

1 Post-Partum Whistle Production in Bottlenose Dolphins

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3 Running Headline: Fripp and Tyack: Maternal Whistle Production in Dolphins

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21 **Abstract**

22 Despite much research on bottlenose dolphin signature whistles, few have
23 investigated the role of maternal whistles in early calf development. We investigated
24 maternal whistle use in the first weeks postpartum for captive dolphins. The overall
25 whistling rate increased by a factor of ten when the calves were born and then decreased
26 again in the third week of the one surviving calf. Adult whistles were distinguished from
27 calf whistles based on the extent of frequency modulation and were further classified into
28 signature and non-signature whistles by comparison to a dictionary of known whistles.
29 The average rate of maternal signature whistle production increased significantly from
30 0.02 whistles per dolphin-minute before the calves were born to 0.2 and 0.3 whistles in
31 weeks 1 and 2, decreasing again to 0.06 in week 3 for the mother of the surviving calf.
32 Percent maternal signature whistles changed similarly. Signature whistle production by
33 non-mothers did not change when the calves were born. A likely function of this increase
34 in maternal signature whistle production is that it enables the calf to learn to identify the
35 mother in the first weeks of life.

36

37 **Keywords:** bottlenose dolphin, *Tursiops truncatus*, vocal behavior, mother-infant,

38 signature whistles, imprinting

39 When mammals approach parturition, their behavior changes in many ways. Bottlenose
40 dolphins, *Tursiops truncatus*, for instance, spend more time alone just before giving birth
41 and a great deal of time rubbing, nursing, and caring for their calf just afterwards (Fripp
42 1999, Mello and Amundin 2005). Dolphin mothers in Shark Bay, Australia also spend a
43 significant amount of time in the calves' first weeks keeping them away from other
44 dolphins (Mann and Smuts 1998). Previous research has suggested that whistle
45 production may increase shortly before parturition (Mello and Amundin 2005). The
46 current study was designed to investigate whistle production during the first weeks
47 following parturition.

48 Signature whistles are individually-distinctive whistles where the unique
49 frequency contour of each dolphin's whistle is highly stereotyped (Caldwell *et al.* 1990).
50 Although dolphins can whistle at birth (Caldwell and Caldwell 1979), they are not born
51 with a stereotyped signature whistle (Caldwell *et al.* 1990, Sayigh 1992), but develop a
52 unique signature whistle by listening to the whistles in their environment (Fripp *et al.*
53 2005). Dolphin calves are also born swimming in a highly social environment. The
54 opportunities for confusion when a calf wanders away from its mother abound. Dolphins
55 in general, and mothers and calves in particular, are known to use signature whistles to
56 keep in contact with each other when separated (Sayigh 1992, Smolker *et al.* 1993, Janik
57 and Slater 1998). Since signature whistles are individually variable, a calf may have to
58 learn to recognize its mother's whistle before it can find her again when separated. We
59 predicted that the need for a calf to learn its mother's signature whistle might elicit an
60 increase in maternal signature whistle production in the calf's first weeks.

61 To investigate post-partum whistle production, four pregnant dolphins in captivity
62 were studied from shortly before to shortly after the births of their calves. Both their
63 overall whistle production and their signature whistle production were quantified.

64

65 **Methods**

66

67 *Data Collection*

68 Whistles were recorded from four pregnant female bottlenose dolphins (*Tursiops*
69 *truncatus*) and their newborn calves, as well as another mother (Sharky) and her seven-
70 month-old female calf (Daphne), at the Kolmårdens Djurpark in Kolmården, Sweden
71 (Table 1). All four newborn calves were male. Calf 1 was born in late April of 1995, and
72 died at 7 days of age. Calves 2, 3, and 4 were born in succession in late May and early
73 June. Calves 2 and 3 died at 9 and 10 days respectively. Calf 4 survived but spent one day
74 (June 9: his 6th) in isolation for medical treatment. Recordings were started in March and
75 continued through the end of Calf 4's third week (March 21 to June 24, Table 1). Sharky
76 and Daphne were moved out of the pool shortly after Calf 1 was born. Similarly, Mother
77 1 was moved out shortly after Calf 2 was born, and Mother 3 was moved out on Calf 4's
78 6th day.

79 Ten-minute focal animal samples (Altmann 1974) were taken on each pregnant
80 mother or newborn calf five times daily, at approximately 0900, 1030, 1330, 1600, and
81 1800 hours. The times were selected to represent all the contexts the dolphins
82 experienced, including presence and absence of trainers and the public, feedings and
83 shows. The breeding pool was closed to the public during the calves' first two weeks and

84 no training was done (only feeding). Dolphins were observed from underwater viewing
85 windows, and behavior was recorded on an IBM Thinkpad 755Cs with The Observer 3.0
86 (Noldus). Acoustic recordings were made from a single hydrophone placed in the corner
87 of the pool near the observation station simultaneously with the behavioral observations.
88 Acoustic recordings were made with a hydrophone from High Tech, Inc. and a Radio
89 Design Labs STM2 preamplifier onto one channel of a Panasonic VHS, PAL-format,
90 stereo VCR.

91 For each calf, focal samples were classified as Pre-Birth, Week 1, Week 2, Week
92 3, or Other (Table 1). Pre-Birth samples included all samples on the calf's mother taken
93 in the 3 weeks before the calf was born. Week 1 included focal samples from that calf in
94 the calf's first 7 days. Week 2 included samples in days 8 through 14, and Week 3
95 included samples in days 15 through 21. Only Calf 4 had samples taken in week 3. Calf 1
96 only had samples taken in week 1. Calves 2 and 3 had samples taken in weeks 1 and 2.
97 Calf 4's Week 1 samples did not include samples from June 9, when Calf 4 was in
98 acoustic isolation. Any samples that did not fit into one of those four categories were
99 classified as "Other" and were not used to evaluate maternal whistle use. Some of these
100 samples were used to evaluate the difference between calf and adult whistles (see
101 "Separating Out Calf Whistles" below).

102

103 *Whistles*

104 A total of 4116 min were digitized from 412 focal samples (Table 1). Recordings were
105 played back on a Samsung SV-300W VCR and filtered with a Frequency Devices 9002
106 programmable filter with a high-pass filter at 2 kHz and a post-filter gain of 5x. Sounds

107 were digitized at 80 kHz onto an IBM PC with a Dalanco Spry model 250 Analog to
108 Digital conversion board. Whistles were then extracted by an automatic extraction and
109 sorting procedure (Fripp 1999). This procedure first extracted all sounds with energy
110 above a pre-set noise threshold and then sorted the sounds by bandwidth. In this way, the
111 sorting procedure separated the broadband burst-pulse sounds and echolocation clicks
112 from the narrowband whistles. A human observer then checked the sound files to
113 eliminate spurious detections. More than 200,000 cuts were made, yielding more than
114 23,000 whistles (Table 1).

115 Files containing whistles were separated into files with single whistles and files
116 with two or more overlapping whistles. Overlapping whistles are whistles that occurred at
117 the same time. While they could often be separated visually (one could see that there
118 were multiple whistles), they could not be separated by the automatic contour extractor
119 (see below). These whistles were therefore excluded from the contour-based analysis, but
120 the number of whistles in these files was counted and added to the number of files
121 containing single whistles to determine the total number of whistles collected.
122 Overlapping whistles were only saved and counted from the May and June recordings
123 (see Table 1).

124 After whistle extraction, the frequency contour of each whistle's fundamental
125 frequency was extracted using the procedure described by Buck and Tyack (1993) (see
126 Figure 1A). With this procedure, the contour is extracted by taking the frequency with the
127 highest amplitude in each time-block of the spectrogram after noise compensation (Buck
128 and Tyack 1993). Spectrograms were produced with an FFT size of 512 samples/block, a
129 step size of 512, a Hamming window, a low frequency cutoff of 4 kHz, a high frequency

130 cutoff of 22 kHz and a band-reject filter that excluded 15.05 to 16.05 kHz (to account for
131 monitor noise). To avoid extracting harmonics and to be sure the contour represents the
132 whistle's fundamental frequency, the extraction program looks for peaks at half and one-
133 third the peak initially detected. Following extraction, contours were visually checked
134 and only contours where the majority of the points fell on the whistle's visible
135 fundamental were included (see Figure 1A). Contours with a few points off the visible
136 fundamental were left as extracted. Correcting these points would have required
137 significant massaging of the data (particularly in the case of Mother 1, who had actual
138 silences in her whistle, see Figure 1A), which we considered inappropriate.

139 The following measures were calculated from the acoustic data: whistle rate per
140 minute, whistle rate per dolphin-minute, average contour length (in ms), and percent of
141 whistles overlapping other whistles. Whistle rate per dolphin-minute was calculated by
142 dividing the whistle rate per minute by the number of dolphins in the group at the time to
143 get an estimate of the average whistle rate per individual. For each measure, a value was
144 calculated for each 10-minute sample. A mean was then calculated for each focal animal
145 for each section (Pre-Birth, Week 1, Week 2, Week 3). All means are presented \pm
146 standard error. An ANOVA was performed using those means (one for each section for
147 each focal). Analysis of signature whistle rate was performed in the same way (see
148 below).

