1   Whistle communication in mammal-eating killer whales (*Orcinus*

2   *orca*): further evidence for acoustic divergence between ecotypes

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19 Running head: Whistles in mammal-eating killer whales

20

21   **Abstract**

22   Public signalling plays an important role in territorial and sexual displays in animals;

23   however, in certain situations it is advantageous to keep signalling private to prevent

24   eavesdropping by unintended receivers. In the northeastern Pacific, two populations of

25   killer whales (*Orcinus orca*), fish-eating 'resident' killer whales and mammal-eating

26   'transient' killer whales, share the same habitat. Previous studies have shown that

27   residents use whistles as private signals during close-range communication, where they

28   probably serve to coordinate behavioral interactions. Here, we investigated the whistling

29   behavior of mammal-eating killer whales and, based on divergent social structures and

30   social behaviors between residents and transients, we predicted to find differences in both

31   whistle usage and whistle parameters. Our results show that, like resident killer whales,

32   transients produce both variable and stereotyped whistles. However, clear differences in

33   whistle parameters between ecotypes show that the whistle repertoire of mammal-eating

34   killer whales is clearly distinct from and less complex than that of fish-eating killer

35   whales. Furthermore, mammal-eating killer whales only produce whistles during 'milling

36   after kill' and 'surface-active' behaviors, but are almost completely silent during all other

37   activities. Nonetheless whistles of transient killer whales may still serve a role similar to

38   that of resident killer whales. Mammal-eating killer whales seem to be under strong

39   selection to keep their communication private from potential prey (whose hearing ranges

40   overlap with that of killer whales), and they appear to accomplish this mainly by

41   restricting vocal activity rather than by changes in whistle parameters.

42

45   **Introduction**

46

47   Acoustic communication often involves several signallers and receivers in a network

48   (McGregor et al. 1999). This is especially pertinent in long-range communication, where

49   a signal might reach a large number of individuals, but it is also relevant at close ranges,

50   where under certain circumstances signals can reach multiple receivers (Peake 2005).

51   Thus, information is sometimes passed on to unintended receivers, so-called

52   eavesdroppers (McGregor et al. 1999; Dabelsteen 2005; Peake 2005), which can be

53   competitors (McGregor et al. 1999; Dabelsteen 2005; Peake 2005), predators searching

54   for prey (e.g., Zuk and Kolluru 1998; Mougeot and Bretagnolle 2000), parasitoids

55   searching for a host (e.g., Zuk and Kolluru 1998; Wagner and Basolo 2007), or potential

56   prey (e.g., Barrett-Lennard et al. 1996; Fenton 2003).

57   For this reason it can be advantageous for senders to either facilitate or counter

58   eavesdropping by altering signal design depending on circumstances. Signals facilitating

59   eavesdropping are called public signals (Dabelsteen 2005). Especially those used as

60   territorial or sexual displays are often designed to reach as many receivers as possible,

61   and examples are sounds of chorusing insects and anurans, bird songs, or acoustic

62   displays in mammals (e.g., Marler and Tenaza 1977; Ryan et al. 1981; Tyack 1998; Slater

63   2003). In certain social interactions, however, it might be advantageous to use signals that

64   counter eavesdropping. This is true for situations where public signalling would incur

65   risks, for example alerting predators, parasitoids, prey, or competitors. Such acoustic

66   signals have been defined as private and they are usually rather quiet, comparatively high

67   in frequency, and highly modulated in order to be more prone to attenuation and

68   degradation over distance (reviewed in Dabelsteen 2005). Furthermore, these kinds of

69   signals are characterized by a high degree of directionality aimed only at the intended

70   receiver (Dabelsteen 2005).

71

72   Acoustic communication in killer whales

73

74   In the inshore waters of the northeastern Pacific, two distinct ecotypes of killer whales,

75   *Orcinus orca*, coexist in sympatry (Ford et al. 1998; Saulitis et al. 2000). Divergence

76   between these ecotypes seems to be primarily driven by differences in feeding ecology,

77   with 'resident' killer whales feeding exclusively on fish and 'transient' killer whales

78   foraging for mammals and the occasional seabird (Ford et al. 1998; Saulitis et al. 2000).

