

1 **Evidence suggests vocal production learning in a cross-fostered Risso's dolphin (*Grampus***
2 ***griseus*)**

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22 **Acknowledgments**

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29 **Abstract**

30 Vocal learning is a rare skill in mammals and we have limited information about the contexts in
31 which they use it. Previous studies suggested that cetaceans in general are skilled at imitating
32 sounds but only few species have been studied to date. To expand this investigation to another
33 species and to investigate the possible influence of the social environment on vocal learning, we
34 studied the whistle repertoire of a female Risso's dolphin (*Grampus griseus*) that was stranded at
35 an early age and was subsequently raised in a group of bottlenose dolphins (*Tursiops truncatus*).
36 We show that this cross-fostered animal produced vocal signals more akin to those of its *Tursiops*
37 poolmates than those of Risso's dolphins in the wild. This is one of very few systematic cross-
38 fostering studies in cetaceans, and the first to suggest vocal production learning in the Risso's
39 dolphin. Our findings also suggest that social experience is a major factor in the development of
40 the vocal repertoire in this species.

41 **Keywords** Bioacoustics, Bottlenose dolphin, *Grampus griseus*, Risso's dolphin, Signature
42 whistles, *Tursiops truncatus*

43

44 **Introduction**

45 Vocal production learning, the ability to modify the acoustic structure of vocalisations after
46 hearing a model sound, is a significant step in the evolution of complexity in communication
47 systems (Janik and Slater 2000). Humans make extensive use of vocal learning to develop
48 speech, but this ability is rare in other animals. Indeed, while many birds are excellent vocal
49 learners, non-human primates and many other mammals are not (Janik and Slater 1997). The only
50 terrestrial, non-human mammals where we find strong evidence for this skill are bats (Knörnschild
51 et al. 2010) and elephants (Poole et al. 2005; Stoeger et al. 2012). However, considerable
52 evidence for vocal production learning can be found in marine mammals (Janik 2014). The best
53 studied species here is the bottlenose dolphin (Richards et al. 1984), where each individual uses
54 vocal learning to develop its own unique signature whistle (Janik and Sayigh 2013). These animals
55 invent their own unique whistle modulation pattern seemingly by modifying whistles they heard
56 early in life (Fripp et al. 2005). In baleen whales, vocal learning contributes to the development of
57 song (Janik 2014) and pinnipeds have been found to copy sounds of other individuals (Reichmuth
58 and Casey 2014). Despite abundant evidence for vocal learning in a few marine mammals, we still
59 know little about vocal learning in the other species and its role in their social lives. To address
60 these gaps, we investigated whether and how vocal learning can influence the vocal repertoire of a
61 member of a species where learning has not been studied, a Risso's dolphin, that has been cross-
62 fostered by a group of bottlenose dolphins. If vocal learning was important in social integration, we
63 would expect the Risso's dolphin to deviate from its natural repertoire to match aspects of the
64 bottlenose dolphin vocalizations and their use.

65

66 **Methods**

67 *Animal history*

68 In summer 2005, a mother-calf pair of Risso's dolphins was found in the harbour of Ancona (44°
69 62' N, 13° 50' E), Italy. The calf was a female, approximately 6 months of age. Both animals were
70 transported to a local dolphin facility for veterinary treatments where they were kept in isolation.
71 Nevertheless, the adult dolphin died after two days due to serious health complications. The

72 orphaned calf was kept in quarantine for 30 days and subsequently moved to the Oltremare
73 marine park in Riccione, Italy. In this new facility, the Risso's dolphin was initially kept with a group
74 of 11 adult bottlenose dolphins (7 males, 4 females). Six of the males were moved to another
75 facility in 2008. At the time of our study in 2011, the bottlenose dolphin group consisted of 1 male,
76 4 females and a one year old male calf. Three of these animals were caught in the Western
77 Atlantic Ocean over 25 years ago, and moved to Italy from Cuba and the USA. All others were
78 born in captivity in Italy.