149

150 *Separating Out Calf Whistles*

151 Because we were interested in changes in the adult repertoire, but with a single
152 hydrophone cannot determine repertoires of individual dolphins, we needed a way to

153 separate calf whistles from the general pool of whistles. Caldwell and Caldwell (1979)
154 described the whistles of newborn bottlenose dolphins as short, quavery, and lacking
155 frequency modulation. This contrasts with the whistles of adult dolphins, which are
156 narrow-band over short time periods and highly frequency modulated over the entire
157 duration of most whistles (Caldwell *et al.* 1990). The Caldwells hypothesized that, using
158 this information, it should be possible to distinguish calf whistles from those made by
159 adults (Caldwell and Caldwell 1979). Following this hypothesis, we used our data to try
160 to separate calf whistles from adult whistles by means of their frequency characteristics.

161 For this test, focal samples were classified into four categories: “Adult Only,”
162 “Neonate Alone,” “No Neonate,” and “Adult + Neonate” (Table 1). The “Adult Only”
163 whistles come from the week immediately before Calf 2 was born, when only four adult
164 dolphins were in the group. The “Neonate Alone” whistles come from Calf 4 at 6-days
165 old, when he was held in a separate pool and out of acoustic contact with any other
166 dolphin. These two periods allowed us to look at known adult whistles and compare them
167 to known calf whistles. During the other two periods there were mixed groups of adults
168 and calves. The “No Neonate” period included the samples from March and the samples
169 from the week before Calf 1 was born. During this time, there were five adult females
170 (four pregnant) and one 7-month old calf in the pool (Table 1). The “Adult + Neonate”
171 period includes all the time when newborn calves were in the pool. The contours from
172 these mixed groups were classified secondarily, using the classification of the known
173 adult and neonate whistles.

174 From the contours in these categories, the contour duration and several frequency
175 parameters were calculated (with a custom program written in Matlab 6.5, Mathworks).

176 The frequency parameters were measured from the quartile contour, which is the contour
177 with the lowest and highest 25% of the frequencies removed. This was done to remove
178 outliers and noise spikes from the contour, which were significant in some contours.
179 Noise spikes occur when the signal-to-noise ratio is unusually low in a particular time-bin
180 of the spectrogram. Although some information was lost in this process, the use of the
181 quartile contour prevented noisy contours from dominating the results. Six parameters
182 were measured from the quartile contour: minimum frequency, maximum frequency,
183 median frequency, frequency range, frequency asymmetry, and sweep rate. Frequency
184 range is a measure of the overall frequencies used in the entire whistle, defined as
185 (maximum frequency)-(minimum frequency). The frequency asymmetry is defined as
186 (median-min)/(max-min). This measure will vary from 0 (median equals minimum) to 1
187 (median equals maximum) (see Fristrup and Watkins 1994). Sweep rate is a measure of
188 frequency modulation, defined as range/duration.

189 Contours from the “Adult Only” and “Neonate Alone” categories were classified
190 by these parameters using linear discriminant analysis (Systat 7.0, SPSS). The centroids
191 of each group were then calculated, and Wilks’ λ was used to test the equality of the
192 centroids. The contours from the two mixed groups, “No Neonate” and “Adult +
193 Neonate,” were classified afterwards using the same discriminant function. To classify
194 these cases, the Mahalanobis distance (defined as $(x-mean)/cov(x-mean)$) from each
195 group mean was calculated for each case. The case was classified into the group whose
196 mean was closer. If the contour was equidistant between groups, no classification
197 decision was made. Later analysis of adult whistle use was done only on contours that
198 were classified as adult by this analysis.

199

200 *Signature Whistle Analysis*

201 In addition to the overall repertoire, we wished to look at the specific changes in
202 signature whistle use. The contours in all sections were therefore classified using
203 dictionary contour comparison (DCC: Buck and Tyack 1993, Fripp *et al.* 2005). To
204 perform DCC, a series of dictionary contours (DCs) are selected to represent the types of
205 whistles generally encountered. All contours are then compared to these DCs using
206 dynamic time warping (DTW), a procedure that correlates the frequencies of two
207 contours after allowing non-linear warping in time (but not in frequency) of one contour
208 to fit the other (Buck and Tyack 1993). The DTW algorithm does not calculate similarity
209 for whistles that differ in duration by more than a factor of two, and assigns a similarity
210 of 0 to those comparisons. Following the DTW, each contour was assigned to the DC
211 with the greatest similarity, so long as that similarity was greater than a predetermined
212 threshold (Fripp *et al.* 2005). If the contour did not have a similarity greater than the
213 threshold with any DC, it was classified as not assigned to a DC. A comparison of
214 methods has shown the combination of DCC and DTW to be a good method for
215 separating known categories of whistles, such as signature whistles (Fripp 1999).

216 For this data set, DCs were selected to represent the signature whistles of all the
217 dolphins in the group (not including the neonatal calves who did not yet have signature
218 whistles). In addition, a few typical non-signature whistle contours were also included,
219 identified as typical by cluster analysis of a random sample of whistles (see Fripp 2005).
220 Signature whistles of the mothers were determined by other researchers, by isolating the
221 mothers after the calves were grown, and are published elsewhere (Mello and Amundin

222 2005). We confirmed these whistles by comparing them to whistles recorded shortly
223 after the calves produced bubblestreams. For each calf, one adult-like whistle
224 consistently showed up among the whistles produced directly after a calf produced a
225 bubblestream. In all cases, these whistles matched the contour of the calf's mother's
226 signature whistle. Because we were recording with only one hydrophone, we had no
227 means to individually identify the producer of any given whistle. Whistles were therefore
228 chosen for the dictionary contours to represent the breadth of whistles heard from the
229 group and the contours of the known signature whistles of the adults.

230 The entire group of DCs is shown in Figure 1B. The DCs included variants of the
231 signature whistles with differing numbers of loops (which is typical, see Caldwell *et al.*
232 1990), because the DTW would consider similar whistles with different numbers of loops
233 to be dissimilar. Unfortunately, the DTW could not distinguish the whistles of Mother 1
234 from those of Mother 3. However, the periods for Calf 1 and Calf 3 did not overlap at all
235 (even the Pre-Birth days), and Mother 1 was removed from the pool a week before Calf 3
236 was born. Therefore, although Mother 3 could be augmenting Mother 1's whistle rate, it
237 is unlikely that Mother 1 impacted Mother 3's rate. The analysis of the DCC classified
238 contours as one of the following: Mother 1/Mother 3, Mother 2, Mother 4, Sharky,
239 Daphne, Non-signature whistle (those contours listed in Figure 1 as "Unidentified"), or
240 not assigned to a DC.

241

242 **Results**

243

244 *Total Whistle Sample*

245 The most striking change between the pre- and post-partum whistle use was that the rate
246 of whistling increased by an order of magnitude when the calves were born, from $0.27 \pm$
247 0.45 whistles per dolphin-minute to 2.86 ± 0.39 (Figure 2A, ANOVA $F(3,7)=9.8$,
248 $P=0.007$). The whistle rate remained high in Week 2 (3.26 ± 0.45) and then decreased
249 again in Week 3 (0.80 ± 0.78). Bonferroni post-hoc tests showed that the Pre-Birth
250 whistle rate was significantly lower than the whistle rate in Weeks 1 and 2 ($P=0.02$).

251 In addition, the whistles themselves changed. The contour length was
252 significantly longer in Week 1 than in the Pre-Birth period, changing from 375 ± 43 ms
253 to 632 ± 37 ms on average (Figure 2B, ANOVA $F(3,7)=10.2$, $P=0.006$). The contour
254 length decreased again in Week 2 (to 523 ± 43 ms) and even more in Week 3 (to $272 \pm$
255 75 ms). Bonferroni tests showed that Week 1 was significantly different from Pre-Birth
256 and Week 3 ($P=0.02$).

257 The percentage of whistles overlapping other whistles also increased, although
258 this difference was not significant (Figure 2C, ANOVA $F(3,7)=2.1$, $P=0.186$). The
259 percent overlap was $5\% \pm 7\%$ in the Pre-Birth period, $23.5\% \pm 6\%$ in Week 1, $26\% \pm 7\%$
260 in Week 2, and $9\% \pm 12\%$ in Week 3. This result may indicate a shift in the dolphins' use
261 of the whistles, although there was a great deal of variation between focal dolphins on
262 this measure.

263 The rate of overlapping whistles, combined with the whistle rate and average
264 duration, can be used to determine whether the whistles are randomly timed with respect

265 to each other. To test this, whistles were randomly placed in a 600 second block of time
266 (equivalent to 10 minutes, the duration of our samples) and the proportion of whistles that
267 overlapped other whistles (i.e. were closer to another whistle than the average whistle
268 duration) was calculated. For each section, the number and duration of whistles were set
269 based on the observed values of whistle rate per minute (note that this is different from
270 whistle rate per dolphin-minute) and average contour length (Table 2). A P-value was
271 generated from the proportion of 10,000 simulations with a greater percentage of
272 overlaps than the observed rate (Table 2). As expected, the overlap rate increased with
273 the increase in number and duration of whistles (from 1% to 12% on average), but the
274 simulated increase was not as great as the observed increase. The observed overlap rate
275 from the Pre-Birth period was not significantly different from the simulated overlap rate
276 ($P=0.07$, Table 2). The observed overlap rates from all three postpartum weeks were
277 significantly higher than the simulated rates, however ($P<0.005$, Table 2). These results
278 indicate that the whistles were randomly timed with respect to each other before the
279 calves were born but were closer together than expected after the calves were born.

