

OPINION¹

Clues of cultural transmission in cooperative foraging between artisanal fishermen and bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae)

Culture has shaped human evolution. As it facilitates the emergence and propagation of adaptive behaviors, it expands the niche and fitness of individuals (BOYD & RICHESON 1996, RICHESON & BOYD 2005). Culture can also shape phenotypes of nonhuman animals (e.g. LALAND & HOPPITT 2003) and the structure of their societies (e.g. CANTOR & WHITEHEAD 2013). Although animal cultures are arguably different from the cumulative and symbolic human cultures (LALAND & GALEF 2009), there is an operational definition of culture, which considers that cultural behavior has two main components: it is socially learned and shared among individuals (e.g. WHITEHEAD & RENDELL 2014).

The evidence for culture among whales and dolphins has been growing as we better understand their memory and learning abilities, and the social complexity of their groups (WHITEHEAD & RENDELL 2014). Experimentation in captivity (e.g. JANIK 2014) and observational studies (e.g. KUCZAJ et al. 2012) have demonstrated that social learning is key in their social lives. Learning from conspecifics is the primary mechanism of sympatric behavioral divergences, rapid spread of innovations, and evolution and maintenance of behavioral variants in wild cetaceans (e.g. CANTOR & WHITEHEAD 2013). For instance, social learning better explains the spread of acoustic communication signals and specialized foraging techniques in humpback whales *Megaptera novaengliae* (Borowski, 1871) (NOAD et al. 2000, ALLEN et al. 2013), orca whales *Orcinus orca* (Linnaeus, 1758) (FORD et al. 1998, DECKEE et al. 2000), and bottlenose dolphins *Tursiops truncatus* (Montagu, 1821) (see WHITEHEAD & RENDELL 2014).

A very distinctive foraging tactic of free-living bottlenose dolphins involves a complex interaction with artisanal fishermen, which is exclusive to a few populations off south Brazil (SIMÕES-LOPES et al. 1998). We showed recently that this behavior is group-specific and shared among some individual dolphins (DAURA-JORGE et al. 2012). But how this foraging tactic is transmitted remains unclear. Here, we discuss observations from our three-decades of studies indicating that the transmission includes learning processes on both sides of the interaction, between dolphins and fishermen. Our argument emphasizes that social learning is a necessary component of this foraging tactic, while the contributions, if any, of genetic and ecological factors are minor. In this case, the dolphin-fishermen coopera-

tion would strengthen the evidence for culture in non-humans (LALAND & GALEF 2009).

The dolphin-human foraging tactic is composed of specialized and coordinated behaviors from both species. To herd mullet (*Mugill* spp.) shoals, solitary or small groups of dolphins engage in circular movements between 20 and 40 m from shore, chasing the fish towards the fishermen. The fishermen stand in lines in shallow waters (<1 m) or on moored canoes (PETERSON et al. 2008) waiting for the dolphins to perform any of the following specific cues: back presentation, head slap, partial emersion, or tail slap (SIMÕES-LOPES et al. 1998). These behaviors are the climax of the interaction, the cues recognized by the fishermen as the right moment for casting their nets. Compared to other dolphin-human interactions – at Morenton Bay, Australia (FAIRHOLME 1856), and El Memghar, Mauritania (BUSNEL 1973) – the cooperative behavior observed in southern Brazil is more synchronized, with mutual responses between fishermen and dolphins.

Although local conditions must be favorable for this cooperative tactic to be of benefit to both dolphins and fishermen, environment alone is unlikely to drive the interaction. First, the cooperative tactic occurs in only four dolphin populations along a 220 km coastline in southern Brazil (Laguna: 28°29'48.14"S, 48°44'57.20"W; Araranguá: 28°53'41.83"S, 49°18'14.31"W; Torres: 29°19'31.62"S, 49°42'44.00"W; Tramandaí: 29°58'34.76"S, 50°7'4.63"W) where key environmental attributes and ecological conditions are very similar – e.g. habitat type, prey availability and behavioral stimulus (SIMÕES-LOPES et al. 1998). This coastal area contains river mouths, lagoons and estuaries with a similar assemblage of prey (including seasonal migration of massive schools of mullet fish) that sustain artisanal fisheries with casting nets. However, there are dolphin populations whose individuals have never engaged in the cooperative foraging. What seems to lack in these dolphin populations is the expertise of how to interact with fishermen. Second, some dolphin populations contain both cooperative and non-cooperative individuals, which makes it even clearer that the influence of the environment is minor. In Laguna, for instance, only 40-45% of the individuals cooperate with fishermen (DAURA-JORGE et al. 2012), although all dolphins are residents of the same lagoon system.

