.737	0.1414	2.428
6	Fast swim	1.389	0.6722	0.254
7	Pinwheeling	1.000	0.1908	1.767
8	Bubble blow	1.000	0.0847	3.224
9	Humping surface	1.000	0.1768	1.886

552

553 **Figure captions**

554 **Fig. 1** The study area, Tramandaí-Armazém estuary, location (A and B) and an aerial perspective of the  
 555 Tramandaí Inlet (C). Black stars indicate the main locations at which fishers stand to throw out their nets.

556 **Fig. 2** Schematic drawing of the three movement patterns performed by dolphins inside the Tramandaí Inlet.  
 557 (a) “Milling” (Shane et al. 1986; Shane 1990; Mann and Sargeant 2003; Lusseau 2006), (b) “prowling” and (c)  
 558 “against-current” (Shane 1990) differ in regularity of movement. Dolphins explore, respectively (a) a wide area  
 559 of the estuary, moving in varied directions, (b) a specific and restricted zone, near sandbanks, and (c) regions  
 560 adjacent to the point where dolphins swim, maintaining their position. The black areas represent the shoreline.

561 **Fig. 3** Partial dependence plots for generalized additive modeling of relative frequency of net casting and  
 562 relative frequency of dolphin behaviors within UAV footage. For each behavior, the corresponding graph shows  
 563 model residuals as dots (in the fitted values scale) and the GAM-fitted smoother is represented by a line 95%  
 564 confidence intervals (grey shaded area). The x-axis represents the behavior frequencies while the y-axis  
 565 corresponds to the estimated degrees of freedom of the smooth function.

566 **Supplementary Information 1** Description, observed quantity and time duration of dolphins' activities and  
567 behavioral events observed on UAV footage.

568 **Supplementary Information 2** Data used for statistical analysis (Generalized Additive Model).

569 **Supplementary Information 3** R script used for statistical analysis (Generalized Additive Model).

570 **Supplementary Information 4** Examples of dolphin behaviors in the Tramandaí Inlet from aerial perspective.

571 **Supplementary Information 5** Model diagnostic plots from *gam.check* (*mgcv* Package) and *acf* (*stats* Package)  
572 functions (R software).

573 **Supplementary Information 6** Organogram presenting how the four generalized behaviors of dolphins  
574 suggested by Simões-Lopes et al. 1998 were interpreted and expanded in this study, as specific behavioral  
575 events.

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