280

281 *Separating Calf Whistles from Adult Whistles*

282 There are two possible explanations for the changes in whistle rate and use discussed
283 above, which are not mutually exclusive. One explanation is that newborn calves whistle
284 a great deal. Because they are newborns, their whistles can be expected to be different
285 from, and be used differently than, the adult whistles. The second explanation is that
286 adults whistle more and differently in the weeks after calves are born.

287 To distinguish between these possibilities, adult and calf whistles need to be
288 separated. Obviously, the best way to do this would be to study individual repertoires.
289 However, with a single hydrophone, there is no way to determine which dolphin
290 produced a given whistle. Other researchers have taken advantage of bubblestreams
291 produced by dolphins to assign individual repertoires (e.g. McCowan and Reiss 1995),
292 but recent research has shown that bubblestreams do not always provide a representative
293 sample of a dolphin's whistle repertoire (Fripp 2005).

294 Previous researchers have suggested that the acoustic characteristics of the
295 whistles could be used to separate adult whistles from calf whistles (Caldwell and
296 Caldwell 1979, Caldwell *et al.* 1990). To determine whether it would be possible to
297 separate neonatal whistles from adult whistles based on their acoustic characteristics, we
298 compared the whistles recorded when only adults were in the pool (Calf 2's Pre-Birth
299 week, see Table 1) to the whistles recorded from a 6-day old neonatal calf in acoustic
300 isolation (Calf 4, see Methods).

301

302 Adult and Neonate Whistles

303 There were clear differences between the adult ("Adult Only") whistles and the neonate
304 ("Neonate Alone") whistles (Figure 3). Neonate whistles were significantly longer than
305 adult whistles on average (507 ± 15 ms vs. 426 ± 17 ms, t-test $t(695)=-3.2$, $P<0.001$),
306 although the adults produced the longest whistles (7% of adult whistles were more than a
307 second long, compared to none of the neonate whistles). Adult whistles had significantly
308 higher quartile frequency ranges than neonate whistles (2.6 ± 0.1 kHz vs. 1.2 ± 0.05 kHz,
309 t-test $t(695)=-9.2$, $P<0.001$). As discussed in the methods, the quartile frequency range is

310 the bandwidth of the central 50% of the frequencies (in other words, with the lowest and
311 highest quartiles of frequencies removed). For whistles with a great deal of frequency
312 modulation, the quartile range will be quite a bit smaller than the apparent frequency
313 range on the figure (e.g. Figure 3A). Adults also had significantly higher sweep rates
314 (10.4 ± 0.7 Hz/ms vs. 4.6 ± 0.5 Hz/ms, t-test $t(695)=-6.0$, $P<0.001$). These results mean
315 that the adult whistles had significantly greater frequency modulation than the neonate
316 whistles, as expected.

317 The discriminant analysis successfully separated the adult whistles from the
318 neonate whistles (Figure 3B). Overall, 79% of the known adult and neonate whistles were
319 classified correctly (76% of adult, 87% of neonate). The discriminant functions relied
320 primarily on the asymmetry and the sweep rate. The duration, frequency range, median
321 frequency, and maximum frequency were also incorporated, although with smaller
322 weights. The mean discriminant function score for adult whistles was -0.53 , while for
323 neonate whistles it was 0.978 (Wilks' $\lambda = 0.658$, $P<0.0001$).

324

325 Mixed Groups

326 The measurements of the whistles in the two mixed groups, “No Neonate” and “Adult +
327 Neonate,” tended to resemble the adult whistles more than the neonatal whistles.

328 However, the average duration of the “Adult + Neonate” whistles was extremely long
329 (646 ± 3 ms), even compared to the “Neonate Alone” whistles. The sweep rate was
330 correspondingly low (5.2 ± 0.1 Hz/ms), most likely the result of the very high durations.

331 Unfortunately, whistles longer than one second were not diagnostic of adult whistles.

332 Approximately 14% of the whistles in the mixed groups were longer than a second, with

333 the long whistles divided between calf and adult whistles by the discriminant analysis.
334 When the whistles from the two mixed groups were classified using the discriminant
335 function determined above, the “No Neonate” contours were classified almost exactly the
336 same as the “Adult Only” whistles: 79% adult and 21% neonate (Figure 3B). The “Adult
337 + Neonate” whistles, on the other hand, appeared to be almost evenly split, with 49%
338 adult and 51% neonate.

339

340 Whistle Rate of Adult Whistles

341 The whistle-rate and contour-length analysis was redone using only adult whistles as
342 determined by the discriminant analysis described above. Average adult whistle rate per
343 dolphin-minute increased in the same way that the overall whistle rate per dolphin-minute
344 had (ANOVA $F(3,7)=13.6$, $P=0.003$; Pre-Birth different from Weeks 1 and 2 by
345 Bonferroni post-hoc tests, $P=0.01$). The adult whistle rate per dolphin-minute is
346 calculated based on the number of adults in the group, not the total number of dolphins.
347 Average adult contour length also increased in the calves’ first weeks (ANOVA
348 $F(3,7)=4.8$, $P=0.041$). These results indicate that the changes in overall whistle rate and
349 use are at least partly due to changes in adult whistling patterns, rather than the whistling
350 behavior of the newborn calves. Because the discriminant analysis relied on whistle
351 contours, overlapping whistles could not be used in this analysis, as overlapping whistles
352 confuse the contour extractor. An analysis of what proportion of overlapping whistles in
353 this time period are calf vs. adult would be interesting, however, and is worthy of later
354 investigation.

355

356 Whistle Rate of Calf Whistles

357 The whistle-rate and contour-length analyses were also redone using only calf whistles as
358 determined by the discriminant analysis of the whistles in the calves' first three weeks.
359 As with adult whistles, the rate of calf whistles per dolphin-minute was calculated based
360 on the number of calves, not the total number of dolphins. The average rate of calf
361 whistles per dolphin-minute was 3.0 ± 0.5 in Week 1, 2.6 ± 0.5 in Week 2 and 1.0 ± 0.9
362 in Week 3. However, this change was not significant, possibly because of the small
363 sample size (total N = 8 focal-week pairs, ANOVA $F(2,5)=2.0$, $P=0.23$). The average
364 calf contour length also started high and then fell, from 620 ± 80 ms in Week 1 to $552 \pm$
365 92 ms in Week 2 to 261 ± 160 ms in Week 3, but again, the change was not significant
366 (ANOVA $F(2,5)=2.0$, $P=0.23$). These results indicate that some aspects of the changes in
367 overall whistle rate and use in the calves' first weeks are also due to changes in calf
368 whistling patterns.

369

370 *Dictionary Contour Comparisons*

371 To categorize whistles by type, all contours were compared to a dictionary of typical
372 contours (Figure 1). Overall, the dictionary contour comparison (DCC) classified 58% of
373 the contours as dictionary contour non-signature whistles and 20% as dictionary contour
374 signature whistles (Table 3). 22% of the contours did not match any of the dictionary
375 contours. Of the contours that were previously classified as "calf" whistles by the
376 discriminant analysis, 90% were non-signature whistles, 9% could not be classified, and
377 only 1% was (incorrectly) classified as signature whistles. These last were all classified
378 as matching Mother 4's signature whistle, which is somewhat similar to non-signature

379 whistle upsweeps that are common among dolphins (see Table 3, Figure 1). Adult
380 whistles were classified as 39% signature whistles, 26% non-signature whistle, and 35%
381 other. The eight contours that were not classified as adult or calf by the discriminant
382 analysis were all similarly not classified by the DCC.

383

384 *Signature Whistle Use*

385

386 Maternal Signature Whistles

387 Adult signature whistle use was investigated using only those contours that were
388 classified both as adult by the discriminant analysis and as a signature whistle by the
389 DCC. The production of signature whistles by each mother was considered relative to the
390 birth of her calf; we classified her signature whistles by the periods described in the
391 methods: Pre-Birth, Week 1, Week 2, and Week 3.

392 The change in maternal signature whistle production was investigated using three
393 measures: the average rate of maternal signature whistles/dolphin-minute, maternal
394 signature whistles as a percent of the total adult whistles, and maternal signature whistles
395 as a percent of the total signature whistles (Figure 4). The average rate of maternal
396 signature whistling increased significantly from the Pre-Birth period to the first few
397 weeks of the calves' lives (ANOVA $P=0.005$, Figure 4A). Interestingly, the highest rate
398 of signature whistles occurred during Week 2; Week 1 was intermediate between Pre-
399 Birth and Week 2. The rate of signature whistling decreased again in Week 3 for Mother
400 4. Maternal signature whistles also increased as a percent of both the total adult whistles
401 and the adult signature whistles (ANOVA $F(3,8)=5.2$ $P=0.03$ and $F(3,8)=6.1$ $P=0.02$,

402 Figure 4B and C). In both cases, the greatest proportion of maternal signature whistles
403 occurred in Week 1, and the proportions declined steadily in Weeks 2 and 3.