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In this case, it is the dolphins' social environment that seems key for the cooperative tactic, because the social relationships among dolphins are segregated between those that cooperate with fishermen and those that do not (DAURA-JORGE et al. 2012).

The formation of such social groupings according to foraging tactic (cooperative vs. non-cooperative) may have emerged by individuals preferentially interacting with those who perform the same foraging tactic (homophily), or by predefined social affiliations during which individuals acquire the tactics of their affiliates (social influence), or more likely by both operating in tandem (DAURA-JORGE et al. 2012, CANTOR & WHITEHEAD 2013). In any case, social interactions would provide opportunities for individuals to learn (observe, imitate, emulate, and/or copy) from one another (CANTOR & WHITEHEAD 2013) while social groupings provide opportunities for selective social learning (KUCZAJ et al. 2012). A parallel case comes from the bottlenose dolphins that use sponges as foraging tools in Shark Bay, Australia. In this population, the sponge foraging skills are socially learned and reinforced by homophily, leading to culturally-segregated social groups of tool-users (KOPPS & SHERWIN 2012, MANN et al. 2012) resembling the distinct social groups of cooperative and non-cooperative dolphins in Laguna (DAURA-JORGE et al. 2012). It is very unlikely that these foraging tactics would emerge, then spread, in these populations without learning.

However, asocial learning alone would not suffice. The cooperative tactic has been maintained across generations of fishermen and dolphins with few changes (SIMÕES-LOPES et al. 1998). Thus, for asocial learning to explain its persistence over the years, many individual dolphins would have to re-create, independently and multiple times, the whole behavioral repertoire involved in the interaction with the fishermen. This scenario is much less parsimonious than dolphins learning the skills and rewards of the interaction by observing their social contacts, and serving as models of this behaviour for younger dolphins. Akin to fishermen, where the cooperative fishing tactic is culturally passed down from generation to generation (fathers to sons) and transferred among peers (PETERSON et al. 2008), social learning seems to be at play among the participating dolphins.

As highly cognitive animals, dolphins develop their behavioral repertoires from early ages, discovering behaviors within their social environment by observing their mothers and other members of their social group (reviewed in KUCZAJ et al. 2012). Therefore, the transmission of the cooperative foraging tactic should not be different. While dolphins can learn horizontally – from their peers, within social modules – the tactic is primarily acquired by calves from their mothers (SIMÕES-LOPES et al. 1998) likely due to the long duration of their social bonds (see also KOPPS & SHERWIN 2012, KUCZAJ et al. 2012). Vertical transmission may suggest a genetic component; however, the strong mother-calf bond underlies mammalian traditions as it creates a very appropriate scenario for social learning (e.g. BOESCH 1991). For instance, in the Shark Bay bottlenose dolphin society, vertical social learning is the primary transmission mechanism of

the skills involved in using sponges as foraging tools (e.g. KOPPS & SHERWIN 2012), outweighing environmental, sex and kinship effects (MANN et al. 2012). Mothers also play an important role in direct instruction and teaching (e.g. THORNTON & RIAHANI 2010). Although relatively rare, teaching has been observed in delphinids (BENDER et al. 2009) and could participate in the transmission of the cooperative foraging tactic (SIMÕES-LOPES et al. 1998).

Female dolphins usually exhibit a higher site fidelity to certain localities (e.g. WELLS et al. 1987), thus contributing to the maintenance of local cultural repertoires. Nevertheless, females can be more prone to innovate (RUSSELL & RUSSELL 1990) and, indeed, we see some variations in the cooperative tactic between populations. The stereotyped behaviors are identical in both populations from south Brazil but their frequency of occurrence is different: head slaps are much more common in Tramandaí (37%) than in Laguna (7%), where back presentation is the most frequent cue used. Moreover, in Laguna, dolphins usually herd fish approaching fishermen obliquely (42%; $n = 2,395$ events), whereas in Tramandaí they mostly do so in parallel (51%, $n = 630$ events) (SIMÕES-LOPES et al. 1998). This variation could result from the high level of residence of the individuals. The two populations are relatively close (220 km apart) with no geographical barriers, but gene flow and movement between them is low and typical only of adult males (COSTA et al. 2015, SIMÕES-LOPES & FABIAN 1999). Thus, if exchanging of information between the population is rare, behavioral variations may arise by individual learning or learning errors, and can be fixed locally by social learning (KRÜTZEN et al. 2011).

