

Scotland's Rural College

Exploration of horizontal information transmission through social learning in juvenile Atlantic spotted dolphins (*Stenella frontalis*)

de Brabanter, GLB; Herzing, DL; Jarvis, S

Published in:
Animal Behavior and Cognition

DOI:
[10.26451/abc.04.04.03.2017](https://doi.org/10.26451/abc.04.04.03.2017)

First published: 01/11/2017

Document Version
Publisher's PDF, also known as Version of record

[Link to publication](#)

Citation for published version (APA):
de Brabanter, GLB., Herzing, DL., & Jarvis, S. (2017). Exploration of horizontal information transmission through social learning in juvenile Atlantic spotted dolphins (*Stenella frontalis*). *Animal Behavior and Cognition*, 4(4), 425 - 441. <https://doi.org/10.26451/abc.04.04.03.2017>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Exploration of Horizontal Information Transmission through Social Learning in Juvenile Atlantic Spotted Dolphins (*Stenella frontalis*)

Gaiane L. B. De Brabanter^{1,2}, Denise L. Herzing^{2,3} and Susan Jarvis^{1,4}

¹ Royal (Dick) School of Veterinary Studies, University of Edinburgh, EH25 9RG, UK

² Wild Dolphin Project, Jupiter FL 33468 USA

³ Dept of Biological Sciences, Florida Atlantic University, Boca Raton, FL 33431 USA

⁴ SRUC, King's Buildings, West Mains Road, Edinburgh, EH9 3JG, UK

1 **Citation** – De Brabanter, G. L. B., Herzing, D. L. & Jarvis, S. (year). Exploration of
2 horizontal information transmission through social learning in juvenile Atlantic spotted
3 dolphins (*Stenella frontalis*).

4

5

6 **Corresponding Author** : Gaiane L. B. De Brabanter, gaianedebra@gmail.com

7

8

9

10

11

12

13

14

15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39

Abstract

Although vertical (mother-to-offspring) information transfer has been reported in dolphins, it is unclear whether horizontal information transfer takes place between peers of non-parental individuals. We hypothesized that horizontal information transmission takes place within juvenile social play-forage subgroups and within pairs of juveniles in the form of social learning, as a way for older juveniles to contribute to the further development of younger juveniles' foraging skills. Since 1985, a long-term study in the Bahamas has involved the collection of underwater videos and sound recordings on the social structure of a resident community of free-ranging Atlantic spotted dolphins *Stenella frontalis*. Foraging behaviors of juvenile dolphins were analyzed in 24 independent foraging events recorded on video from 1994 to 2013. Forty-nine juveniles in total were observed, including eight individually identified juveniles foraging alone, eight individually identified juveniles foraging in pairs, and 33 juveniles foraging in eight subgroups of three or more dolphins. The comparison of older juveniles' behavior against younger juveniles' behavior in juvenile play-forage subgroups suggested the potential for horizontal transmission of information about prey location. However, we found no direct evidence for social learning or of teaching in pairs. This new information about wild Atlantic spotted dolphin social structure is a starting point in horizontal information transmission research and is important in terms of cognitive processes and welfare implications.

Keywords : Atlantic spotted dolphins, juvenile, social learning, horizontal transmission

40 In animal societies, social structure and social interactions influence the direction of
41 information transmission within a group (Coussi-Korbel & Frigaszy, 1995). The term 'vertical
42 transmission' refers to information transmission between generations, e.g., piglets learning
43 about foraging from the mother (Oostindjer et al., 2011). The term 'horizontal transmission',
44 however, is used to describe information transmission within generations and between
45 individuals of the same age, e.g., domestic hens influencing food preferences of observing
46 hens by providing visual clues (Sherwin et al., 2002). Sometimes, the spread of novel
47 behaviors within groups can contribute to the diffusion of maladaptive foraging behaviors,
48 e.g., when dogs prefer to use a less adaptive behavior gained from observing a demonstrator
49 (Pongracz et al., 2003). However, horizontal information transmission has many benefits and
50 is likely to be adaptive when transmitted information is of transient value, e.g. when different
51 foraging strategies are used following temporary local variations in the environment (Laland
52 et al., 1996).

53 In a cetacean society, social information can be transmitted vertically and horizontally
54 (Herzing, 2005). In a Bahamian community of free-ranging Atlantic spotted dolphins, *Stenella*
55 *frontalis*, sexually mature females have a calf every three and a half year on average with a
56 subsequent juvenile period of approximately three years (Elliser & Herzing, 2014; Herzing,
57 1997). During the juvenile period, the mother teaches the calf how to fish, and, by the time
58 weaning occurs, the calf has become an independent forager partly as a result of vertical
59 transmission (Bender et al., 2009).

60 Horizontal transmission was observed among juvenile dolphins in both interactive and
61 non-interactive situations (Herzing, 2005). In this dolphin community, calves become
62 independent at three or four years old, a year marked by a reduction in nursing, an increase in
63 time spent alone and in time spent foraging in proximity of conspecifics other than the mother,
64 including in juvenile play-forage subgroups (Miles & Herzing, 2003).

65 Whereas vertical transmission contributes to the development of calves' foraging
66 behavior (Bender et al., 2009), young dolphins' acquired foraging skills may vary at weaning.
67 Yet, in order to survive, dolphins must become competent foragers irrespective of the length
68 and the skills acquired by the end of the nursing period. Whether, and how, horizontal
69 transmission of social information between juvenile dolphins may contribute to the
70 development of foraging skills in young juveniles is currently poorly understood. Therefore,
71 the aim of the present study is to characterize horizontal transmission, and identify potential
72 underlying social-cognitive mechanisms thereof in the free-ranging Bahamian community of
73 Atlantic spotted dolphins.

74 Every individual has a role in its social network (Lusseau & Newman, 2004). One of
75 the ways one can explore and understand the mental mechanisms underlying animals'
76 perception, processing, and transmission of information is by measuring the model's and the
77 learner's behavior (Herman, 1980; Herzing, 2006). The social-cognitive mechanisms by which
78 animals learn individually and from one another have been widely studied (Heyes & Galef,
79 1996). An animal can make use of the experience of a conspecific by acquiring information
80 and new behaviors through relatively simple cognitive processing or via more sophisticated
81 cognitive processes (Galef & Giraldeau, 2001). An observing animal can be subject to social
82 influence by simply being in the same environment as a demonstrator through exposure
83 (Whiten & Ham, 1992). The presence of a demonstrator can also simply affect an observer's
84 motivation through social enhancement (Hoppitt & Laland, 2008; Visalberghi, 1987; Whiten
85 & Ham, 1992); and it can direct an observer's attention to parts of the environment that were
86 not previously noticed through local enhancement (Galef & Giraldeau, 2001; Hoppitt &
87 Laland, 2008). Equally, a demonstrator's behavior can direct an observer's attention towards
88 an object, irrespective of where the object is subsequently located through stimulus
89 enhancement (Heyes, 1994; Palameta & Lefebvre, 1985; Whiten & Ham, 1992).

90 Greater cognitive mechanisms give rise to social learning, defined as the acquisition of
91 knowledge of skills, by indirect observation or interaction with a conspecific (Nicol, 2006).
92 Social learning is differentiated from enhancement mechanisms described above, as in all
93 social learning cases, the model's influence on the learner results in the learner learning as a
94 result of experiencing the social situation (Galef & Laland, 2005; Nicol, 2006; Whiten, 2000).
95 Social learning mechanisms include imitation (Whiten & Ham, 1992; Whiten et al., 2004;
96 Zentall, 2003), goal emulation (e.g., Tomasello et al., 1987) and observational conditioning
97 (e.g., Mineka & Cook, 1988; Tanida & Nagano, 1998). Social learning provides an alternative
98 of reduced costs for the learner to individual associative learning (e.g., trial-and-error
99 learning), while offering a way to continue developing adaptive behavior from the presence of
100 others (Nicol, 1995). Teaching is another form of social learning, and is defined as guided
101 instruction, as a modification of the teacher's behavior at a cost to the teacher in the presence
102 of naïve observers, according to the definition proposed by Caro and Hauser (1992).