79   The precise taxonomic status of different killer whale ecotypes is under debate with some

80   researchers postulating separate species status (Morin et al. 2010). Like most other

81   delphinids, killer whales produce three different types of acoustic signals: echolocation

82   clicks, pulsed calls and whistles (Popper 1980; Ford 1989; Janik 2009). While

83   echolocation clicks are used primarily for navigation and prey detection, both pulsed calls

84   and whistles serve as social signals. Most social sounds in killer whales are pulsed calls,

85   which are thought to help maintain group cohesion, coordinate behaviors, and mediate

86   group recognition (Ford 1989, 1991; Miller 2002; Thomsen et al. 2002). Based on

87   spectrographic contour and signal repetitiveness, they can be classified as discrete,

88   aberrant, or variable (Ford 1989; Rehn et al. 2007). Each resident killer whale kin-group

89   (matriline) has a matriline-specific dialect, a unique set of discrete pulsed call types(Ford

90   1989, 1991) with closely related matrilines having similar dialects (Ford 1991; Barrett-

91   Lennard 2000; Deecke et al. 2010). Furthermore, in resident killer whales, discrete pulsed

92   calls seem to function as public signals, as they are high intensity signals that are audible

93   over several kilometers underwater and are predominantly used for long-range

94   communication (Ford 1989, 1991; Miller 2002, 2006; Thomsen et al. 2002). Transient

95   killer whales have a more flexible social structure with some juvenile dispersal from

96   matrilines (Baird and Whitehead 2000; Baird and Dill 1996; Ford et al. 1998; Ford and

97   Ellis 1999) and all members of a population appear to share at least some call types

98   (Deecke 2003). Transient killer whales also run the risk of alerting potential prey to their

99   presence, because all of their prey have excellent underwater hearing ability (reviews in

100   Au et al. 2000; Berta et al. 2006) and respond to transient pulsed calls with anti-predator

101   behavior (Deecke et al. 2002). Accordingly, mammal-hunting killer whales show greatly

102   reduced rates of echolocation (Guinet 1992; Barrett-Lennard et al. 1996), and usually

103   restrict calling to the time after a successful kill or periods of social interaction (Guinet

104   1992; Deecke et al. 2005; Saulitis et al. 2005).

105

106   Whistle communication in killer whales

107

108   Killer whale whistles are highly modulated signals that show some degree of

109   directionality, and have lower sound pressure levels and higher fundamental frequencies

110   compared to pulsed calls (Ford 1989; Thomsen et al. 2001; Miller 2002; 2006; Riesch et

111   al. 2006, 2008). Fundamental frequencies of resident whistles range from around 2 to 17

112   kHz (Ford 1989; Thomsen et al. 2001). Samarra et al. (2010) recently described whistles

113   with frequencies of 17 - 75kHz from some North Atlantic populations, but found that

114   such ultrasonic whistles did not occur in recordings of North Pacific residents or

115   transients. Although the vast majority of resident whistles seem to be variable in nature,

116   several stereotyped whistle types have been described that are often emitted in complex

117   sequences (Riesch et al. 2006, 2008). Compared to pulsed calls, killer whale whistles

118   show all the characteristics of private signals designed to limit the number of

119   eavesdroppers (Holland et al. 1998; Dabelsteen 2005; Riesch et al. 2008). However, the

120   whistling behavior of transients has not been investigated so far.

121   In the present study we conducted an in-depth analysis of whistle structure of

122   mammal-eating killer whales and analyzed the behavior context in which transient killer

123   whales engage in whistle communication. We then compared both the behavior context

124   and the whistle structure to findings in fish-eating resident killer whales. Since fish-eating

125   and mammal-eating killer whales clearly differ in their social structure and social

126   behavior, we predicted to find differences in whistle usage between the two ecotypes.

127   Because of greater costs from eavesdropping prey, we expected to find (1) that whistle

128   characteristics of mammal-eating killer whales should show even stronger shifts toward

129   those of private signals than observed in fish-eating killer whales, (2) that like pulsed

130   calls, overall whistle rates of transients should be lower than those of residents, and (3)

131   that transient killer whales should use whistles preferentially to pulsed calls in contexts

132   associated with active search for prey.