404

405 Signature Whistle Use by Non-Mothers

406 To determine whether the change in whistle production was confined to mothers, the
407 signature whistle use of other dolphins was investigated over the same periods. Because
408 of the sequential nature of the births, signature whistle use by non-mothers could only be
409 tested in the Pre-Birth vs. Week 1 periods for certain combinations of calves and dolphins
410 (Table 4). Non-neonates (adults and 7-month old Daphne) had to be in the pool for both
411 the Pre-Birth period and at least some portion of the calf's first week. Adults could not
412 be caring for a neonate during either period. Because the whistles of Mother 1 and
413 Mother 3 could not be distinguished, neither could be used for the other's calf. Analysis
414 of this data set showed that the dolphins did not change their rate of signature whistle
415 production when calves that were not their own were born (paired t-test $t(6)=1.4$, $P=0.21$,
416 see Table 4). This result is consistent with the increase in maternal signature whistles as a
417 percent of the total signature whistles heard (Figure 4C).

418

419 Calf 4's Unusual First Week

420 Calf 4 had a rather unusual first week, which merits a separate discussion. This calf was
421 born approximately a week after Calf 2 died. As soon as Calf 4 was born, before Mother
422 4 could turn around to find him, Mother 2 took him with her to the surface. Calf 4
423 remained with Mother 2 until his 6th day, when he was removed from the pool for

424 medical treatment. When he was returned to the group later that day, Mother 2 ignored
425 him and Mother 4 reclaimed him. He remained with Mother 4 until weaning.

426 These unusual circumstances allow us to look at postpartum signature whistle use
427 with respect to whether or not the mother is actually caring for a calf (Figure 5). Mother
428 4's signature whistle rate was high on day 1 (during much of which Mother 4 was in
429 labor) and again starting on day 7 (Figure 5). On the days when Mother 4 was not caring
430 for her calf, her signature whistle rate decreased again. This indicates that for Mother 4,
431 increased signature whistling was related to actually caring for her calf. Her signature
432 whistle rate increased when she began caring for the calf again, on day 7. In fact, her
433 signature whistle rate on day 7 was unusually high, higher than any of the other mothers
434 on any day of their calves' lives (0.7 whistles/dolphin-min *vs.* max = Mother 3 d9, 0.64;
435 average max = 0.35). Although there was some variability (esp. an unusually high whistle
436 rate for both adults on day 13, see Figure 5), for the most part Mother 4's signature
437 whistle rate decreased slowly over the calf's next two weeks.

438 Interestingly, Mother 2 did not increase her signature whistle rate when she was
439 caring for Calf 4 (Figure 5). This may have indicated that she was treating Calf 4 as if he
440 was Calf 2, who would have been two weeks old. Based on Mother 4's behavior, two
441 weeks may be beyond the time when the mothers are increasing their signature whistle
442 production. Alternatively, she could have considered caring for Calf 4 somehow different
443 from caring for her own calf and therefore behaved differently. However, a separate
444 analysis was done of the dolphins' non-vocal behavior, including time as nearest
445 neighbor, nursing, affiliative contact such as rubbing, and retrieving which is a maternal

446 behavior (Fripp 1999). Mother 2's non-vocal behavior toward Calf 4 was equivalent to
447 the maternal behavior she showed to her own calf (Fripp 1999).

448

449 **Discussion**

450 In this study, dolphin mothers produced more signature whistles in the first week of their
451 calves' lives than they had previously. By the third week of the calf's life, the only
452 mother of a surviving calf had returned to her previous rates of signature whistle
453 production. Only mothers changed their rate of signature whistle production after their
454 own calf was born: dolphins did not change their rate of signature whistle production
455 when calves were born to other dolphins.

456 Many things change when calves are born and changes in vocal behavior are to be
457 expected. Mothers, and other dolphins, might be expected to produce more or different
458 whistles when swimming with newborn calves than when swimming only with adults.
459 Previous work has recorded changes in adult whistling behavior shortly after calves are
460 born (e.g. Sayigh 1992, Mello and Amundin 2005), but the exact nature of these changes
461 was not clear. One hypothesis is that the mother could be using her signature whistle to
462 communicate with the other adults. In that case, however, one would predict that all the
463 dolphins would increase their signature whistle rate, not just the mother. Probably the
464 most obvious hypothesis is that the increase in only maternal signature whistle production
465 could be explained by the need for a mother to keep in contact with her calf. Signature
466 whistles are known to be used for this purpose (Sayigh 1992). However, the decrease in
467 signature whistle production by Mother 4 in week 3 does not fit that hypothesis, as calves
468 actually wander further from their mothers as they get older (Mann and Smuts 1998). If

469 the result that mothers do not keep up their increased signature whistle production
470 represents a general trend, another hypothesis is necessary.

471

472 *Alternative Hypothesis I: Imprinting*

473 Mann and Smuts (1998) suggested another hypothesis that may help explain this pattern.

474 They found that dolphin mothers (*Tursiops sp.*) in Shark Bay, Australia do not allow their
475 newborns to spend time alone with other dolphins, although they do tolerate non-social
476 separations. The mothers' intolerance of social separations changes to tolerance in the
477 calf's second week. Mann and Smuts (1998) hypothesized that this shift reflects a period
478 of imprinting during which calves learn to recognize their mothers' signature whistles.

479 Bottlenose dolphins are highly social, living in a fission-fusion society where a
480 calf will encounter many other dolphins before it is weaned (Wells 2003). The
481 combination of precocious locomotion (i.e. the ability to swim at birth) and sociality is
482 associated with imprinting in other species (Hess 1959). A calf can easily get separated
483 from its mother and find itself among many other dolphins. Imprinting allows young
484 animals to learn to recognize their mothers quickly and avoid confusion.

485 Mann and Smuts' (1998) imprinting hypothesis predicts an increase in maternal
486 signature whistle production in the first week of a calf's life. This increase should be
487 followed by a decline shortly after mothers begin tolerating social separations. High rates
488 of signature whistles may continue for a short time to reinforce the learning, but once
489 learning has occurred, the mother should produce fewer signature whistles. Signature
490 whistle production by other animals in the group should not change during this time.

491 Our results show a clear increase in maternal signature whistle production without
492 a corresponding increase in non-maternal signature whistle production. These results
493 support the imprinting hypothesis: our interpretation is that bottlenose dolphin calves
494 imprint on their mothers' signature whistles in the first week of their lives, and their
495 mothers facilitate this process by producing their signature whistles at higher than normal
496 rates for the calves to learn. The results from Mother 4 suggest that the mothers are
497 decreasing their signature whistle production again in week 3, which is predicted by the
498 imprinting hypothesis of Mann and Smuts (1998). Unfortunately, with only one calf
499 surviving to week 3, and a calf with an unusual first week at that, this evidence is not
500 particularly strong. Future work to determine whether most mothers decrease their
501 signature whistle production in week 2 or 3 is necessary to truly test this hypothesis.

502

503 Learning to Recognize your Mother

504 Vocal recognition between mothers and infants has been seen in other species of
505 mammals, especially species of pinnipeds and bats (e.g. McCulloch and Boness 2000,
506 Balcombe and McCracken 1992). In most of these cases, however, it is primarily the
507 mother who recognizes the calls of the infants, not the other way around (McCulloch and
508 Boness 2000), although in some species the recognition is mutual (Trillmich 1981;
509 Gisiner and Schusterman 1991, Balcombe and McCracken 1992, Insley 2001).

510 The phenomenon of imprinting as a specialized learning mechanism whereby
511 infants learn to recognize their mothers was first described in birds (Lorenz 1937). Early
512 discussions of imprinting described it as a fairly rigid phenomenon, occurring primarily
513 in birds, characterized by a constrained sensitive period, and irreversible (Lorenz 1937).

514 Since then, imprinting has been described in other taxa, including a number of ungulates,
515 which are related to dolphins, and other mammalian species (e.g. Hess 1959, Altmann
516 1963, Alcock 1998, Thewissen *et al.* 2001). Imprinting by infants appears to be more
517 common in species that are highly social and those with precocious locomotion (Hess
518 1959). Dolphins fit both patterns (Wells 2003).

519 In some bird species, the critical period for imprinting is as short as a few hours
520 (Lorenz 1937). In some mammals, the critical period for imprinting is the first few
521 weeks of life (e.g. days 5-14 for the shrew, Alcock 1998). The one-to-two week critical
522 period suggested by Mann and Smuts (1998) is therefore in line with durations reported
523 for other mammalian species. In addition, ungulates sometimes hide with their young
524 until imprinting is complete (e.g. Hersher *et al.* 1963a). The dolphin mothers' intolerance
525 of social separations (Mann and Smuts 1998) may reflect a similar process. Since
526 Lorenz's time, additional evidence has also shown the sensitive period of imprinting is
527 often more flexible than originally thought (Hersher *et al.* 1963b).