More than the mere presence of culture in an animal population, it is the effects of culture on ecology, population biology, and genetic evolution that are more relevant (e.g. WHITEHEAD 2009). We propose that the dolphin-human interaction has such consequences, as the cooperation is beneficial to both parties. Cooperatively, fishermen more easily catch the shoals herded into the muddy waters where visibility is limited, and dolphins more easily catch fish disoriented by the nets; overall, both parties seem to increase their catch of larger fish (SIMÕES-LOPES et al. 1998). An additional benefit suggests that dolphins which cooperatively forage, reduce their spatial range, while dolphins that do not participate have larger home ranges and foraging areas (DAURA-JORGE et al. 2012). If the cooperative tactic is indeed effective, one can expect effects on individual fitness, and ultimately on genetic and population structures. Given the apparent benefits, it is still puzzling why some dolphins never cooperate with fishermen, resulting in social segregation within a population (as in Laguna; DAURA-JORGE et al. 2012). We submit two non-exclusive hypotheses for the restricted spread of the cooperative tactic in a population (both of which remain to be tested). First, learning takes time and is energetically costly; and interacting with fishermen may have the additional risk of entanglement in casting nets. Thus, not all individuals may be prone to invest in the acquisition of the cooperative tactic. Second, the environment may have reached its capacity, meaning that spots

for cooperative fishing are limited and cannot support an entire population of cooperative dolphins. In this case, competition would have made independent foraging (i.e. not cooperating with fishermen) an equally advantageous tactic for some dolphins.

In summary, we identified the following evidence in favor of the cultural transmission of the cooperative foraging tactic among dolphins: stereotyped and synchronized behaviors, which are shared among subsets of the population and maintained across generations via social learning, primarily from mother to calves. A very similar mechanism operates on the fishermen side: the techniques are local traditions passed from more experienced individuals to others through learning and teaching (PETERSON et al. 2008). To date, the evidence comes from field observations. However, as more individual data on the dolphins become available, it will be possible to test and quantify the precise contribution of social learning in producing the cooperative tactic in comparison to other factors – such as sex, kinship, and habitat use, which can influence social relationships and cultural transmission (e.g. MANN et al. 2012). Additionally, modeling techniques (e.g. CANTOR et al. 2015) can shed light on the origins and spread of the cooperation between dolphins and humans. Continuing to provide evidence for cultural transmission of behaviors that have critical implications for fitness in the wild will consolidate the evidence for social learning as an evolutionary force outside our species, and aid research aiming to understand the potential common origins of culture (e.g. LALAND & GALEF 2009).