79

80 *Data collection at Oltremare marine park*

81 We conducted behavioural observations on close contact swimming (< 1m) of the Oltremare
82 dolphins over several days from 30 Nov 2009 to 26 Feb 2010. This behaviour is an indicator of a
83 close social relationship in dolphins (Connor et al. 2000). Dolphins were observed as one group
84 (66 hours) or in two groups separated by a gate (32 hours with 2 males separated from the rest of
85 the group). The Risso's dolphin was in the same pools as its preferred social partner, a female
86 named Pelé, in all observation periods. In April 2011, we collected audio and video recordings
87 during 30 different recording sessions over 14 consecutive days. We used an acoustic recording
88 array consisting of four HTI-94-SSQ hydrophones (frequency response 2Hz to 30kHz \pm 1dB). The
89 hydrophone output signals were recorded with a Tascam DR-680 digital recorder (sampling rate 96
90 kHz). During recording sessions, the Risso's dolphin and the bottlenose dolphins were free to swim
91 in the main pool and all four holding pools of the facility. However, we analysed only segments
92 when one animal was isolated from the group by choosing to swim alone in one of three holding
93 pools that we fitted with individual hydrophones. This allowed us to match vocalisations to the
94 emitter by using a time-of-arrival difference analysis of the acoustic signals to hydrophones (Janik
95 et al. 2000). Over the period of recordings, the whistles of the Risso's dolphin were collected in 17
96 separate sessions, while each of the six poolmates was recorded for an average of 4 ± 2 (mean \pm
97 SD) different sessions.

98

99 *Acoustic recordings of wild Risso's dolphins*

100 Acoustic recordings in the Canary Islands were conducted continuously on a dispersed 4-
101 hydrophone array, recording to a laptop with an Edirol FA-101 sound card. The acoustic array had
102 3 hydrophones tensioned to chains at 2 m of depth (2 HTI-96-MIN and one HTI-94-SSQ, frequency
103 response 2Hz-to-30kHz \pm 1dB), and a fourth hydrophone at 10 m of depth (SRD hydrophone
104 HS/150, frequency response 1kHz-to-100kHz \pm 1db). Recordings were collected for as long as
105 possible in a sea state of 3 or less (Beaufort scale) in dry weather using sampling rates of 96 kHz
106 (33% of recordings) and 192 kHz (67% of recordings). Signal to noise ratio (SNR) was calculated
107 for each of the 115 recorded whistles in a total recording time of 45 hours in the presence of
108 Risso's dolphins. Only 62 of these had a SNR of 6dB or above which was our criterion for inclusion
109 in the analysis.

110

111 *Acoustic analysis*

112 Audio segments containing whistles were visually selected by inspection of spectrograms
113 (Hanning window, FFT size 512, 100% window width) using Adobe Audition 2.0. For each whistle,
114 we extracted the pitch contour of the fundamental frequency using the beluga toolbox (available for
115 download at: <http://biology.st-andrews.ac.uk/soundanalysis/>) for MATLAB[®]. From each whistle
116 contour extracted with beluga, we measured the following 12 acoustic parameters using
117 automatized procedures in MATLAB[®]: start frequency, end frequency, minimum frequency,
118 maximum frequency, mean frequency, frequency range (maximum – minimum), duration, time to
119 minimum frequency, time to maximum frequency, number of inflections in the contour (i.e. any
120 change of slope from positive to negative or vice versa), number of steep sections in the contour
121 (i.e. frequency change > 500Hz between one point and the following), and number of steps in the
122 contour (i.e. steep sections preceded or followed by at least 25 ms of frequency modulation of less
123 than 100 Hz).

124

125 *Statistical analysis*

126 After parameter standardization, we performed a principal component analysis (PCA) on all
127 acoustic parameters using an orthogonal varimax rotation. The PCA reduced the original set of

128 acoustic measurements to a new set of uncorrelated principal components (PCs). The scores of
129 these PCs were then used to calculate pairwise Euclidean distances for each whistle of the Risso's
130 dolphin with those of the captive bottlenose dolphins and wild conspecifics. All analyses were
131 performed in SPSS v. 20 (SPSS, Inc. 2010).