528 In his discussion of imprinting, Lorenz (1937) comments that the irreversibility of
529 the process is what sets imprinting apart from other types of associative learning. It is not
530 yet clear how irreversible the process of learning a mother's signature whistle is in
531 dolphins. However, an investigation of previous evidence in bottlenose dolphins may
532 illuminate this question. The theft, or attempted theft, of newborn dolphins, as occurred
533 with Calf 4, has been reported previously (e.g. Dudok van Heel and Meyer 1974, Prescott
534 1977, Shallenberger and Kang 1977, Thurman and Williams 1986, Mann and Smuts
535 1998). Most interestingly, these incidents almost always occur in the first day of the
536 calf's life. If the imprinting hypothesis holds, this may indicate that after the calf has

537 imprinted on its mother, such theft is much more difficult. The fear of such theft may
538 drive the maternal intolerance of early social separations (Mann and Smuts 1998). The
539 shift to tolerance at the end of the first week might then be explained by the completion
540 of a relatively irreversible imprinting process.

541 The theft and subsequent return of Calf 4 may also illuminate the flexibility of the
542 imprinting process. Mann and Smuts (1998) reported a shift in maternal tolerance of
543 social separations starting as early as days 4 to 7. In this study, however, maternal
544 signature whistle production remained high through the second week (days 8 to 14).
545 Mother 4's increased signature whistle production after Calf 4 returned to her and
546 through his second week may indicate that the critical period can last as long as two
547 weeks, although that length of time is not always necessary. The constant exposure to
548 other dolphins that a calf experiences in captivity may also necessitate a longer period of
549 exposure to the mother's whistle than would be required in the wild, or possibly by a lone
550 mother-calf pair in captivity. Flexibility in imprinting critical periods has been reported
551 for other species as well (Bateson 1979, Hersher *et al.* 1963b).

552

553 *Alternative Hypothesis II: Modeling Signature Whistles for Male Calves*

554 A second alternative hypothesis is raised by the observation that all four of these calves
555 were male. Dolphin signature whistles develop over the course of the calf's first year of
556 life, and the contour of the signature whistle is learned from the whistles the calf hears in
557 its first few months (Sayigh *et al.* 1990, Fripp *et al.* 2005). Previous research has shown
558 that male calves are more likely than female calves to develop signature whistles similar
559 to their mothers' signature whistles (Sayigh *et al.* 1995). An increase in maternal

560 signature whistle production with a male calf may therefore be related to the mother
561 using her signature whistle as a model for the son's future signature whistle. The short-
562 lived nature of the increase, potentially demonstrated here by Mother 4, could indicate
563 that the most important time for learning one's future signature whistle is the first few
564 weeks. An early period of learning for a vocalization that only appears later is well
565 known from studies of birdsong (e.g. Marler 1970, Kroodsma and Pickert 1984).
566 However, the exposure to song needed for young birds is not so early or so short-lived.
567 Most birds are exposed to song tutoring for their entire time in the nest and often some of
568 their fledgling stage (Marler 1970, Kroodsma and Pickert 1984). One might expect,
569 therefore, that tutoring of male dolphins would continue for longer than two to three
570 weeks, especially considering how much longer dolphin calves are dependent on their
571 mothers (3 to 5 years, Wells 2003).

572 The fact that the current study was done in captivity is an argument against this
573 hypothesis however. Sayigh's work showed that while free-ranging males were more
574 likely to have signature whistles similar to their mothers, captive-born males were not
575 (Sayigh 1992). However, if the mothers' behavior has an innate basis, they may produce
576 more signature whistles for their male calves regardless of the situation. Therefore, while
577 being in captivity is an argument against this hypothesis, it is not strong evidence to
578 discount this hypothesis. Future work investigating maternal signature whistle use with
579 female calves is the best way to answer this question. This hypothesis predicts that
580 mothers should only increase their signature whistle production with male calves and not
581 with females.

582

583 *Caveats*

584 Certain methodological issues must be addressed when discussing these results.
585 Dolphins are known to mimic each other's signature whistles (Tyack 1986). To classify
586 the whistles, we matched the contours to the known contours of the dolphins' signature
587 whistles. We therefore could not distinguish between maternal signature whistle
588 production and mimicry of the mother's signature whistle by other dolphins. However, at
589 most, signature whistle mimicry has been reported to account for 25% of the signature
590 whistles recorded (Tyack 1986). The increase in maternal signature whistle use was far
591 greater than 25%. However, a short-lived increase in signature whistle mimicry related
592 to the novelty of the new calf cannot be discounted here. An investigation of individual
593 whistle use is needed to distinguish that hypothesis but awaits the advent of new
594 technology to allow us to assign whistles to individuals (see Fripp 2005 for a discussion
595 of this problem).

596 We must also consider the deaths of three of the four calves. Data for week 3
597 were only available for one calf, and this calf had a very unusual first week. His mother
598 also showed the highest whistle rate of all the mothers, raising the concern that she may
599 be dominating the results. Re-analysis of the results shows that not to be the case. The
600 other three mothers increased their signature whistle production in the first two weeks of
601 their calves lives as well ($F(2,5)=6.9$, $P=0.04$ without Mother 4), and their signature
602 whistles comprised a greater proportion of all the signature whistles produced during the
603 calves first two weeks ($F(2,5)=8.0$, $P=0.03$ without Mother 4). Because only the one calf
604 survived to week 3, we can only see the week 3 decrease from that calf's mother.
605 However, Mother 2's behavior while caring for Calf 4 (not increasing her signature

606 whistle rate) also suggests a decrease in signature whistle use as a calf grows older.
607 Alloparenting, taking care of other animals' infants, is often seen among postpartum
608 females (Hrdy 1977, McBride & Kritzler 1951, Riedman & Le Boeuf 1982). Several
609 researchers have suggested that these females are hormonally "primed" to respond to
610 young infants (Hrdy 1977, Riedman & Le Boeuf 1982). The recent loss of Calf 2 may
611 have primed Mother 2 to respond when Calf 4 was born. She therefore may have been
612 treating Calf 4 as if he were Calf 2. If the whistling behavior of mothers is also
613 hormonally primed by the timing of birth, then Mother 2 may have been beyond the
614 typical period of high whistle rates.

615 Another issue that needs to be addressed is the DCC's confusion of Mother 1's
616 whistles with Mother 3's. As was stated before, Mother 1 was moved out a week before
617 Calf 3 was born. The increase in production of Mother 1/Mother 3 whistles in Calf 3's
618 first weeks is therefore attributable to Mother 3, not Mother 1. Signature whistles
619 produced by Mother 3 could have contributed to the increase in Mother 1 signature
620 whistles following Calf 1's birth. However, no other dolphin increased her signature
621 whistle production following the birth of another dolphin's calf (note that that analysis
622 did not include Mother 3 at Calf 1's birth). It is therefore unlikely that Mother 3 would
623 have changed her signature whistle production when Calf 1 was born.

624 The final methodological issue that needs to be addressed is the fact that this work
625 was done in captivity. It is possible that these results are an artifact of life in captivity
626 where animals are in constant acoustic contact with each other. It is possible that the
627 only way to differentiate the mother in this environment is through high whistle rates.
628 However, this hypothesis would not predict a decrease in whistling when the calf is only

629 three weeks old. Additionally, changes in adult whistling behavior shortly after calves
630 are born have been recorded in the wild as well (Sayigh 1992). Although animals are not
631 is as constant acoustic contact with each other in the wild, there are many other dolphins
632 around and many opportunities for a calf to be lost in the wild. We would therefore
633 expect that a calf would have a similar, if not greater, need to recognize its mother as it
634 has in captivity.

635

636 *Separation of Calf and Adult Whistles*

637 In the current study, the extent of frequency modulation could be used to distinguish
638 neonate whistles from adult whistles by discriminant analysis, as predicted by Caldwell
639 and Caldwell (1979). Although the discriminant analysis classified the majority of the
640 known whistles properly, 24% of the “known adult” whistles were classified as neonatal.
641 One possible reason for this is the connection between the pools at Kolmårdens Djurpark.
642 Although Daphne, the seven-month-old calf, had been moved into another pool, that pool
643 was not acoustically isolated from the study pool. Whistles from that calf may have been
644 heard in the study pool even when only adults were physically present in the study pool.
645 This is a likely explanation for why the “Adult Only” and “No Neonate” categories
646 appear so similar. It is important to note, however, that the whistles from the “Neonate
647 Alone” category come from a pool that was acoustically isolated from the rest of the
648 facility. All the whistles in that category were produced by the single calf in that pool.

649 The discriminant analysis indicated that the “Adult + Neonate” contours were
650 approximately half adult and half neonate. That result is interesting considering that on
651 most days there was only one neonate in a group of two to four adults. This may indicate

652 that the neonates were far more vocal than the adults. Alternatively, the adults may have
653 been imitating the neonatal sounds, although this seems unlikely. More likely, some of
654 the whistles classified as neonate in this context were misclassified. Since 24% of the
655 “Adult Only” whistles were classified as neonate (and 13% of the “Neonate Alone”
656 whistles were classified as adult), we should expect some of the mixed whistles to be
657 misclassified. Additionally, the postpartum increase in duration may be partly due to an
658 increase in the number of loops in the adult whistles. As noted in the results, this could
659 cause a corresponding decrease in the sweep rate, which could cause the whistle to be
660 misclassified, as sweep rate was one of the major parameters used by the discriminant
661 analysis.