103 Cognitive processes in animals have been extensively studied in several primate
104 species (Tomasello & Call, 1997; Whiten & Ham, 1992), yet most literature on cetacean
105 cognition comes from studies on bottlenose dolphins *Tursiops truncatus* kept in laboratory
106 environments (Herman, 2010). Furthermore, research on social-cognitive processes in wild
107 populations may be slow due to the kind of data collection necessary for the analysis of
108 behavior. Laboratory studies show that dolphins understand basic grammatical structure and
109 aspects of semantic reference in the learning of an artificial language (Herman et al., 1993,
110 1984; Mercado et al., 1999). Dolphins also memorize and remember sounds and actions
111 (Herman & Gordon, 1974; Thompson & Herman, 1981, 1977) and questions about the extent
112 to which dolphins are self-aware continue to be debated (Harley, 2013; Reiss & Marino,
113 2001), but they can understand symbolic references to their own different body parts (Herman
114 et al., 2001) and are able to utilize pointing gestures for referencing purposes (Herman et al.,

115 1999; Xitco et al., 2004). Such skills may underlie a dolphin's ability to synchronize known
116 and novel behaviors (Pack & Herman, 2006).

117 Existing long-term datasets have facilitated research on social-cognitive processes in
118 wild populations and the exploration of detailed underwater behavior of free-ranging
119 cetaceans. In settings where natural behaviors are expressed and social-cognitive abilities can
120 be tested, behavioral studies suggest that dolphins tackle environmental challenges and
121 manage complex social lives using advanced cognitive skills (Emery & Clayton, 2004;
122 Marino et al., 2007). In fact, the dolphin brain may have evolved to its current size in response
123 to multiple social requirements of living in a complex society, such as being able to
124 communicate, collaborate and compete among individuals (Connor, 2007; Connor et al.,
125 1992), and possibly due to the development and use of echolocation also (Jerison, 1986;
126 Ridgway, 1986; Wood & Evans, 1980). Dolphins learn, use, and mimic signature whistles to
127 call each other (Janik, 2000; Janik et al., 2006), organize synchronized and collaborative
128 feeding (e.g., Duffy-Echevarria et al., 2007), and may even teach foraging techniques (Bender
129 et al., 2009; Rendell & Whitehead, 2001) and tool-use (Krützen et al., 2005) to their offspring.

130 Social-cognitive information transmission mechanisms can take place between
131 individuals among small groups, communities, and larger societies, while leading to
132 information transmission at a cultural level (Franz & Matthews, 2010; Laland & Janik, 2006;
133 Norris & Dohl, 1980; Whitehead & Rendell, 2015). Horizontal transmission could facilitate
134 the continuing development of foraging behavior in young dolphins by allowing young
135 dolphins to develop their potential from interaction with more competent models, resulting in
136 a steady state of behavioral development where young juveniles have reached the foraging
137 competency required for survival (Kuczaj et al., 2005). The structure of a marine mammal
138 society is complex and responds to a variety of factors, including human activity (Ansmann et
139 al., 2012; Chilvers & Corkeron, 2001; Chilvers et al., 2003; Elliser & Herzing, 2014; Mann &

140 Watsoncapps, 2005). Understanding social-cognitive processes occurring within the social
141 structure is important from a cognitive, welfare, educational, and evolutionary perspective
142 (Mendl & Paul, 2004). Cognitive development and social structure are crucial to the
143 perpetuation of survival skills (Snyder et al., 1996; Whitehead et al., 2004) and better
144 understanding can contribute to the improvement of housing, management, and handling of
145 captive and rescued animals (Barber, 2009; Jiang et al., 2007; Wechsler & Lea, 2007). In
146 stranded dolphins being rehabilitated, the ability to catch live prey independently is one of
147 many criteria that must be met in order to determine whether a rescued animal is fit for release
148 (Barnett, 2002). Knowledge about the social-cognitive mechanisms underlying foraging
149 behavior development in free-ranging populations is thus key to maximize the rate of
150 successful rescue and rehabilitation of stranded animals. It may also shed light on unidentified
151 evolutionary advantages of social information transmission.

152 The objectives of this study were to research horizontal information transmission
153 through social-cognitive mechanisms among free-ranging juvenile Atlantic spotted dolphins.
154 Horizontal information transmission among juvenile Atlantic spotted dolphins may occur in
155 the following contexts: 1) through play-forage sequences of interactive juvenile subgroups,
156 e.g., via repetition of body movements by older juveniles towards a location, object or
157 individual worthy of attention, or by older juveniles initiating a foraging behavior; and 2)
158 through foraging performances in pairs, e.g., via noticeably different foraging performance
159 duration by old juveniles when foraging in the presence of a young dolphin. Information
160 transfer may occur via social learning by less experienced juveniles, where the younger
161 juveniles benefit from observing their conspecifics' foraging experience; and possibly through
162 demonstration by experienced juveniles, where the instructor's foraging behavior changes in
163 the presence of naïve observers (Bender, 2012; Heyes, 1994). A set of 24 video sequences
164 was analysed to test for the presence of horizontal information transmission firstly in play-

165 forage subgroups (Study One), and secondly, in pairs (Study Two), with a focus on behavioral
166 modifications in older juveniles. The primary hypothesis was that older juveniles contribute to
167 the further development of young dolphins' foraging performance, through social learning
168 processes facilitated by behavioral modifications of more experienced juveniles.

169 **Study One**

170 Study One (Subgroups) tested the hypothesis that play-forage juvenile subgroups
171 provide a platform for horizontal social information transmission through social-cognitive
172 processes.

173 **Methods**

174 **Study site, dolphin community and subjects.**

175 The community of free-ranging Atlantic spotted dolphins on Little Bahama Bank
176 (LBB) in the Bahamas has been observed every summer since 1985 for 4-5 months. LBB is a
177 shallow sandbank with waters 6 to 16 metres deep, surrounded by steep drop offs into the 500
178 metres deep waters of the Gulfstream. The location has extensive underwater visibility for
179 observations and the study area covers approximately 500 km² north of Grand Bahama Island.
180 The bottom is primarily sandy, with zones of rock, reef and patches of seagrass (*Thalassia*
181 *testudinum*). The life history, including non-invasive genetic analysis, (Elliser & Herzing,
182 2012, 2013, 2016 & 2016; Green, Herzing & Baldwin, 2007 & 2011) and the development
183 and use of social and acoustic behaviors of this community of Atlantic spotted dolphins have
184 been documented extensively (Au & Herzing, 2003; Herzing, 2000, 2004, 2005; Herzing &
185 Brunnick, 1997; Herzing & dos Santos, 2004; Herzing & Elliser, 2013; Herzing & Johnson,
186 1997; Herzing, Moewe & Brunnick, 2003; Lammers, Au & Herzing, 2003; Miles & Herzing,
187 2003; Welsh & Herzing, 2008).

188 The community includes approximately 100 individuals on any given year, although
189 up to 330 have been identified over the decades (Elliser & Herzing, 2014). Age class

190 coloration is modified relative to that described for pantropical spotted dolphin *Stenella*
191 *attenuata* (Perrin, 1970), with four consecutive developmental color classes identified for
192 increasing levels of age-related skin pigmentation: two-tone, speckled, mottled and fused
193 (Herzing, 1997). Both studies contained individuals of the two earliest age classes: the two-
194 tone phase (neonates and calves, ≤ 4 yr) and the speckled phase (4-9 year-old independent
195 juveniles), with a large majority of dolphins belonging to the second earliest age class (due to
196 juvenile subgroup analysis) and with the exception of one individual who belonged to the
197 mottled phase (young adult, between 10 and 16 years old). Two-tone calves are grey-white
198 and spotless. Speckled juveniles have at least two black spots on the ventral surface and
199 several light grey spots on the dorsal surface. Before the speckled phase, the dolphins depend
200 on their mother for survival; by the end of the speckled phase, dolphins move into their young
201 adult stage (Herzing, 1997). Underwater footage was selected for the presence of benthic
202 foraging behavior (Figure 1). Location of the prey was identifiable in most video recordings
203 and when not, prey location was determined according to marks in the sand and dolphin body
204 movements.