132

133 **Results**

134 Each of the bottlenose dolphins primarily used one individually distinctive and unique signature
135 whistle when swimming alone (time analysed = 01 h 15 m 59 s; $N_{\text{whistles}} = 151$ (8-40 per animal))
136 (Fig. 1a). The cross-fostered Risso's dolphin also produced only one unique whistle type (Fig. 1b)
137 when swimming in isolation (time analysed = 02 h 54 m 24 s; $N_{\text{whistles}} = 192$), similar to the use of
138 signature whistles found in bottlenose dolphins. Descriptive statistics of the whistle parameters for
139 this type are presented in Table 1a. Interestingly, recurring whistle contours in our sample of wild
140 Risso's dolphin whistles were rare (Fig. 1c) (time analysed = 45 h; $N_{\text{whistles}} = 62$).

141

142 The PCA reduced the 12 acoustic parameters measured from the fundamental frequency to
143 four independent PCs. These four components explained 81.93% of the total variance (PC1 =
144 24.56%, PC2 = 22.88%, PC3 = 19.82%, PC4 = 14.68%). Table 2 shows the factor loadings for
145 each principal component. In particular, the main separating PC (PC1) represented primarily
146 maximum frequency, mean frequency, frequency range, duration and time to maximum frequency.
147 In the space defined by the PCs, the signature whistles of the Risso's dolphin made a distinctive
148 cluster within the range of variation of bottlenose dolphin vocalisations, and they were separated
149 from the cluster made by whistles from wild conspecifics recorded in the Canary Archipelago (Fig.
150 2). Mean Euclidean distances indicated that similarity was higher between the whistles of the
151 captive Risso's dolphin and those of the bottlenose dolphins (2.87 ± 0.004 ; mean \pm SE pairwise
152 distances) than between the whistles of the captive and the wild Risso's dolphins (3.074 ± 0.009).
153 Interestingly, the whistle parameters of the Risso's dolphin whistle most closely matched those of
154 an adult female (Pelé) that she spent most of her contact time with (time spent at more than 1 m
155 from conspecifics: 74%, time close to Pelé only: 15%, time close to other dolphins: 11%) and those

156 of the one adult male that stayed in the pool for the whole study period even though she was not
157 observed to interact with him.

158

159 **Discussion**

160 The evidence presented here suggests that Risso's dolphins are capable of vocal learning. We
161 analysed the whistle repertoire of a female that became orphaned at an early age and grew up in a
162 community of captive bottlenose dolphins. We found that the cross-fostered Risso's dolphin
163 produced almost exclusively one whistle type when in isolation, similar to the use of signature
164 whistles found in bottlenose dolphins (Janik and Sayigh 2013). Interestingly, recurring whistle
165 contours in our sample of wild Risso's dolphin whistles were rare. Together with the very low
166 whistle rate we found for wild Risso's dolphins in the Canary Islands, this may indicate an absence
167 of signature whistles in wild Risso's dolphins. However, Risso's dolphin behaviour in the Canaries
168 may differ from that in other geographic locations. A signature whistle has been found in one other
169 captive Risso's dolphin but this animal was also housed with bottlenose dolphins (Caldwell et al.
170 1969). Killer whales have also been found to change their vocal behaviour when housed with
171 bottlenose dolphins (Musser et al. 2014), further supporting the importance of the social
172 environment for repertoire development in delphinids. It remains to be seen whether Risso's
173 dolphins use signature whistles when with conspecifics.

174

175 Overall, our results show that the whistles of the cross-fostered Risso's dolphin were much
176 closer to those of its bottlenose dolphin pool mates than to wild Risso's dolphins from the Canary
177 Islands (Figure 2). This was also confirmed by the analysis of Euclidean distances, chosen as a
178 similarity measure. While the Canary Island population may differ from Risso's dolphins in the
179 Adriatic Sea, a comparison of our data with published data from wild Risso's dolphin from the
180 Azores and from Scotland (Rendell et al. 1999) also suggests that the cross-fostered individual
181 used its pool mates as a model for its whistle. Table 3 shows that average values for start, end,
182 minimum, maximum, and mean frequency of the captive Risso's dolphin whistles were
183 considerably closer to the average bottlenose dolphin whistles from its pool than to those from

184 these other conspecific populations. Little is known about wild Risso's dolphin vocalizations and
185 their social organization appears to be different from that of well-known vocal learners like
186 bottlenose dolphins or killer whales (*Orcinus orca*) (Hartmann et al. 2008). Risso's dolphins live in
187 relatively stable, non-matrilineal groups. Thus, it is difficult to speculate how Risso's dolphins would
188 use vocal learning in the wild.