662 Our results indicate that adult whistles change depending on context (pre- vs.
663 post-partum), as do previous results (Janik *et al.* 1994, Janik and Slater 1998). Since all
664 the known neonate whistles in this sample were from a single calf in a particular context,
665 alone with no adults in visual or acoustic contact, contextual changes in calf whistles may
666 have impacted our results as well. A follow-up study investigating the differences in the
667 whistles used by adults and calves in different contexts would be therefore useful.
668 However, the current study demonstrates a method whereby unidentified whistles can be
669 classified as probably produced by an adult or a young calf. This ability should aid in the
670 understanding of bottlenose dolphin vocal and behavioral development.

671

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681

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770 **Tables**

771 Table 1: Periods with different calves during which whistles were sampled.

Dates (1995)	10' Focal Samples	Whistles	Mother 1 and Calf 1 ^a	Mother 2 and Calf 2 ^a	Mother 3 and Calf 3 ^a	Mother 4 and Calf 4 ^a	Sharky and Daphne ^b	Discrim Analysis Period
March 21 - 29	80	> 1,138 ^c	<i>Other</i>	<i>Other</i>	<i>Other</i>	<i>Other</i>	Present	No Neonate
April 18, 24	32	> 330 ^d	Pre-Birth	<i>Other</i>	<i>Other</i>	<i>Other</i>	Present	No Neonate
April 25, 28, 29	52 ^e	> 524 ^d	Week 1	<i>Other</i>	<i>Other</i>	<i>Other</i>	Present 1 st day	Adult + Neonate
May 16, 18, 20, 21	60	636	<i>Other</i>	Pre-Birth	Pre-Birth	Pre-Birth	Not Present	Adult Only
May 22, 24, 28	45	3,465	Present 1 st day	Week 1	Pre-Birth	Pre-Birth	Not Present	Adult + Neonate
May 29	15	2,862	Not Present	Week 2	Pre-Birth	Pre-Birth	Not Present	Adult + Neonate
May 30; June 1, 2	40	6,439	Not Present	<i>Other</i>	Week 1	Pre-Birth	Not Present	Adult + Neonate
June 4	15	1,810	Not Present	<i>Other</i>	Week 1	Week 1	Not Present	Adult + Neonate
June 6, 8	30	3,757	Not Present	<i>Other</i>	Week 2	Week 1	Not Present	Adult + Neonate
June 9	4	250						Neonate Alone
June 10	5	519	Not Present	<i>Other</i>	Not Present	Week 1	Not Present	Adult + Neonate
June 12, 14, 16, 18	19	1,244	Not Present	<i>Other</i>	Not Present	Week 2	Not Present	Adult + Neonate
June 20, 22, 24	15	360	Not Present	<i>Other</i>	Not Present	Week 3	Not Present	Adult + Neonate
33 recording days	412	23,334						

772 ^aSections for each calf only include focal samples on that calf or that calf's mother.

773 ^bDaphne was seven months old and therefore was not a subject of this study. Sharky is her mother.

774 ^cNot all the whistles from this section were saved, due to computer error.

775 ^dNot all the overlapping whistles from these sections were saved, due to computer error.

776 ^eOne sample during this period was cut short (by 4.25') due to equipment failure, so only 515.75' were recorded from these 52 samples.

777 Table 2: Results of Randomization Trials for Whistle Overlaps

Section	Input Numbers			Results			
	Whistles	Length	% Overlap	Mean	Range	> Observed	P-value
Pre-Birth	11	375 ms	5%	0.6%	0-18%	670 (6.7%)	0.07
Week 1	125	631 ms	23%	12.2%	4-24%	2 (0.02%)	0.0002
Week 2	94	523 ms	26%	7.7%	0-21%	0 (0.0%)	0.000
Week 3	24	272 ms	9%	1.0%	0-17%	21 (0.2%)	0.002

778

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779 Table 3: Dictionary Contour Comparisons

Whistle Type*	Type of Dictionary Contour:			Total
	Signature Whistle	Non-Signature Whistle	None	
Adult	39% (2,935)	26% (1,989)	35% (2,594)	100% (7,518)
Calf	1% (69)	90% (6,564)	9% (691)	100% (7,324)
No Decision	0%	0%	100% (8)	100% (8)
Overall	20% (3,004)	58% (8,553)	22% (3,293)	100% (14,850)

780 *Whistle type determined by discriminant analysis (see “Separating Calf Whistles from Adult Whistles”).

781

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782 Table 4: Non-Maternal Signature Whistles per Dolphin-Minute

Calf	Signature whistle Type	Pre-Birth Rate*	Week 1 Rate*
Calf 1	Mother 2	0.01	0.00
	Mother 4	0.00	0.00
	Sharky	0.00	0.01
	Daphne	0.00	0.00
Calf 2	Mother 1/Mother 3	0.02	0.12
	Mother 4	0.02	0.01
Calf 3	Mother 4	0.02	0.07
Average		0.01	0.03

783 *Pre-Birth and Week 1 rates were **not** significantly different by paired t-test ($t(6)=1.4$, $P=0.21$). $N=7$

784 dolphin-calf pairs, with a total of 377 whistles, averaging 54 whistles/dolphin-calf pair.

785

786 **Figure Legends**

787

788 Figure 1: Contours

789 A. Sample Spectrograms and Contours. Spectrograms and matching contours of two of
790 the whistles used to make dictionary contours from the signature whistles of Mother 1
791 and Mother 3.

792 B. Dictionary Contours. The contours used as dictionary contours for the dictionary
793 contour comparison. The labeled contours include variants of the signature whistle from
794 each dolphin. “Unidentified” contours were typical whistles but could not be identified as
795 the signature whistle of a specific dolphin. Note that the analysis of the dictionary
796 contours could not distinguish Mother 1 from Mother 3.

797

798 Figure 2. Whistle Count Analysis for May and June. For each plot, each bar represents
799 the average of the three focals, each focal having been averaged over all the focal
800 samples from that mother-calf pair, when the calf was living. These plots include all
801 whistles except contour length, which includes only usable contours.

802 A. Average whistles/dolphin-minute. ANOVA, $F(3,7)=9.8$, $P = 0.007$; Bonferroni post
803 hoc tests show that Pre-Birth is significantly different from Weeks 1 and 2.

804 B. Average contour length. ANOVA, $F(3,7)=10.2$, $P = 0.006$; Bonferroni post hoc tests
805 show that Week 1 is significantly different from Pre-Birth and Week 3.

806 C. Percent Overlaps. ANOVA, $F(3,7)=2.1$, $P = 0.186$.

807

808 Figure 3. Separating Adult and Calf Whistles.

809 A. Sample Contours

810 Adult Only: Examples of whistles from the week immediately before Calf 2 was born,
811 when four adult females were in the group. These were classified as “Adult” by the
812 discriminant analysis.

813 Neonate Alone: Examples of whistles produced by a 6-day-old male, Calf 4, acoustically
814 isolated from the rest of the group. These were classified as “Calf” by the discriminant
815 analysis.

816 B. Discriminant Analysis Separating Adult and Calf Whistles; Discriminant analysis was
817 done using “Adult Only” and “Neonate Alone” categories, with a 79% accuracy rate. “No
818 Neonate” and “Adult + Neonate” sections were then classified based on the previous
819 discriminant analysis.

820

821 Figure 4: Maternal Signature Whistle Use. For each plot, each bar represents the average
822 of the four focal dolphins, each focal having been averaged over all the focal samples on
823 that mother-calf pair, when the calf was living. These plots include only usable contours
824 that have been classified as adult by the discriminant analysis and as maternal signature
825 whistles by the dictionary contour comparisons.

826 A. Average maternal signature whistles/dolphin-minute. ANOVA, $F(3,8)=9.4$, $P = 0.005$;

827 Bonferroni post hoc tests show that Pre-Birth is significantly different from Week 2.

828 B. Maternal signature whistles as a percent of all adult whistles. ANOVA, $F(3,8)=5.2$,

829 $P=0.028$; Bonferroni post hoc tests show that Pre-Birth is significantly different from

830 Week 1.

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831 C. Maternal signature whistles as a percent of all signature whistles. ANOVA,
832 $F(3,8)=6.1$, $P=0.019$; Bonferroni post hoc tests show that Pre-Birth is significantly
833 different from Week 1.

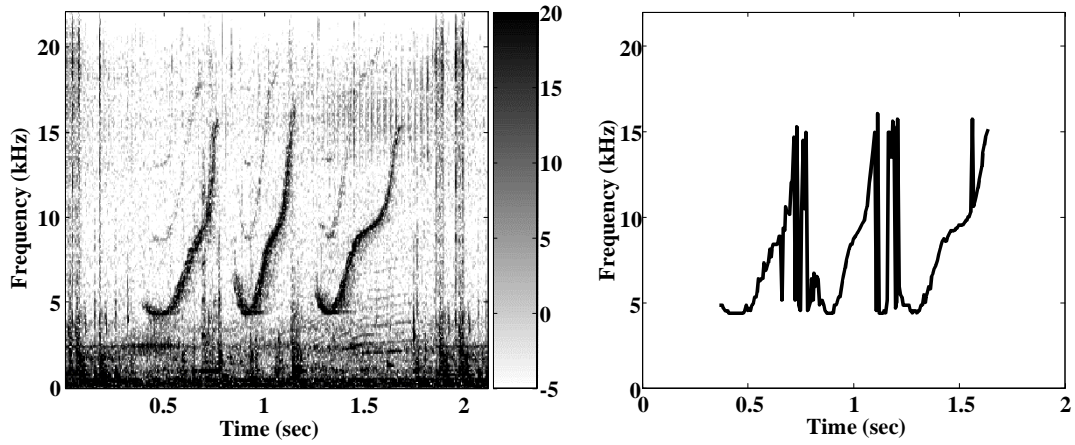
834

835 Figure 5: Signature Whistle Use in Calf 4's First Week: Average signature
836 whistles/dolphin-minute. Each point represents the average for that mother of all the Calf
837 4 focal samples on that day. Only usable contours that were classified as adult by the
838 discriminant analysis and as signature whistles by the dictionary contour comparisons
839 have been included. Mother 2 stole Calf 4 from Mother 4 at birth and returned him on
840 day 6.