205

206 **Figure 1** – A spotless two-tone calf digs in the sand for fish while being watched by an elder
207 dolphin. Credit: Wild Dolphin Project

208

209 **Materials.**

210 ***Data collection.*** Video and audio sequences recorded by Wild Dolphin Project

211 researchers using various types of underwater cameras with attached hydrophone during

212 summer field seasons from year 1994 to 2013 were extracted from the Wild Dolphin Project

213 database for this study.

214 ***Experimental treatments and video standardization.*** A *play-forage juvenile subgroup*

215 was defined as a group of three to five juveniles who display foraging behavior while socially

216 interacting and swimming together at the bottom of the sea. The relative age of the juveniles

217 in each group is visibly distinguishable via skin pigmentation and/or body size in cases where

218 individual identification was unavailable. A *benthic foraging sequence in juvenile subgroup*
 219 was defined as the period between the start and the end of a benthic-feeding event in subgroup.
 220 The sequence starts when an individual initiates scan, dig or chase. The sequence ends when
 221 one of the following cases occurred: fish chase is over because fish escapes or is ingested,
 222 subgroup dissolves or subgroup leaves benthic area. The videos ($n = 8$) were selected for the
 223 presence of foraging juveniles and were included in the analysis as long as the focal juveniles
 224 did not go out of the video for more than three seconds in play-forage subgroups.

225 **Procedure.**

226 **Behavioral definitions.** Benthic foraging was defined as searching and eating benthic
 227 fish such as flounder (family *Bothidae*), snakefish (family *Synodontidae*) and razorfish
 228 (family *Clinidae*). A foraging bout was divided into four distinct phases: scan for the prey, dig
 229 the prey out of the sand, chase the prey and ingest the prey (Bender et al., 2009). The benthic
 230 foraging behaviors were recorded as described in Table 1.

231 **Table 1 – Ethogram of benthic foraging behaviors in subgroups.**

Foraging Behavior	Definition	Modifier *	
Scan	The dolphin repeatedly moves its head horizontally or vertically while swimming by the sea floor, using buzz sounds at times	Initiate ¹	
			Follow ²
Dig	The dolphin introduces its rostrum into the sand, leading to exposure of the prey. The body is most often oriented vertically or obliquely with the rostrum in contact with the sand and oscillating up, down and sideways	Initiate	
			Follow
Chase	The dolphin swims closely behind the benthic fish (after the fish being dug up) – usually occurs prior to catching the fish with the mouth	Initiate	
			Follow
Body-orienting movements (BOM)		Point of focus	Category (and name) of BOM
Focus	After the prey is dug out of the sand, the dolphin's body position remains oriented towards the prey, with the rostrum directly pointing at the fish and with a distance of half a body length from the prey	Prey	Prey-directed movement (prey-focus)

	The dolphin body position is oriented towards its peer with the rostrum directly pointing at the peer and with a distance of half a body length from the peer	Peer	Peer-directed movement (peer-focus)
Turn	The dolphin reorients its body position so as to follow a prey closely by turning sharply and effecting a rotation from 45° to 360°/complete turnaround. This results in the dolphin's body axis parallel to the fish body axis and the dolphin is located within a radius of at minimum half a body length of the prey (or closer)	Prey	Prey-directed movement (prey-turn)
	As for prey turn, but oriented towards peer	Peer	Peer-directed movement (peer turn)
* Modifiers			
¹ Initiate	A dolphin <i>initiates</i> a foraging behavior in a social subgroup when it begins performing scan, dig or chase.		
² Follow	A dolphin <i>follows</i> when it starts performing the same foraging behavior as the one any peer previously started performing. A foraging behavior was no longer considered as <i>followed</i> if five seconds or more had elapsed since the behavior was initiated.		

232

233 ***Video analysis, type of scoring and method of recording.*** One observer, the first
234 author, compared the behavior of older juveniles versus young dolphins within eight play-
235 forage juvenile subgroups (2.22 minutes of footage in total, involving 33 dolphins) scoring for
236 seven benthic foraging behaviors, during eight independent benthic foraging sequences. The
237 relative age of each juvenile in each group was visibly distinguishable via skin pigmentation
238 and/or body size. When available, juvenile identity was determined using data from the Wild
239 Dolphin Project preliminary video log and visible body marks. The video sequences were
240 watched in a randomized order using QuickTime Player. Each juvenile of a subgroup was
241 monitored throughout the benthic foraging sequence and was given an age category. The
242 youngest and (when applicable) the second youngest individuals of the subgroup were merged
243 in the *young* category, while the oldest (and when applicable) the second and third oldest
244 individuals of the subgroup were merged in the *old* category. The observer scored for seven
245 behaviors (scan, dig, chase, prey-focus, prey-turn, peer-focus and peer-turn) as events: each
246 event scored in a category of foraging behavior and body-orienting movement (described in
247 Table 1). The four body-orienting movements (peer-focus, prey-focus, peer-turn and prey-

248 turn) were merged in two movement categories. Prey-focus and prey-turn were merged into
249 the *prey-directed movements* category, while peer-focus and peer-turn were merged into the
250 *peer-directed movements* category. The observer applied modifiers (initiate and follow) to the
251 analysis of scan, dig and chase in juvenile subgroups. The data collected were categorical.

252 **Statistical analysis.**

253 With the categorical data obtained from play-forage subgroup analysis, we tested for
254 association between age category and the focus of body-orienting movements (prey/peer)
255 using a first chi-square test. A second chi-square test (for association between age category
256 and *prey-directed* movements, prey-focus and prey-turn), and a third chi-square test (for
257 association between age category and *peer-directed* movements, peer-focus and peer-turn)
258 were carried out. Finally, a Fisher's exact test for association was carried out between age
259 category (young/old) and behavior modifier (initiate/follow).

260 **Results**

261 For inter-observer reliability, one independent observer scored two videos of each
262 treatment group (25% of the videos, $n = 2$). There was a significant correlation between the
263 observations by the first author and the independent observer ($r^2 = 0.93$).

264 **Comparison of foraging behavior of old juveniles versus young juveniles in** 265 **juvenile subgroup.**

266 The duration of a benthic foraging sequence in juvenile subgroups was 10 to 37
267 seconds ($x_{mean} = 19.3$; $SE = 4.37$). The first chi-square showed that, whereas there was no
268 effect of point of focus (*peer* or *prey*) for younger juveniles, there was a significant effect for
269 older juveniles with older juveniles looking more at the prey than peers: there was an
270 association between age and the point of focus *prey* for both body-orienting movements
271 (*focus* and *turn*), with the total count of *focus* and *turn* showing that older juveniles performed
272 more *prey-directed* movements than *peer-directed* movements ($\chi^2(1) = 4.96$, $p = 0.03$, $N = 64$),

273 thereby focusing significantly more on the prey than on their companions. The second and
 274 third chi-square tests showed that there was no effect of body-orienting movement type (*focus*
 275 or *turn*) for younger juveniles or older juveniles, i.e., there was no significant difference
 276 between the number of *focus* or *turn* performed by younger and older juveniles. Respectively,
 277 older juveniles performed 22 *prey-directed* movements of which 13 were *prey-focus* and nine
 278 were *prey-turn* ($\chi^2(1) = 1.303, p = 0.249, N = 39$), while only performing seven *peer-directed*
 279 movements of which six were *peer-focus* and one was *peer-turn* ($\chi^2(1) = 0.503, p = 0.462, N =$
 280 25). In comparison, young juveniles performed 17 *prey-directed* movements and 18 *peer-*
 281 *directed* movements. The data presented in Table 2 show the distribution of body-orienting
 282 movements by older juveniles per point of focus.