133

134   **Material and methods**

135

136   Analysis of whistle structure

137

138   We screened approximately 60 hrs of recordings of West Coast Transient killer whales

139   for whistles using real-time spectrographic analysis (Raven version 1.2.1, Cornell Lab of

140   Ornithology, 2005). Whistles were then classified into variable and stereotyped.

141   Stereotyped whistles had a discrete spectrographic contour and were found repeatedly in

142   12 or more recordings (see also supplementary Table S1). Variable whistles, on the other

143   hand, did not have stereotyped contours and were thus only found once and in a single

144   recording. We named stereotyped whistles alphanumerically as TW1 (transient whistle

145   type 1), TW2, and so on (see also Riesch et al. 2006, 2008). Original whistle

146   categorization was conducted by only one of the authors (R.R.), but was subsequently

147   confirmed by a test for interobserver reliability (see below).

148   For the analysis of whistle structure we measured bioacoustic parameters of all

149   whistles that had adequate signal-to-noise ratios. Using the 'selection and measurements'

150   functions in Raven, version 1.2.1, we measured start frequency, end frequency, minimum

151   frequency, maximum frequency, frequency bandwidth, dominant frequency, and whistle

152   duration. Furthermore, following the definition of Steiner (1981), we counted the number

153   of frequency modulations (i.e., changes of direction in the fundamental frequency from

154   rising to falling and vice versa).

155   Recordings came from the entire known range of West Coast Transients between

156   Monterey Bay, California and Glacier Bay, Alaska. Approximately 41 hrs of these were

157   made during dedicated focal follows conducted in 1999-2008 by one of the authors (V.

158   Deecke). During focal follows, the animals were followed in small (6-7m) boats and

159   recordings were made using dippable (Offshore Acoustics) hydrophones or towable

160   hydrophone arrays (Benthos AQ-4 elements with Texas Instruments INA106 or Magrec

161   HP-02 pre-amplifiers) onto DAT (Sony TCD-D8 and Sony PCM-M1) or solid-state

162   recorders (Alesis ADAT HD-24 or Marantz PMD671). All systems used for this analysis

163   had a flat (± 3dB) frequency response from 0.1 to 20kHz. To increase sample size,

164   additional 18 hrs of transient recordings (obtained 1970-2002) were provided by fellow

165   researchers (see acknowledgements for a complete list of names). These were made using

166   a variety of recording systems, all of which had a flat frequency response from 0.1 to 12

167   kHz, although for some systems the range of the flat response extended up to 20 kHz.

168

169   Test of Interobserver Reliability

170

171   We used a subset of 45 randomly chosen whistles to confirm our initial classification of

172   whistle categories, following a well-established protocol (for detail see Janik 1999;

173   Riesch et al. 2006; Rehn et al. 2007). In short, we presented spectrograms (fast Fourier

174   transformation size: 4096 samples, frame length: 512 samples, overlap between frames:

175   75%, normalization: Hamming) of mammal-eating killer whale whistles to three

176   observers. All whistles were printed on separate 8 x 10 cm sheets, and spectrograms were

177   presented in a random order. All observers were naïve to spectrographic analysis and

178   were asked to divide the whistles independently by their spectrographic contour and

179   length into as many categories as appropriate to them. We then used Kappa statistic to

180   test for interobserver reliability (Siegel and Castellan 1988).

181

182   Behavior context of transient killer whale whistles

183

184   Since information on distance and behavior of recorded animals was not always available

185   for recordings contributed by other researchers, this analysis was restricted to recordings

186   made during dedicated focal follows. These were made between 1999 and 2008 in

187   Southeast Alaska and British Columbia by V. Deecke. When killer whales were

188   encountered, the identity and size of the group were confirmed by taking identification

189   photographs of all individuals for comparison with existing catalogues (Ford and Ellis

190   1999; Ellis et al. 2008). While following a group, it's behavior was noted on each

191   approach and distance to the nearest animal was estimated on each surfacing or measured

192   using laser rangefinders (Bushnell Yardage Pro 1000 or Leica Geovid 7x42 BDA)

193   whenever possible. Behavior was classified as 'travel', 'slow travel', 'milling', and

194   'surface-active' according to the group's swim speed, synchronicity of surfacing, and

195   directionality and occurrence of surface-active behaviors (slapping the surface with tail or

196   pectoral fin, breaching, etc.). Milling behavior following a confirmed predation event was

197   listed as a separate behavior category 'milling after kill'. See Deecke et al. (2005) for

198   additional detail on distance estimation and the classification of behaviors.