841 Figure 1: Contours

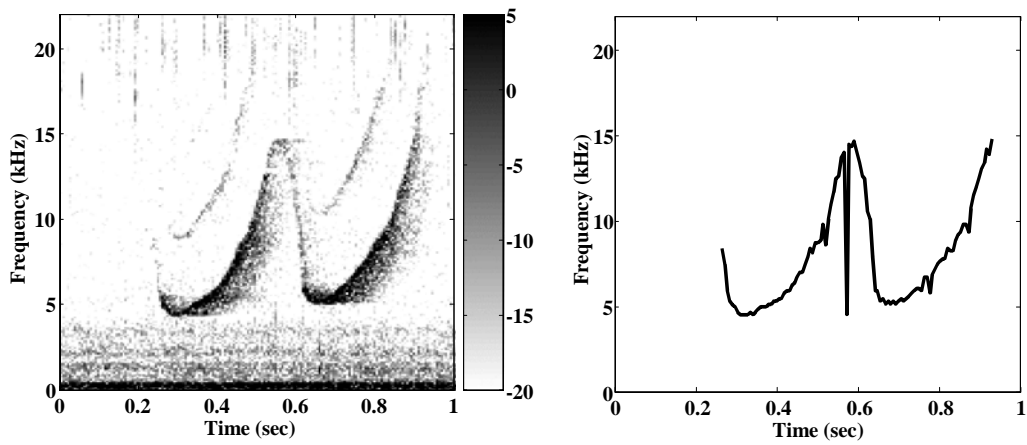
842 A. Sample Spectrograms and Contours.

843 Mother 1



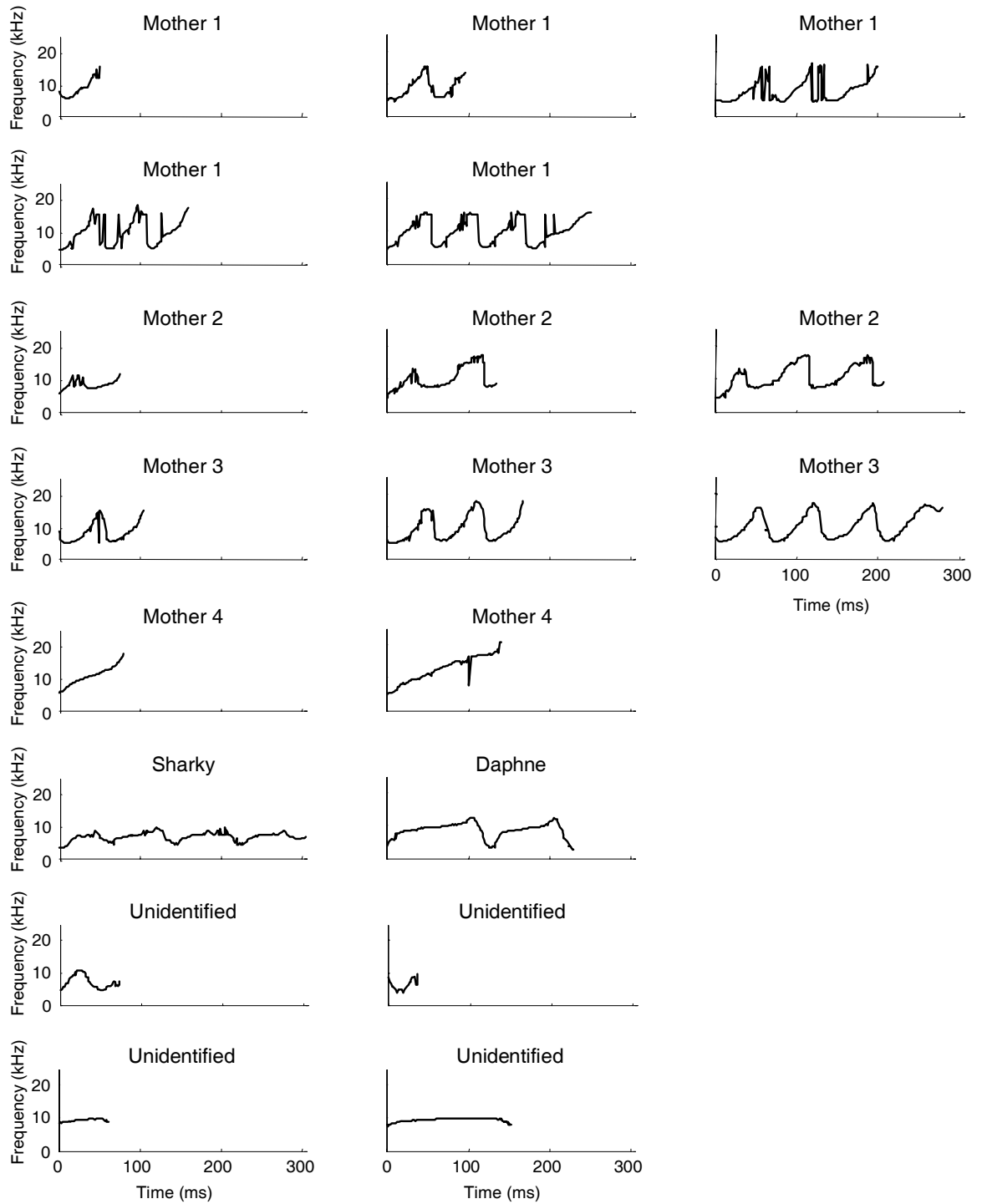
844

845 Mother 3



846

847 B. Dictionary Contours.

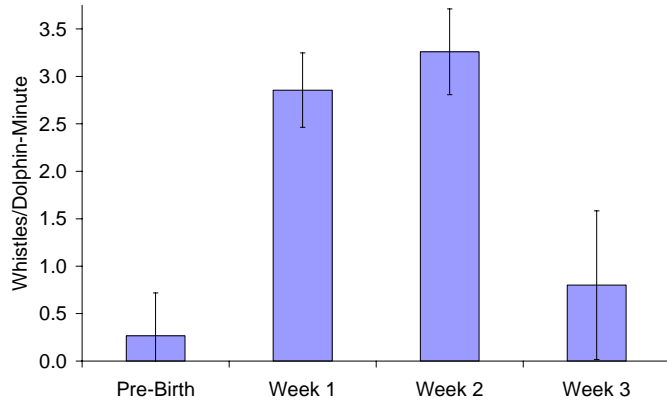


848

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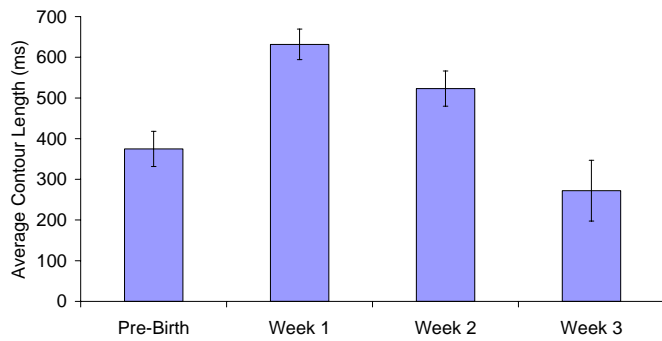
849 Figure 2

850 A. Average whistles/dolphin-minute



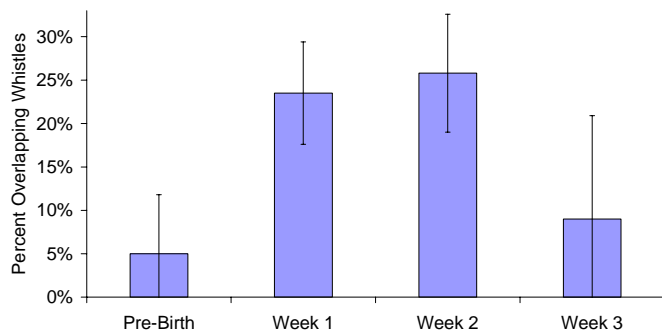
851

852 B. Average contour length.



853

854 C. Percent Overlaps.



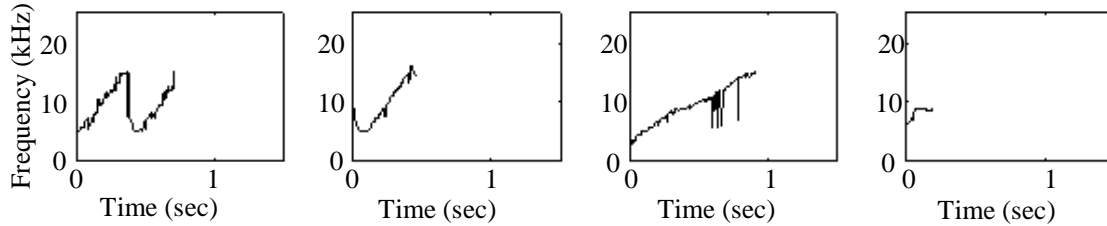
855

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856 Figure 3. Separating Adult and Calf Whistles.