283 **Table 2 – Data showing association between body-orienting movements and points of**
 284 **focus performed by old juveniles in social play-forage subgroups.** Pearson's chi-squared
 285 statistic χ , degree of freedom, p value (p) and total count (N) in above paragraph.
 286

Category of body-orienting movements	Focus	Turn	Total
Prey-directed movement	13	9	22
Peer-directed movement	6	1	7

287
 288 The Fisher's exact test showed that there was no association between age category
 289 (young/old) and behavior modifier (initiate/follow). The relationships between age and
 290 modifier were not significant (scan: $p = 0.32$; dig: $p = 0.62$; and chase: $p = 0.27$). Older
 291 juveniles were not more likely to initiate the performance of any foraging behavior, and young
 292 juveniles were not more likely to follow foraging behaviors previously performed.

293

294

295

296

Study Two

297

Study Two (Alone versus in Pairs) tested the hypothesis that older juveniles modify

298

their behavior in the presence of a young dolphin (young juvenile or calf) during a

299

standardized foraging event.

300

Methods

301

Study site, dolphin community, subjects and data collection were as in Study One.

302

Materials.

303

Experimental treatments and video standardization. A *juvenile foraging alone* was

304

defined as a foraging sequence in which the juvenile forages exclusively alone, without

305

physical or social interaction with other dolphins; no dolphin gets closer than two body-

306

lengths of the subject throughout the foraging event. *Juveniles foraging in pairs* were defined

307

as a foraging sequence during which one pair of juveniles forage together; where an older

308

juvenile forages in the presence of a calf or young juvenile. The two-tone calf or the young

309

juvenile are always visibly smaller than the old speckled juvenile via skin pigmentation and

310

body size. This type of sequence includes some level of physical and social interaction. A

311

complete foraging sequence was defined as the period between the start and the end of the

312

benthic feeding event. A sequence starts when the dolphin begins to scan the bottom using

313

echolocation, accompanied by buzz sounds at times, and makes scanning horizontal head

314

movements. A sequence ends when one of the following cases occurs: fish gets away, fish is

315

ingested, dolphin swims upwards from the bottom so the head is higher than the fluke while

316

moving for three seconds, or the dolphin moves at least one body length away from the sea

317

floor. The videos ($n = 16$) were included in the analysis as long as the focal juveniles did not

318

disappear from the frame of the video for more than five seconds when foraging alone and in

319

pairs.

320 **Procedure.**

321 *Behavioral definitions.* Study Two compared scan, dig and chase exclusively in
322 juveniles foraging alone versus in pairs. Scan, dig and chase were defined as in Study One
323 (Table 1).

324 *Video analysis, type of scoring, and method of recording.* To ensure independence of
325 the samples within and across the two treatment groups, one observer, the first author,
326 determined the identity of 19 dolphins (including all eight juveniles foraging alone and all
327 eight older juveniles foraging in pairs) out of the 24 dolphins involved in the video selection,
328 including age and gender, using data from the Wild Dolphin Project preliminary video log and
329 visible body marks. The video sequences were watched in a randomized order, using
330 QuickTime Player. The duration of the complete foraging sequence and the duration of each
331 foraging behavior performed by juveniles alone and the older juvenile of each pair were
332 recorded continuously using a stopwatch. The observer compared the duration of three
333 foraging states (scan, dig and chase as defined in Table 1) of eight juveniles foraging alone
334 (total of 4.96 minutes) versus eight old juveniles foraging in pairs (total of 3.68 minutes)
335 during distinct complete foraging sequences ($n = 16$). The observations were scored as states:
336 the behaviors were measured in duration, i.e., the time during which a specific foraging
337 behavior continues. The data collected for foraging state were continuous (in seconds).

338 **Data handling and statistical analysis.**

339 Raw data were transformed to obtain the percentage of time spent performing each
340 type of feeding behavior during a complete foraging sequence. Our two sets of percentage
341 data collected from complete foraging sequences were independent and continuous. An
342 Anderson-Darling normality test was used and found to be non-normal (see Results) and
343 therefore a Kruskal-Wallis test was used to test for difference in the mean percentage of time

344 spent performing foraging behaviors between Alone and Pairs. Minitab 17.1.0 was used for all
345 statistical analysis.

346 **Analysis of the relationships between foraging behaviors.**

347 For further investigation into the relationship between the variables across the whole
348 juvenile population, a Spearman's correlation test was used on the 16 juvenile dolphins (the 8
349 Alone and the 8 older juveniles in Pairs) recorded. These tests were performed on the whole
350 dataset to understand how foraging behaviors related to one another when juveniles foraged in
351 pairs.

352 **Results**

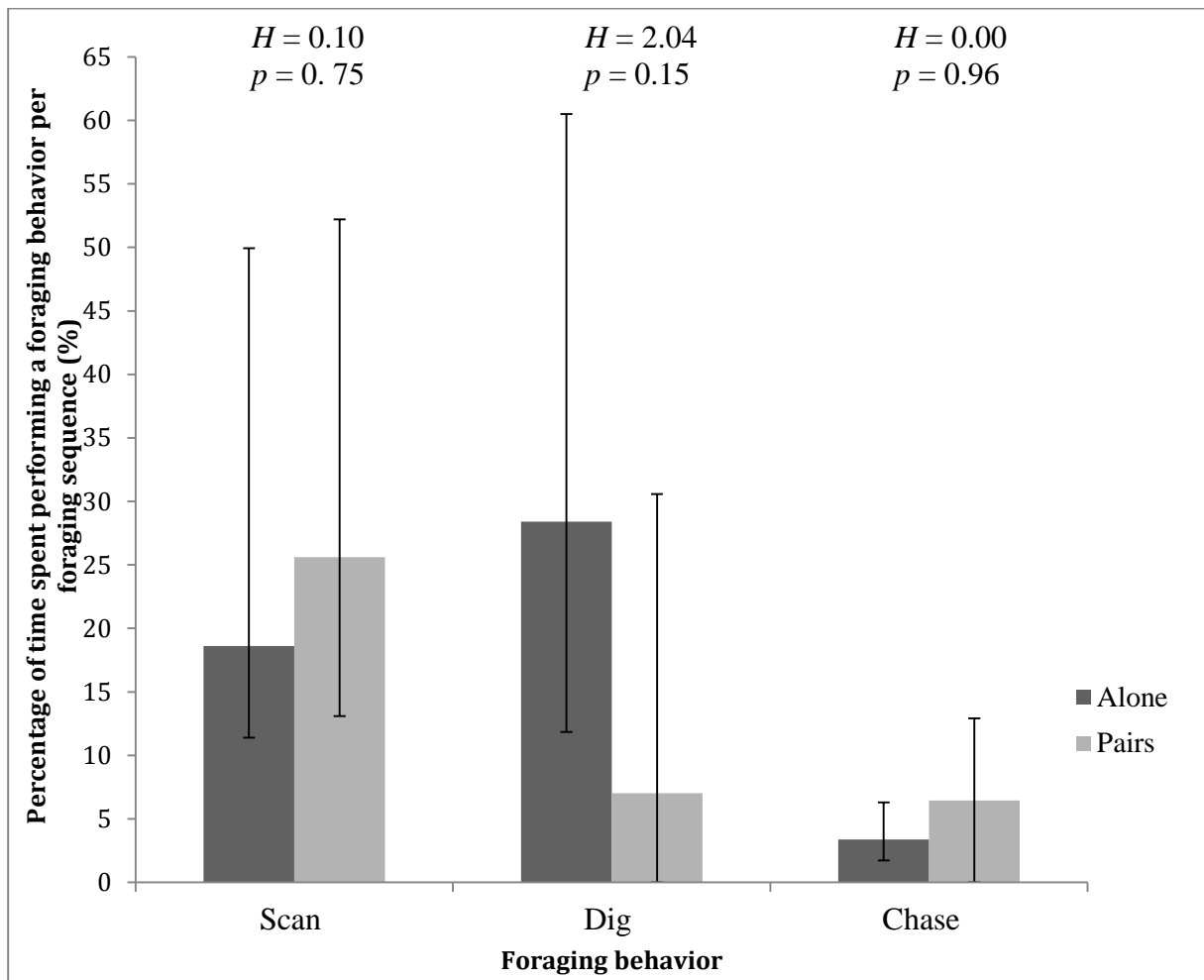
353 Inter-observer reliability was assessed as in Study One with one independent observer
354 scoring two videos of each treatment group (25% of the videos, $n = 4$). There was a
355 significant correlation between the observations by the first author and the independent
356 observer ($r^2 = 0.98$).