199   While pulsed calls of resident killer whales carry far underwater (detectable over

200   several kilometers: Miller 2006), whistles and transient pulsed calls are often relatively

201   faint (Thomsen et al. 2001; Deecke et al. 2005; Miller 2006). Hence, to minimize the

202   number of missed sounds, we restricted this analysis to sections of recordings where at

203   least one individual was within 500 m of the hydrophone. These sections were then

204   further separated according to behavioral category.

205   To compare levels of whistle activity between different behavior contexts, and to

206   be able to compare our findings to whistle activity in resident killer whales, we followed

207   the protocol of Thomsen et al. (2002). In a first step, we divided all selected sections into

208   discrete subsamples that were characterized by the same behavior context. We then

209   divided all samples of the same encounter from the same behavioral category into 3-min

210   sample intervals. Finally, from each pool of 3-min samples that we thus derived for each

211   encounter and each behavioral category, we now selected every other 3-min sample

212   interval for further analysis. If total recording time for a behavioural category from one

213   encounter was shorter than 6 min total, we analyzed only the central 3-min, while

214   sections shorter than 3-min were discarded. This resulted in 244 samples from 29

215   encounters. For each sample we counted the number of pulsed calls, total whistles, and

216   whistle sequences (a sequence consisted of at least two whistles that occurred within 5 s

217   of each other; sensu Riesch et al. 2008), and then calculated the number of whistles and

218   whistle sequences per animal per minute. To avoid pseudoreplication, we pooled all

219   samples from the same encounter and same behavior context, which means that all data

220   points within a behavioral category are independent, but some data points in different

221   behavioral categories stem from the same encounter. Since whistle behavior was not

222   normally distributed, we tested for differences in whistle activity with a Kruskal-Wallis

223   *H*-test, and then used Dunn's multiple comparisons to identify homogeneous subsets.

224

225   Comparison of variable vs. stereotyped and resident vs. transient killer whale whistles

226

227   Prior to all multivariate analyses, whistle parameters (start frequency, end frequency,

228   minimum frequency, maximum frequency, frequency range, dominant frequency, whistle

229   duration, and frequency modulations) were z-transformed to normalize the variables with

230   regards to differences in the unit of measure and in variance (Gotelli and Ellison 2004).

231   We tested for differences in bioacoustic parameters between variable and stereotyped

232   whistles of mammal-eating killer whales by means of a multivariate GLM (MANOVA)

233   with z-transformed whistle parameters as dependent variables, and whistle type

234   ('variable' vs. 'stereotyped') as fixed factor. In a similar MANOVA model, we

235   subsequently tested for differences between stereotyped transient whistle categories with

236   z-transformed whistle parameters as dependent variables, and stereotyped whistle

237   categories ('TW1', 'TW2' or 'TW3') as fixed factor.

238   To provide an intuitive metric for differences between stereotyped whistles of

239   transient killer whales, we conducted discriminant function analysis (DFA) on z-

240   transformed whistle parameters. We used a jack-knife ('leave–one–out') sampling

241   scheme as a cross–validation technique (i.e., each case is classified by the functions

242   derived from all cases other than that case). *A priori* probabilities were calculated based

243   on group–sizes, and these were then used to calculate the proportional-by-chance

244   accuracy by summing the squares of all prior probabilities. An overall classification

245   success for the model was provided, and the grouping variable was stereotyped whistle

246   category ('TW1', 'TW2', or 'TW3').

247   We extracted and reanalyzed bioacoustic parameters of northern and southern

248   resident killer whales from a previous study (Riesch et al. 2006), and tested for

249   differences between stereotyped whistles of different killer whale populations by means

250   of a full-factorial multivariate GLM (MANOVA). The dependent variables were again z-

251   transformed whistle parameters, and population ('transient', 'northern resident' or

252   'southern resident') was the fixed factor.