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LITERATURE CITED

- ALLEN J, WEINRICH M, HOPPITT W, RENDELL L (2013) Network-Based diffusion analysis reveals cultural transmission of lobe-tail feeding in humpback whales. **Science** **340**: 485-488. doi: 10.1126/science.1231976
- BENDER CE, HERZING DL, BJORKLUND DF (2009) Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. **Animal Cognition** **12**: 43-53. doi: 10.1007/s10071-008-0169-9
- BOESCH C (1991) Teaching among wild chimpanzees. **Animal Behaviour** **41**: 530-532. doi: 10.1016/S0003-3472(05)80857-7
- BOYD R, RICHESON PJ (1996) Why culture is common, but cultural evolution is rare. **Proceedings of the British Academy for the Humanities and Social Sciences** **88**: 77-93
- BUSNEL RG (1973) Symbiotic relationship between man and dolphin. **Transactions of the New York Academy of Sciences** **35**: 112-131. doi: 10.1111/j.2164-0947.1973.tb01511.x
- CANTOR M, WHITEHEAD H (2013). The interplay between social networks and culture: theoretically and among whales and dolphins. **Philosophical Transactions of the Royal Society B** **368**: 20120340. doi: 10.1098/rstb.2012.0340
- CANTOR M, SHOEMAKER L, CABRAL R, FLORES CO, WHITEHEAD H (2015) Multilevel animal societies can emerge from cultural transmission. **Nature Communications** **6**: 8091. doi: 10.1038/ncomms9091
- COSTA APB, FRUET P, DAURA-JORGE FG, SIMÕES-LOPES PC, OTT PH, VALIATI VH, DE OLIVEIRA LR (2015) Bottlenose dolphin communities from the southern Brazilian coast: do they exchange genes or are they just neighbours? **Marine and Freshwater Research** **66**: 1201-1210. doi: 10.1071/MF14007
- DAURA-JORGE FG, CANTOR M, INGRAM SN, LUSSEAU D, SIMÕES-LOPES PC (2012) The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. **Biology Letters** **8**: 702-705. doi: 10.1098/rsbl.2012.0174
- DEECKE VB, FORD JK, SPONG P (2000) Dialect change in resident killer whales: implications for vocal learning and cultural transmission. **Animal Behaviour** **60**: 629-38. doi: 10.1006/anbe.2000.1454
- FAIRHOLME JKE (1856) The blacks of Morenton Bay and the porpoises. **Annals and Magazine of Natural History** **114**: 497-498. doi: 10.1080/00222935708693977
- FORD JK, ELLIS GM, BARRETT-LENNARD LG, MORTON AB, PALM RS, BALCOMB III, KC (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. **Canadian Journal of Zoology** **76**: 1456-1471.
- JANIK VM (2014) Cetacean vocal learning and communication. **Current Opinion in Neurobiology** **28**: 60-65. doi: 10.1016/j.conb.2014.06.010
- KRÜTZEN M, WILLEMS EP, VAN SCHAIK CP (2011) Culture and geographic variation in orangutan behavior. **Current Biology** **21**: 1808-1812. doi: 10.1016/j.cub.2011.09.017
- KOPPS AM, SHERWIN WB (2012) Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. **Animal Behaviour** **84**: 1347-1362. doi: 10.1016/j.anbehav.2012.08.029
- KUCZAJ II, STAN A, YEATER D, HIGHFILL L (2012) How selective is social learning in dolphins? **International Journal of Comparative Psychology** **25**: 221-236. Available online at: <http://eprints.cdlib.org/uc/item/9z25m1rq>
- LALAND KN, GALEF BG (2009) **The question of animal culture**. Cambridge, Harvard University Press, 355p.
- LALAND KN, HOPPITT W (2003) Do animals have culture? **Evolutionary Anthropology** **12**: 150-159. doi: 10.1002/evan.10111
- MANN J, STANTON MA, PATTERSON EM, BIENENSTOCK EB, SINGH LO (2012) Social networks reveal cultural behaviour in tool-using dolphins. **Nature Communications** **3**: 980. doi: 10.1038/ncomms1983
- NOAD MJ, CATO DH, BRYDEN MM, JENNER MN, JENNER KCS (2000) Cultural revolution in whale songs. **Nature** **408**: 537. doi: 10.1038/35046199

- PETERSON D, HANAZAKI N, SIMÕES-LOPES PC (2008) Natural resource appropriation in cooperative artisanal fishing between fishermen and dolphins (*Tursiops truncatus*) in Laguna, Brazil. **Ocean Coastal Management** 51: 469-475. doi: 10.1016/j.ocecoaman.2008.04.003
- RICHERSON PJ, BOYD R (2005) **Not by genes alone: How culture transformed human evolution**. Chicago, University of Chicago Press.
- RUSSELL C, RUSSELL WMS (1990) Cultural evolution of behavior. **The Netherlands Journal of Zoology** 40: 745-762.
- SIMÕES-LOPES PC, FABIAN ME (1999) Residence patterns and site fidelity in bottlenose dolphins, *Tursiops truncatus* (Montagu) (Cetacea, Delphinidae) off Southern Brazil. **Revista Brasileira de Zoologia** 16: 1017-1024. doi: 10.1590/S0101-81751999000400012
- SIMÕES-LOPES PC, FABIAN ME, MENEGHETI JO (1998) Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. **Revista Brasileira de Zoologia** 15: 709-726. doi: 10.1590/S0101-81751998000300016
- THORNTON A, RAIHANI NJ (2010) Identifying teaching in wild animals. **Learning & Behavior** 38: 297-309. doi: 10.3758/LB.38.3.297
- WELLS RS, SCOTT MD, IRVINE AB (1987) The social structure of free-ranging bottlenose dolphins. **Current Mammalogy** 1: 247-305.
- WHITEHEAD H (2009) How might we study culture? A perspective from the ocean, p. 125-152. In: LALAND RN, GALEF B (Eds.) **The question of animal culture**. Cambridge, Harvard University Press.
- WHITEHEAD H, RENDELL L (2014) **The cultural lives of whales and dolphins**. Chicago, University of Chicago Press.
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