357 **Comparison of juvenile behavior foraging alone versus in pairs**

358 The duration of foraging states in pairs ranged from 0 second (when a foraging
359 behavior was not performed) to 27.8 seconds ($x_{mean} = 6.72$; $SE = 1.03$). An Anderson-Darling
360 normality test revealed that percentage of scan and chase in pairs and percentage of dig alone
361 were normal (respectively, $p = 0.15$; $p = 0.13$; and $p = 0.6$); however, percentage of scan and
362 chase alone and percentage of dig in pairs were non-normal (respectively, $p = 0.03$; $p < 0.005$
363 and $p = 0.05$).

364 There was no significant difference in the percentage of time spent scanning, digging
365 and chasing between the two treatment groups. The Kruskal-Wallis test results are included in
366 Figure 2. The subjects from the Alone and Pair treatments spent a similar amount of time
367 scanning. Digging was the foraging behavior performed the longest by juveniles foraging
368 alone. There was a trend for the older juveniles in pairs to spend less time digging but it was

369 not statistically significant. Chasing had the shortest duration of all foraging behaviors
 370 performed.



371
 372 **Figure 2** – Median percentage of time spent scanning, digging and chasing per complete
 373 foraging sequence between the Alone and Pairs (older juvenile). Median with interquartile
 374 range and Kruskal-Wallis test results (t statistic (H) and p value (p) above the corresponding
 375 foraging behavior.

376
 377
 378 **Relationships between foraging behaviors.**

379 There was a significant positive relationship with a good level of association between
 380 digging and chasing within individuals, as shown by the Spearman rank correlation results
 381 presented in Table 2. We also found a significant negative relationship with a moderate level of
 382 association between scanning and digging, and a significant negative relationship with a
 383 moderate level of association between scanning and chasing.

	Scan	Dig
Dig	$r_S = -0.564$ $p = 0.02$ *	
Chase	$r_S = -0.573$ $p = 0.02$ *	$r_S = 0.549$ $p = 0.03$ *

384
385 **Table 3 – Correlation matrix of Spearman rho values (r_S) and p values (p) for foraging**
386 **behaviors performed by all subjects in the Alone and Pairs (older juvenile) ($n = 16$) during a**
387 **complete foraging sequence.**
388

389 Discussion

390 Results of the present study suggest that horizontal information transmission is
391 possible within play-forage juvenile dolphin subgroups. In social subgroups, older juveniles
392 performed significantly more prey-oriented movements than peer-oriented movements,
393 compared to young dolphins. The significant repetition of body-orienting movements of the
394 older dolphins focused on the prey rather than on their companions. Older juveniles enhanced
395 prey location information by turning their head (*prey focus*) and body (*prey turn*) towards the
396 benthic fish, thereby providing visual cues for prey detection to young dolphins. However, we
397 found no evidence for teaching *per se* of foraging behaviors in subgroups, or in pairs. First,
398 older juveniles did not initiate foraging behaviors nor did younger juveniles follow the
399 foraging behaviors of older juveniles in subgroups (Study One). Second, older juveniles did
400 not alter their scanning, digging and chasing time in presence of young dolphins during a
401 complete foraging sequence (Study Two). The correlation test outlined that juvenile dolphins
402 tend to perform digging and chasing together; two active behaviors used for feeding purposes
403 that result in the ingestion of the prey, unlike scanning, which involves the use of
404 echolocation at times that is used for exploratory purposes and prey-finding in the context of
405 foraging.

406 The results of Study One (Subgroups) identified one significant difference in the
407 behavior of older juveniles with regards to prey. However, the data collected on the initiation

408 and following of foraging behaviors showed no evidence for teaching of foraging behaviors in
409 subgroups, i.e., older juveniles did not initiate foraging behaviors, and younger juveniles did
410 not follow them, and Study Two (Alone versus Pairs) suggests that older juveniles do not
411 modify foraging performance time in presence of a younger dolphin. The implications of our
412 study therefore suggest that horizontal transmission is present, with social information transfer
413 possibly occurring through social enhancement and social learning, but not to the extent
414 where older juveniles teach, *per se*, foraging to younger juveniles. Challenging to identify in
415 wild populations (Thornton & Raihani, 2010), teaching would allow young juveniles to
416 acquire foraging skills more rapidly (Caro & Hauser, 1992). An analogy to social situations
417 where young chimpanzees received less attention than same-age and older individuals in
418 social subgroups (Biro et al., 2003) may be drawn with juvenile subgroups of Atlantic spotted
419 dolphins, as older juveniles focused on the prey and they did not demonstrate foraging to the
420 younger juveniles in social subgroups.

421 At this stage, our study remains inconclusive regarding the possible occurring social
422 learning mechanisms, due to small sample size and inability to manipulate behaviors and
423 conditions. A larger sample size of our standardized footage for the analysis of juveniles
424 foraging in pairs might have increased the power of efficiency of the Kruskal-Wallis tests,
425 and reduced the variability of results in Figure 2. Future research is necessary to characterize
426 possible social learning mechanisms in juvenile dolphins' play-forage subgroups, to
427 determine what effect the repeated body-orienting movements performed by the older
428 juveniles have on young dolphins' learning, and to what extent such an effect affects young
429 dolphins' foraging competence. Many avenues demand to be explored for the potential social-
430 cognitive processes underlying horizontal transmission to be identified. Social cognitive
431 processes, such as social enhancement (e.g., exposure) and social learning (e.g., imitation and
432 goal emulation) may underpin horizontal transmission among juvenile subgroups but it is not

433 yet understood which exactly, and how. Exposure may occur, for juvenile play-forage
434 subgroups constitute a favorable environment for social enhancement and older juveniles'
435 behavior provide visual cues. Stimulus enhancement may be present: the focus of older, and
436 supposedly more experienced, juveniles on the prey may help observing young juveniles to
437 detect, pinpoint and identify fish more rapidly while limiting unnecessary exploration, as is
438 the case among certain avians with grains (Nicol & Pope, 1994 & 1999; Palameta & Lefebvre,
439 1985). It may be that, through goal emulation, the young juveniles benefit from opportunities
440 to associate prey-orienting behavior with a successful outcome (success being the ingestion of
441 food) when seeing older juveniles directing attention towards the fish and eating it, i.e., young
442 dolphins may emulate the goal behind *prey focus* and *prey turn* performances (Yeater &
443 Kuczaj, 2010). The potential for presence of stimulus enhancement and goal emulation
444 mechanisms in Atlantic spotted dolphin society seem analogous to the social learning
445 mechanisms evoked in young primates (Tomasello et al., 1987; Whiten, 2000), despite
446 different physical environments. Young dolphins may also learn by imitation and by
447 observational conditioning despite the highly social and playful foraging context.

448 Benthic foraging sequences in juvenile subgroups are highly social contexts in which
449 sonorous interaction, play and possibly some level of competition can occur at the same time.
450 Examples for future questions could include: when do old juveniles perform more prey-
451 orienting movement: in social subgroups, in pairs or alone; are there differences between
452 young dolphins' behavior as a function of presence or time spent with older juveniles in the
453 play-forage subgroup? Further, the trend of older juveniles to spend less time digging in pairs
454 was non-significant but suggestive, and therefore worthy of additional study. It may also be
455 that older juveniles' repeated prey-oriented movements in play-forage subgroups are part of
456 horizontal transmission processes that are associated with social aspects not tested for, e.g.,
457 acoustic communication development.