253   Finally, we tested for differences between stereotyped whistles from different

254   killer whale ecotypes by conducting another jack-knife DFA. *A priori* probabilities were

255   again calculated based on group–sizes, the grouping variable was population ('transient',

256   'northern resident', or 'southern resident') and the dependent variables were the same as

257   for the previous DFA.

258   All statistical analyses were conducted using PASW Statistics 18.0.2 for Mac

259   (SPSS Inc. 2010), with the exception of the Kruskal-Wallis *H*-test and Dunn's multiple

260   comparisons, which were calculated using InStat 3.0b for Mac (GraphPad Software, Inc.

261   2003).

262

263   **Results**

264

265   Transient killer whale whistles

266

267   We measured bioacoustic parameters of 1,218 whistles. Most of these (897) appeared to

268   be variable in structure with no apparent similarities in spectrographic contour, while 321

269   could be grouped into one of three discrete whistle categories: TW1, TW2, and TW3

270   (Fig. 1). These whistles were comprised of 'chirps' with a U- to W-shaped frequency

271   contour and were often multilooped (i.e., repetitive sequences of the same whistle type;

272   Fig. 1). However, all stereotyped whistles were also found as isolated whistles. Overall,

273   42% (507 whistles) of all analyzed transient whistles were produced as isolated signals,

274   while 58 % (711 whistles) were produced as part of whistle sequences. These sequences

275   consisted of 3.48±2.13 (mean±SD) individual whistles, the interval between consecutive

276   whistles within the sequence was 0.42±0.77 s, and on average 6.00±3.55 animals

277   (encounters with reliable animal count: $N = 21$) were present during recordings that

278   contained whistle sequences. Average intervals between isolated whistles lasted

279   102.33±153.16 s and on average 4.90±2.28 animals were present during recordings

280   containing isolated whistles (encounters with reliable animal count: $N = 30$). Variable and

281   stereotyped whistles differed significantly in their whistle parameters (MANOVA: $F_{8,1209}$

282    $= 27.393$, $P < 0.001$): In general, variable whistles tended to be longer in duration than

283   stereotyped whistles, had slightly higher maximum frequencies, and exhibited more

284   frequency modulations (Table 1). We could not find any indication for differences in

285   whistle repertoires between different transient groups (online supplementary Table S1).

286   Instead, all three stereotyped whistles appear to be part of the same, shared repertoire.

287   The MANOVA confirmed that stereotyped whistle categories differed

288   significantly in their whistle parameters ($F_{16,622} = 19.995$, $P < 0.001$), and post-hoc

289   analysis revealed that this was due to significant differences in acoustic parameters

290   between at least two whistle types (Fisher's Least Significant Differences: all

291   comparisons $P \leq 0.021$; except for TW1 vs. TW2 (end frequency, maximum frequency,

292   and frequency modulations), TW1 vs. TW3 (start frequency, minimum frequency, and

293   dominant frequency), and TW2 vs. TW3 (whistle duration), all $P > 0.120$).

294   The DFA classified 70.4 % of all stereotyped whistles into the correct whistle

295   category (compared to the proportional-by-chance probability of 36.9 %; Fig. 2A), the

296   variable with the most discriminatory power was start frequency (*Wilks' lambda* = 0.931,

297     $F_{2,318}$ = 11.829, P < 0.001; see online supplementary Table S2), and individual

298   classification success was 94.2 % for TW1, 67.1 % for TW2, and 35.1 % for TW3 (Fig.

299   2A).

300   In two different recordings, we found one whistle each that closely resembled

301   stereotyped whistles of resident killer whales in spectrographic contour, and bioacoustic

302   parameters. One resembled whistle W6 of the northern resident killer whales, the other

303   SW1 of the southern resident killer whales (Riesch et al. 2006; see online supplementary

304   Fig. S1). For both recordings, no resident killer whales were observed during the

305   recorded encounter with transients (V. Deecke, pers. observation, and J. K. B. Ford, pers.

306   communication).