189

190 In conclusion, our results provide evidence that the cross-fostered Risso's dolphin developed a
191 signature whistle and used overall whistle parameters that were more similar to bottlenose
192 dolphins than to those used by wild Risso's dolphins. Cross-fostering is one of the few strong
193 approaches to the study of vocal learning and as shown here can add information on the role of
194 social partners in its usage. Our study only describes one animal and can therefore only suggest
195 the influence of vocal learning on whistle development. Changes in vocalizations could be
196 achieved through copying as in vocal production learning, or through selection of pre-existing
197 vocalization patterns as would be the case in contextual learning. The large differences in
198 parameters, especially in start frequency and frequency range, between the cross-fostered animal
199 and the three wild populations of Risso's dolphins suggest that this is a case of vocal production
200 learning rather than using already existing whistles from a pre-existing repertoire. However, future
201 studies need to address the role of signature vocalizations in this species as well as the
202 mechanism of learning with a larger sample size.

203

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Tables

Table 1. (a) Descriptive statistics of whistle parameters. (b) Mean values and standard deviation of whistle parameters from captive bottlenose and Risso's dolphins and wild Risso's dolphins recorded in the Azores and Scotland by Rendall et al. (1999). Shaded boxes indicate parameters in which the cross-fostered Risso's dolphin was more similar to the captive bottlenose dolphins than to the wild Risso's dolphins.

		Start frequency (Hz)	End frequency (Hz)	Minimum frequency (Hz)	Maximum frequency (Hz)	Mean frequency (Hz)	Frequency range (Hz)	Duration (ms)	Time to minimum frequency (ms)	Time to maximum frequency (ms)	Number of inflections in the contour	Number of steep sections	Number of steps in the contour
(a)													
Risso's dolphins recorded in the Canary Archipelago (n=62)	Mean	11461	12810	10094	15205	12471	5110	506	228	298	1	1	0
	St.Dev.	2781	4310	2476	3932	2823	2976	220	248	248	2	2	2
Cross-fostered Risso's dolphin (n=192)	Mean	6006	7769	5771	16852	12372	11080	757	95	615	1	2	2
	St.Dev.	1015	1300	872	1474	852	1708	114	239	117	0	1	1
Bottlenose dolphin Pelé (n=26)	Mean	6748	6863	5165	19080	11283	13915	432	360	252	3	10	7
	St.Dev.	833	1179	1116	1515	926	1450	100	152	172	1	4	3
Bottlenose dolphin 2 (n=40)	Mean	8276	9680	6187	9952	7014	3764	130	16	181	1	2	1
	St.Dev.	600	894	139	1002	339	984	34	9	114	0	1	0
Bottlenose dolphin 3 (n=8)	Mean	8818	10635	4471	10635	7048	6164	1353	712	231	2	4	3
	St.Dev.	380	814	1828	814	204	752	130	49	432	1	3	2
Bottlenose dolphin 4 (n=27)	Mean	16115	6620	6576	17688	10941	11111	539	500	39	1	1	1
	St.Dev.	1248	110	124	982	299	984	46	50	16	1	1	1
Bottlenose dolphin 5 (n=28)	Mean	6862	13110	6034	15407	10023	9373	701	232	461	3	7	5
	St.Dev.	1572	3799	1247	2668	1467	2788	155	250	181	1	4	3
Bottlenose dolphin 6 (n=22)	Mean	9096	5380	5214	11150	7385	5936	788	729	82	1	1	0
	St.Dev.	1605	347	344	1737	647	1577	132	123	55	1	1	1
(b)													
Risso's dolphins recorded in the Azores (n = 82) and Scotland (n = 1182)	Mean	12100	10830	8830	13440	11300	4610	530					
	St.Dev.	2160	3330	2710	2690	2290	2680	260					
Cross-fostered Risso's dolphin (n=192)	Mean	6006	7769	5771	16852	12372	11080	757					
	St.Dev.	1015	1300	872	1474	852	1708	114					
Oltremare bottlenose dolphins (n = 151)	Mean	9258	8611	5819	14129	9065	8309	521					
	St.Dev.	3507	3149	940	3998	2011	4024	324					