458 Whereas age influenced the frequency of body-orienting movements in juvenile
459 subgroups, gender, personality, novelty of behavior and environmental context are likely to
460 have intervened in horizontal information transmission as well (Kuczaj et al., 2012; Laland,
461 2004; Wilson et al., 1994). Dolphins, like other animal species, develop and conserve various
462 kinds of personality traits across time (Highfill & Kuczaj, 2007). In captivity, both old and
463 bold bottlenose calves are likely to be observed and imitated by young calves (Kuczaj et al.,
464 2006). Moreover, calves are prone to spontaneously produce as well as imitate novel
465 behaviors, particularly novel play behaviors performed by other calves (Kuczaj & Yeater,
466 2006). In the context of wild juvenile subgroups, young juveniles did not appear to reproduce
467 *per se* familiar foraging behaviors, possibly because the subjects had already been taught
468 scanning, digging and chasing by their mother in the same environmental context and were
469 independent foragers (Bender et al., 2009). The kind of teaching provided by experienced
470 adults before weaning is very important in foraging behavior development (Bender et al.,
471 2009), but it is possible that simple cognitive processing suffice to allow young dolphins to
472 gain information between themselves, as is the case for young wild chimpanzees foraging for
473 termites (Londsorf, 2006). However, it may be that young juveniles chose a salient individual
474 among the subgroup members according to criteria that our study did not measure (e.g.,
475 novelty of behavior, familiarity with the peer, personality), with any influence of the model on
476 the young juvenile's behavior being due to factors not yet identified.

477 Foraging appears to be socially taught and learned in the Bahamian Atlantic spotted
478 dolphin society (Bender et al., 2009) and prey information is possibly shared in the social
479 community within juvenile subgroups through horizontal transmission. Competence as a
480 forager is a developmental outcome that clearly benefits dolphins individually. If, as for cats
481 (Bateson, 2015), we can assume that the level of overall foraging competence at adulthood
482 has evened early individual variations in foraging skills, then young or less experienced

483 dolphin calves catch up with adult foraging ability by the time they are fully grown. The
484 formation of play-forage juvenile subgroups following the weaning period, by providing a
485 platform for horizontal transmission, would support the continuing development of foraging
486 behavior in spite of individuals having possibly different types of early experience with their
487 mothers. Horizontal information transmission in juvenile subgroups could play a role in the
488 preservation of the cultural benthic feeding traits in the Atlantic spotted dolphin culture, as a
489 result of a complex process emerging from the relationships between young society members,
490 while contributing to survival.

491 To conclude, our study identified foraging behaviors potentially involved with
492 horizontal information transfer in juvenile play-forage subgroups in a free-ranging community
493 of Atlantic spotted dolphins. Horizontal transmission in this context is suggestive of several
494 types of underlying social enhancement and, social learning mechanisms. However, our study
495 does not support teaching by older juveniles and remains inconclusive as to the extent to
496 which young dolphin learning occurs. Our findings are important in terms of social-cognitive
497 development, welfare, educational, and evolutionary implications for this wild Atlantic
498 spotted dolphin community, and is a starting point in research into horizontal information
499 transmission. Future research is needed to identify social information transmission
500 mechanisms and to determine the extent of young dolphins' learning from older juvenile's
501 repeated movements, and to what extent older juveniles influence juveniles' foraging
502 competence.

503 **Acknowledgments**

504 Many thanks to the Wild Dolphin Project for sharing their long-term database for this study.
505 Research for the study was conducted under a research permit from the Bahamian Department
506 of Fisheries.

507
508

References

- 509
510
511 Ansmann, I. C., Parra, G. J., Chilvers, B. L. & Lanyon, J. M. (2012). Dolphins restructure
512 social system after reduction of commercial fisheries. *Animal Behaviour*, 84, 575–581.
- 513 Au, W. W. L. & Herzing, D. L. (2003). Echolocation signals of wild Atlantic spotted dolphin
514 (*Stenella frontalis*). *Journal of the Acoustical Society of America*, 113, 598-604.
- 515 Barber, J.C. (2009). Programmatic approaches to assessing and improving animal welfare in
516 zoos and aquariums. *Zoo Biology*, 28, 519–530.
517
- 518 Barnett, J., (2002). Evaluation of rehabilitation as an option for stranded dolphins, porpoises
519 and whales. (pp. 1–91). Retrieved from Resources and Downloads :
520 <http://www.bdmlr.org.uk/>
521
- 522 Bateson, P. (2015). *The domestic cat: the biology of its behaviour*. Cambridge University
523 Press.
524
- 525 Bender, C. E. (2012). Social play as a tool for developing social-cognitive skills in a wild
526 population of Atlantic spotted dolphins (*Stenella frontalis*). Florida Atlantic University.
527 Unpublished.
528
- 529 Bender, C. E., Herzing, D. L. & Bjorklund, D. F. (2009). Evidence of teaching in Atlantic
530 spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their
531 calves. *Animal Cognition*, 12, 43–53.
532
- 533 Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T.
534 (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence
535 from field experiments. *Animal Cognition*, 6, 213–223.
536
- 537 Caro, T. M. & Hauser, M. D. (1992). Is there teaching in nonhuman animals?. *The Quarterly*
538 *Review of Biology*, 67, 151–174.
539
- 540 Chilvers, B. L. & Corkeron, P. J. (2001). Trawling and bottlenose dolphins' social structure.
541 *Proceedings of the Royal Society: Biological Sciences*, 268, 1901–1905.
542
- 543 Chilvers, B. L., Corkeron, P. J. & Puotinen, M. L. (2003). Influence of trawling on the
544 behaviour and spatial distribution of Indo-Pacific bottlenose dolphins (*Tursiops*
545 *aduncus*) in Moreton Bay, Australia. *Canadian Journal of Zoology*, 81, 1947–1955.
546
- 547 Connor, R. C. (2007). Complex alliance relationships in bottlenose dolphins and a
548 consideration of selective environments for extreme brain size evolution in mammals.
549 *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362,
550 587-602.
551
- 552 Connor, R. C., Smolker, R. A., Richards, A. F. (1992). Dolphin alliances and coalitions. In
553 *Coalitions and alliances in human and other animals* (pp. 415-443). Oxford University
554 Press.
555

- 556 Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and
557 social learning. *Animal Behaviour*, 50, 1441-1443.
558
- 559 Duffy-Echevarria, E. E., Connor, R. C. & St. Aubin, D. J. (2007). Observations of strand-
560 feeding behavior by bottlenose dolphins (*Tursiops truncatus*) in Bull Creek, South
561 Carolina. *Marine Mammal Science*, 24, 202–206.
562
- 563 Elliser C. R. & Herzing, D. L. (2012). Community structure and cluster definition of Atlantic
564 spotted dolphins, *Stenella frontalis*, in the Bahamas. *Marine Mammal Science*, 28, e486-
565 e502.
- 566 Elliser C. R. & Herzing, D. L. (2013). Social structure of Atlantic spotted dolphins, *Stenella*
567 *frontalis*, following environmental disturbance and demographic changes. *Marine*
568 *Mammal Science*, 30, 329-347.
- 569 Elliser, C.R. & Herzing, D. L. (2014). Long-term social structure of a resident community of
570 Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas 1991-2002. *Marine*
571 *Mammal Science*, 30, 308–328.
- 572 Elliser C. R. & Herzing, D. L. (2016). Long-term interspecies association patterns of Atlantic
573 bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella*
574 *frontalis*, in the Bahamas. *Marine Mammal Science*, 32, 38-56.
- 575 Elliser C. R. & Herzing, D. L., (2016). Changes in interspecies association patterns of Atlantic
576 bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella*
577 *frontalis*, after demographic changes related to environmental disturbance. *Marine*
578 *Mammal Science*.
- 579 Emery, N.J. & Clayton, N.S. (2004). The mentality of crows: convergent evolution of
580 intelligence in corvids and apes. *Science*, 306, 1903–1907.
- 581 Franz, M. & Matthews, L. J. (2010). Social enhancement can create adaptive, arbitrary and
582 maladaptive cultural traditions. *Proceedings of the Royal Society of London: Biological*
583 *Sciences*, 277, 3363-3372.
584
- 585 Galef, B. G. & Giraldeau, L. A. (2001). Social influence on foraging in vertebrates: causal
586 mechanisms and adaptive functions. *Animal Behaviour*, 61, 3-15.
- 587 Galef, B. G. & Laland, K. N. (2005). Social learning in animals: empirical studies and
588 theoretical models. *Bioscience*, 55, 489-499.
- 589 Green, M. L., Herzing, D. L. & Baldwin, J. D. (2007). Noninvasive methodology for the
590 sampling and extraction of DNA from free-ranging Atlantic spotted dolphins (*Stenella*
591 *frontalis*). *Molecular Ecology Notes*, 7, 1287-1292.
- 592 Green, M. L., Herzing, D. L. & Baldwin, J. D. (2011). Reproductive success of male Atlantic
593 spotted dolphins (*Stenella frontalis*) revealed by noninvasive genetic analysis of
594 paternity. *Canadian Journal of Zoology*, 89, 239-253.
595