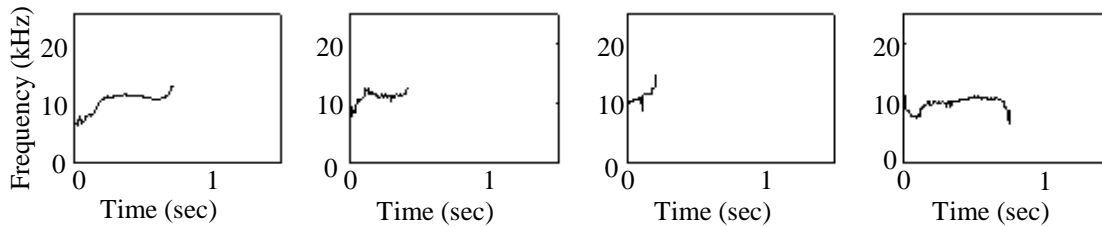
857 A. Sample Contours

858 Adult Only:



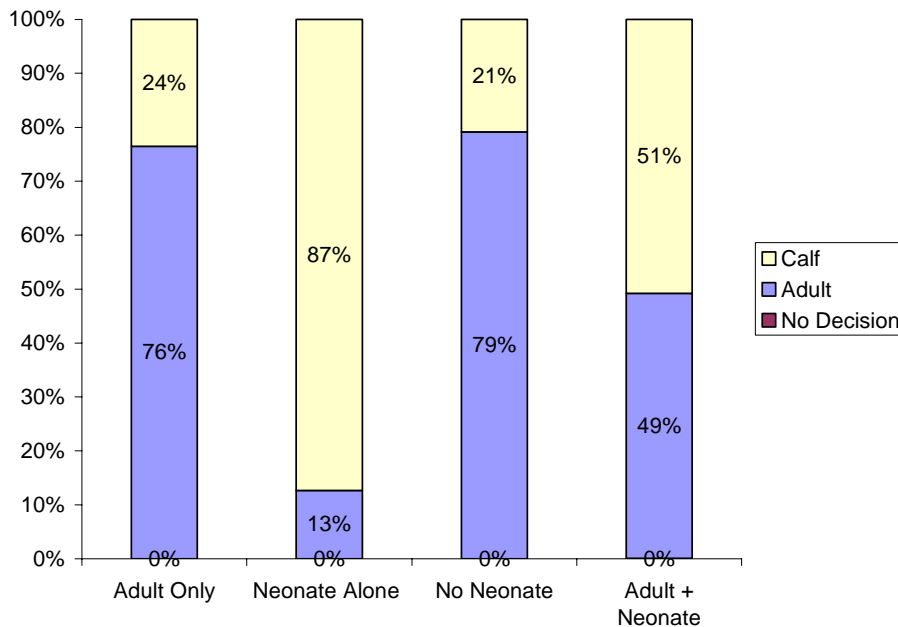
859

860 Neonate Alone:



861

862 B. Discriminant Analysis Separating Adult and Calf Whistles

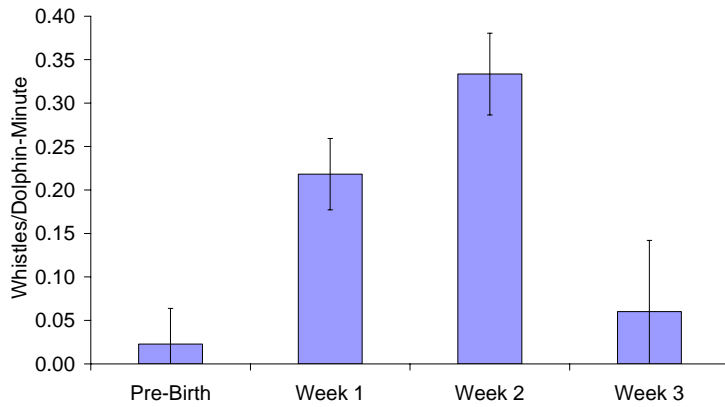


863

Fripp and Tyack: Maternal Whistle Production in Dolphins

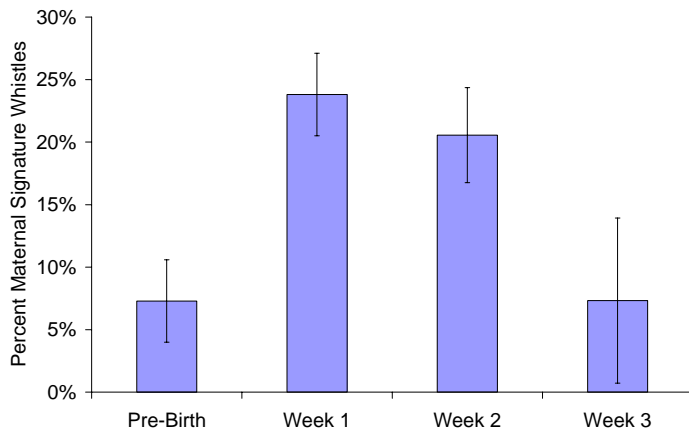
864 Figure 4: Maternal Signature Whistle Use.

865 A. Average maternal signature whistles/dolphin-minute.



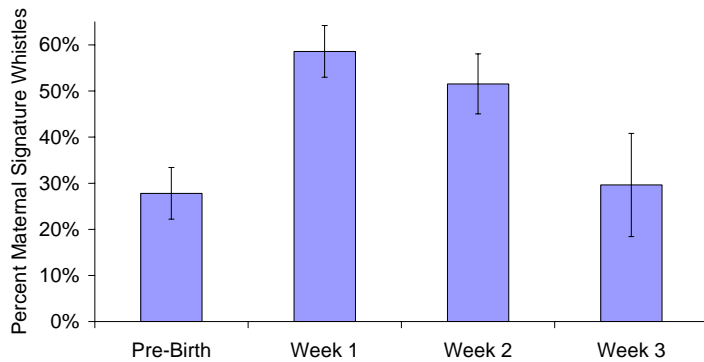
866

867 B. Maternal signature whistles as a percent of all adult whistles.



868

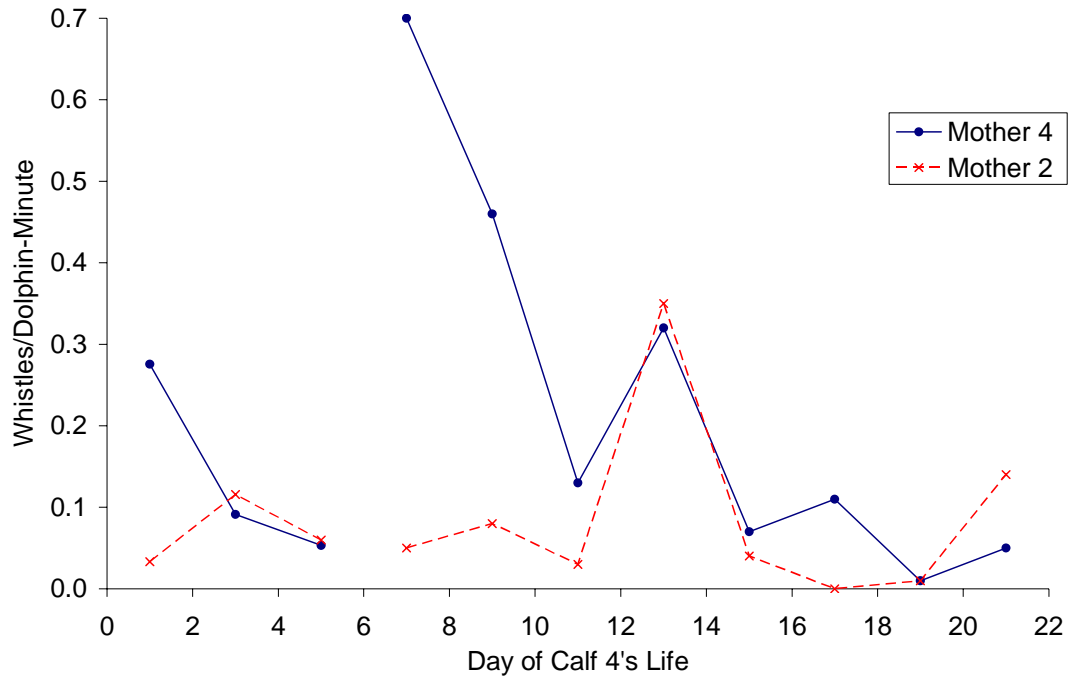
869 C. Maternal signature whistles as a percent of all signature whistles.



870

871 Figure 5: Signature Whistle Use in Calf 4's First Week: Average signature

872 whistles/dolphin-minute.



873

874