Table 2. Results of the principal component analysis with varimax rotation. The table shows factor loadings of the acoustic parameters on the principal components showing eigenvalues > 1 (PC1-PC4) extracted from the PCA. Bold text indicates the largest factor loadings ($r > 0.5$).

Acoustic parameter	Principal Component			
	1	2	3	4
Start frequency	-0.072	-0.269	0.529	-0.728
End frequency	0.009	0.124	0.831	0.210
Minimum frequency	0.098	-0.283	0.885	0.180
Maximum frequency	0.879	0.317	0.194	-0.043
Mean frequency	0.877	0.014	0.376	0.119
Frequency range	0.742	0.442	-0.312	-0.061
Duration	0.614	-0.049	-0.475	-0.048
Time to minimum frequency	-0.014	0.020	-0.285	-0.852
Time to maximum frequency	0.644	0.070	-0.179	0.627
Number of inflections in the contour	0.086	0.720	0.001	-0.058
Number of steep slope sections	0.126	0.952	-0.044	0.040
Number of contour jumps	0.157	0.921	0.077	-0.105

Figure Captions

Fig. 1 Pitch contours extracted for the signature whistles of the six bottlenose dolphins (a; * indicates the whistles of Pelé) and the Risso's dolphin (b). The contours of the whistles recorded from wild Risso's dolphins in the Canary Archipelago are presented as a comparison (c)

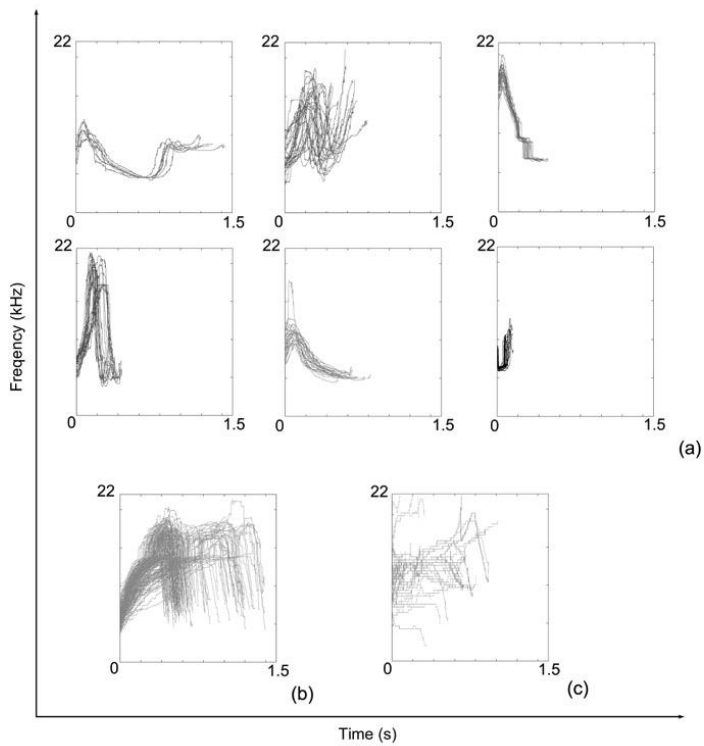


Fig. 2 Whistles plotted in the space defined by principal components. The signature whistles of the captive Risso's dolphin made a distinctive cluster within the range of variation of bottlenose dolphin vocalisations, which was separated from the cluster made by whistles from wild conspecifics