- 596 Harley, H. E. (2013). Consciousness in dolphins? A review of recent evidence. *Journal of*
597 *Comparative Psychology A*, 199, 565-582.
598
- 599 Herman, L. M. (1980). *Cetacean behavior: mechanisms and functions*. Krieger Publishing
600 Company.
- 601 Herman, L. M. (2010). What laboratory research has told us about dolphin cognition.
602 *International Journal of Comparative Psychology*, 23, 310–330.
603
- 604 Herman, L. M., Abichandani, S. L., Elhajj, A. N., Herman, E. Y. K., Sanchez, J. L. & Pack,
605 A. (1999). Dolphins (*Tursiops truncatus*) comprehend the referential character of the
606 human pointing gesture. *Journal of Comparative Psychology*, 113, 347–364.
607
- 608 Herman, L. M. & Gordon, J. A. (1974). Auditory delayed matching in the bottlenose dolphin.
609 *Journal of Exp Anal Behaviour*, 21, 19–26.
610
- 611 Herman, L. M., Kuczaj, S. & Holder, M. D. (1993). Responses to anomalous gestural
612 sequences by a language- trained dolphin: evidence for processing of semantic relations
613 and syntactic information. *Journal of Experimental Psychology*, 122, 184–194.
614
- 615 Herman, L. M., Matus, D. S., Herman, E. Y. K., Ivancic, M. & Pack, A. A. (2001). The
616 bottlenosed dolphin's (*Tursiops truncatus*) understanding of gestures as symbolic
617 representations of its body parts. *Animal Learning & Behavior*, 29, 250–264.
618
- 619 Herman, L. M., Richards, D. G. & Wolz, J. P. (1984). Comprehension of sentences by
620 bottlenosed dolphins. *Cognition*, 16, 129–219.
621
- 622 Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella*
623 *frontalis*): age classes, color phases, and female reproduction. *Marine Mammal Science*,
624 13, 576–595.
625
- 626 Herzing, D. L. (2000). Acoustics and social behavior of wild dolphins: implications for a
627 sound society. In *Hearing by whales and dolphins*, (pp. 225-272). Springer New York.
- 628 Herzing, D. L. (2004). Social and non-social uses of echolocation in free-ranging *Stenella*
629 *frontalis* and *Tursiops truncatus*. In *Advances in the study of echolocation in bats and*
630 *dolphins* (pp. 404-410). University of Chicago Press.
- 631 Herzing, D. L. (2005). Transmission mechanisms of social learning in dolphins: underwater
632 observations of free- ranging dolphins in the Bahamas. *Autour de l'éthologie et de la*
633 *cognition animale*, 185–193.
634
- 635 Herzing, D. L. (2006). The currency of cognition: assessing tools, techniques, and media for
636 complex behavioral analysis. *Aquatic Mammals*, 32, 544–553.
637
- 638 Herzing, D. L. & Brunnick, B. J. (1997). Coefficients of association of reproductively active
639 female Atlantic spotted dolphins, *Stenella frontalis*. *Aquatic Mammals*, 23, 155-162.

- 640 Herzing, D.L. & dos Santos, M. (2004). Functional aspects of echolocation in dolphins. In
641 *Advances in the study of echolocation in bats and dolphins* (pp. 386-393). University of
642 Chicago Press.
- 643 Herzing, D. L. & Elliser, C. R. (2013). Directionality of sexual activities during mixed species
644 encounters between Atlantic spotted dolphin (*Stenella frontalis*) and bottlenose dolphin
645 (*Tursiops truncatus*). *International Journal of Comparative Psychology*, 26, 124-134.
646
- 647 Herzing, D. L. & Johnson, C. M. (1997). Interspecific interactions between Atlantic spotted
648 dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the
649 Bahamas, 1985-1995. *Aquatic Mammals*, 23, 85-99.
- 650 Herzing, D. L., Moewe, K. & Brunnick, B.J. (2003). Interspecies interactions between Atlantic
651 spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*, on
652 Great Bahama Bank, Bahamas. *Aquatic Mammals*, 29, 335-341.
- 653 Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological*
654 *Reviews of the Cambridge Philosophical Society*, 69, 207-231.
655
- 656 Heyes, C. M., Galef, B. G. (1996). Social learning in animals: the roots of culture. London
657 Academic Press.
658
- 659 Highfill, L. E. & Kuczaj II, S. A. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have
660 distinct and stable personalities?. *Aquatic Mammals*, 33, 380-389.
661
- 662 Hoppitt, W., Laland, K. N. (2008). Social processes influencing learning in animals: a review
663 of the evidence. *Advances in the study of behavior*, 38, 105-165.
664
- 665 Janik, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*).
666 *Science*, 289, 1355-1357.
667
- 668 Janik, V. M., Sayigh, L. S. & Wells, R. S. (2006). Signature whistle shape conveys identity
669 information to bottlenose dolphins. *Proceedings of the National Academy of Sciences*,
670 103, 8293-8297.
671
- 672 Jerison, H. J. (1986). The perceptual world of dolphins. In *Dolphin cognition and behaviour:*
673 *a comparative approach* (pp. 141-166). Lawrence Erlbaum.
674
- 675 Jiang, Y., Lück, M. & Parsons, E. C. M. (2007). Public awareness, education, and marine
676 mammals in captivity. *Tourism Review International*, 11, 237-249.
677
- 678 Krutzen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. (2005).
679 Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National*
680 *Academy of Sciences of the United States of America*, 102, 8939-8943.
681
- 682 Kuczaj, S. A., Yeater, D. B. & Highfill, L. (2012). How selective is social learning in
683 dolphins?. *International Journal of Comparative Psychology*, 25, 221-236.
684
- 685 Kuczaj II, S. A. & Yeater, D. B. (2006). Dolphin imitation: who, what, when, and why?
686 *Aquatic Mammals*, 32, 413-422.

- 687
688 Kuczaj, S. A., Makecha, R., Trone, M., Paulis, R. D. & Ramos, J. (2006). Role of peers in
689 cultural innovation and cultural transmission: evidence from the play of dolphin calves.
690 *International Journal of Comparative Psychology*, 19, 223–240.
691
- 692 Kuczaj, S. A., Paulos, R. D., Ramos, J. A. (2005). Imitation in apes, children and dolphins:
693 implications for the ontogeny and phylogeny of symbolic representation. In *Emory*
694 *symposia in cognition* (pp. 221-243). Lawrence Erlbaum Associates Publishers.
695
- 696 Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, 32, 4-14.
697
- 698 Laland, K. N. & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology &*
699 *Evolution*, 21, 542-547.
700
- 701 Laland, K. N., Richerson, P. J. & Boyd, R. (1996). Developing a theory of animal social
702 learning, in C. M. Heyes & B. G. Galef, Jr. (Eds) *Social learning in animals: the roots*
703 *of culture* (pp. 129-154). London Academic Press.
- 704 Lammers, M. O., Au, W. W. L. & Herzing, D. L. (2003). The broadband social acoustic
705 signaling behavior of spinner and spotted dolphins. *Journal of the Acoustical Society of*
706 *America*, 114, 1629-1639.
- 707 Lonsdorf, E. V. (2006). What is the role of mothers in the acquisition of termite-fishing
708 behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)?. *Animal Cognition*, 9,
709 36–46.
710
- 711 Lusseau, D. & Newman, M. E. J. (2004). Identifying the role that animals play in their social
712 networks. *Proceedings of the Royal Society of London: Biological Sciences*, 271, S477–
713 S481.
714
- 715 Mann, J. & Watsoncapps, J. (2005). Surviving at sea: ecological and behavioural predictors of
716 calf mortality in Indian Ocean bottlenose dolphins. *Animal Behaviour*, 69, 899–909.
717
- 718 Marino, L., Connor, R. C., Fordyce, R. E., Herman, L. M., Hof, P. R., Lefebvre, L., Lusseau,
719 D., McCowan, B., Nimchinsky, E., Pack, A., Rendell, L., Reidenberg, J. S., Reiss, D.,
720 Uhen, M. D., Van der Gucht, E. & Whitehead, H. (2007). Cetaceans have complex
721 brains for complex cognition. *PLoS Biology*, 5, e139.
722
- 723 Mendl, M., & Paul, E. (2004). Consciousness, emotion and animal welfare: insights from
724 cognitive sciences. *Animal Welfare*, 13, 17-25.
725
- 726 Mercado, E., Uyeyama, R. K., Pack, A. & Herman, L. M. (1999). Memory for action events
727 in the bottlenosed dolphin. *Animal Cognition*, 2, 17–25.
728
- 729 Miles, J. & Herzing, D.L. (2003). Underwater analysis of the behavioural development of
730 free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age).
731 *Aquatic Mammals*, 29, 363–377.
732
- 733 Mineka, S. & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys.
734 In *Social learning: psychological and biological perspectives* (pp. 51-73).

735
736 Norris, K. S. & Dohl, T. P. (1980). The structure and function of cetacean schools. In L.
737 Herman (ed.) *Cetacean behavior: mechanisms and functions* (pp. 211-261). Wiley, New
738 York.
739
740 Nicol, C. (1995). The social transmission of information and behaviour. *Applied Animal*
741 *Behaviour Science*, 44, 79-98.
742
743 Nicol, C. (2004). Development, direction, and damage limitation: social learning in domestic
744 fowl. *Learning & Behavior*, 32, 72-81.
745
746 Nicol, C. (2004). *Welfare of the laying hen* (pp. 177-190). CABI Publishing.
747
748 Nicol, C. (2006). How animals learn from each other. *Applied Animal Behaviour Science*, 100,
749 58-63.
750
751 Nicol, C. J. & Pope, S. J. (1994). Social learning in small flocks of laying hens. *Animal*
752 *Behaviour*, 47, 1289-1296.
753
754 Nicol, C. J. & Pope, S. J. (1999). The effects of demonstrator social status and prior foraging
755 success on social learning in laying hens. *Animal Behaviour*, 57, 163-171.
756
757 Oostindjer, M., Bolhuis, J. E., Mendl, M., Held, S., van der Brand, H. and Kemp, B. (2011).
758 Learning how to eat like a pig: effectiveness of mechanisms for vertical social learning
759 in piglets. *Animal Behaviour*, 82, 503-511.
760
761 Pack, A. & Herman, L. M. (2006). Dolphin social cognition and joint attention: our current
762 understanding. *Aquatic Mammals*, 32, 443-460.
763
764 Palameta, B. & Lefebvre, L. (1985). The social transmission of a food-finding technique in
765 pigeons: what is learned?. *Animal Behaviour*, 33, 892-896.
766
767 Perrin, W. F. (1970). Color pattern of the Eastern pacific spotted porpoise *Stenella graffmani*
768 *Lonnberg* (Cetacea, Delphinidae). *Zoologica*, 54, 135-149.
769
770 Pongrácz, P., Miklósi, Á., Kubinyi, E., Topál, J. & Csányi, V. (2003). Interaction between
771 individual experience and social learning in dogs. *Animal Behaviour*, 65, 595-603.
772
773 Reiss, D. & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: a case of
774 cognitive convergence. *Proceedings of the National Academy of Sciences*, 98, 5937-
775 5942.
776
777 Rendell, L. & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain*
778 *Sciences*, 24, 309-382.
779
780 Ridgeway, S. H. (1986). Physiological observations on dolphin brains. In *Dolphin cognition*
781 *and behaviour: a comparative approach* (pp. 31-59). Lawrence Erlbaum.
782
783 Sherwin, C. M., Heyes, C. M. and Nicol, C. J. (2002). Social learning influences the
784 preferences of domestic hens for novel food. *Animal Behaviour*, 63, 933-942.

785
786 Snyder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone,
787 William, D. & Miller, B. (1996). Limitations of captive breeding in endangered species
788 recovery. *Conservation Biology*, 10, 338–348.
789
790 Tanida, H. & Nagano, Y. (1998). The ability of miniature pigs to discriminate between a
791 stranger and their familiar handler. *Applied Animal Behaviour Science*, 56, 149–159.
792
793 Thompson, R. K. R. & Herman, L. M. (1981). Auditory delayed discriminations by the
794 dolphin: nonequivalence with delayed-matching performance. *Animal Learning &
795 Behavior*, 9, 9–15.
796
797 Thompson, R. K. R. & Herman, L. M. (1977). Memory for lists of sounds by the bottle-nosed
798 dolphin: convergence of memory processes with humans?. *Science*, 195, 501–503.
799
800 Thornton, A. & Raihani, N.J. (2010). Identifying teaching in wild animals. *Learn Behav*, 38,
801 297–309.
802
803 Tomasello, M. & Call, J. (1997). *Primate cognition*. Oxford University Press, USA.
804
805 Tomasello, M., Davis-Dasilva, M., Camak, L. & Bard, K. (1987). Observational learning of
806 tool-use by young chimpanzees. *Human Evolution*, 2, 175–183.
807
808 Visalberghi, E. (1987). Acquisition of nut-cracking behaviour by two capuchin monkeys
809 *Cebus appella*. *Folia Primatologica*, 49, 168-181.
810
811 Von Bertalanffy, L. (1950). The theory of open systems in physics and biology. *Science*, 111,
812 23–29.
813
814 Whitehead, H., Rendell, L., Osborne, R.W. & Wursig, B. (2004). Culture and conservation of
815 non-humans with reference to whales and dolphins: review and new directions.
816 *Biological Conservation*, 120, 431–441.
817
818 Whitehead, H. & Rendell, L. (2015). *The cultural lives of whales and dolphins* (pp. 10-44).
819 University of Chicago Press.
820
821 Wechsler, B. & Lea, S. E. G. (2007). Adaptation by learning: its significance for farm animal
822 husbandry. *Applied Animal Behaviour Science*, 108, 197–214.

823 Welsh, L.S. & Herzing, D.L. (2008). Preferential association among kin exhibited in a
824 population of Atlantic spotted dolphins (*Stenella frontalis*). *International Journal of
825 Comparative Psychology*, 21, 1-11.

826 Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, 24, 477–508.
827
828 Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal
829 kingdom: reappraisal of a century of research, in P. J. B. Slater, J. S. Rosenblatt, C. Beer
830 & M. Milinski (eds.) *Advances in the study of behavior* (pp. 239–283). San Diego
831 Academic Press.

- 832 Whiten, A., Horner, V., Litchfield, C. A., Marshall-Pescini, S. (2004). How do apes ape?
833 *Learning & Behavior*, 32, 36-52.
834
- 835 Wilson, D. S., Clark, A. B., Clark, A., Coleman, K. & Dearstyne, T. (1994). Shyness and
836 boldness in humans and other animals. *Trends in Ecology & Evolution*, 9, 442–446.
837
- 838 Wood, F. G. & Evans, W. E. (1980). Adaptiveness and ecology of echolocation in toothed
839 whales. In *Animal sonar systems* (pp. 381-426). Plenum Press.
840
- 841 Xitco, M. J., Gory, J. D. & Kuczaj, S. A. (2004). Dolphin pointing is linked to the attentional
842 behavior of a receiver. *Animal Cognition*, 7, 231–238.
843
- 844 Yeater, D. B. & Kuczaj II, S. A. (2010). Observational learning in wild and captive dolphins.
845 *International Journal of Comparative Psychology*, 23, 379–385.
846
- 847 Zentall, T. R. (2003). Imitation by animals: how do they do it? *Current directions in*
848 *Psychological Science*, 12, 91-95.
849
850
851