307

308   Test for interobserver reliability

309

310   The visual inspection method showed that observers overall agreed on the classification

311   of stereotyped whistles versus variable whistles. If only stereotyped whistle types were

312   considered independently and all variable whistles were considered as a single residual

313   class, the degree of interobserver reliability was very high (Kappa statistic: κ =0.88,

314   Z=8.47, P<0.0001; Table 2). However, two observers placed two stereotyped whistles

315   from category TW3 into a separate whistle category and one observer placed two variable

316 whistles into their own stereotyped whistle category (Table 2; online supplementary Fig.

317 S2).

318

319 Behavior context of transient killer whale whistles

320

321 Most whistling occurred during 'milling after kill' (median whistle rate: 0.14 whistles per

322 animal per min; interquartile range (IQR): 0.05-0.48) and 'surface-active' (median: 0.00

323 whistles per animal per min; IQR: 0.00-1.01), while transients were usually silent during

324 'milling' (median: 0.00 whistles per animal per min; IQR: 0.00-0.05), 'slow travel'

325 (median: 0.00 whistles per animal per min; IQR: 0.00-0.00), and 'travel' (median: 0.00

326 whistles per animal per min; IQR: 0.00-0.01). Accordingly, we found significant

327 differences between whistling rates across behavioral categories (Kruskal-Wallis H-test:

328 $H_4 = 19.622$, $P = 0.0006$), and 'milling after kill' had significantly higher whistling rates

329 than 'slow travel' (Dunn's test: $Q_{11,10} = 3.486$, $P < 0.001$) and 'travel' ($Q_{11,17} = 3.277$, $P <$

330 0.01). All other comparisons were not significant (Fig. 3).

331

332 Comparison of resident and transient killer whale whistles

333

334 In the GLM, 'population' had a significant influence on stereotyped whistle parameters

335 ($F_{16,1502} = 180.096$, $P < 0.001$), and post-hoc analysis revealed that this was due to

336 significant differences in most acoustic parameters between all three populations

337 (Fisher's Least Significant Differences: all comparisons $P \leq 0.001$ except for end

338 frequency, northern residents vs. transients, $P = 0.253$; minimum frequency, northern

339   residents vs. southern residents, $P = 0.062$; and frequency modulations, northern vs.

340   southern residents, $P = 0.072$).

341   The DFA classified 91.7 % of all stereotyped whistles into the correct group

342   (compared to the proportional-by-chance probability of 45.1 %; Fig. 2B) and the

343   variables with the most discriminatory power were maximum frequency (*Wilks' lambda*

344   $= 0.468$, $F = 430.555$, $P < 0.001$) for discriminant function 1, and whistle duration

345   (*Wilks' lambda* $= 0.363$, $F = 665.804$, $P < 0.001$; see online supplementary Table S3) for

346   discriminant function 2. Classification success was highest for transient whistles (98.8

347   %), second best for northern resident whistles (88.9 %) and lowest for southern resident

348   whistles (66.7 %). Furthermore, differences between ecotypes and within ecotypes

349   clearly follow a different trajectory: transient whistles differed from those of residents

350   mainly in whistle duration, end frequency and maximum frequency, while northern

351   residents differed from southern residents mainly in whistle duration and bandwidth (Fig.

352   2B).

353

354   **Discussion**

355

356   We investigated whistle communication in mammal-eating killer whales from the

357   northeastern Pacific and found that similar to fish-eating resident killer whales, transients

358   also use a combination of variable and stereotyped whistles, and have a tendency to emit

359   whistles as whistle sequences (Riesch et al. 2006, 2008). Using three different statistical

360   methods (MANOVA, DFA, and the test for interobserver reliability) we found evidence

361   for pronounced differences between variable and three distinct stereotyped whistle

362   categories. However, all West Coast transients seem to share the same whistle repertoire,

363   and the behavior context, as well as the bioacoustic parameters of transient whistles, are

364   clearly distinct from those in resident killer whales.

365   Whistles of the type TW3 clearly exhibit the most intra-category variability (Fig.

366   1C), which led to low classification success in the DFA and to two observers dividing

367   TW3s into two distinct subcategories (online supplementary Figure S2). Based on those

368   results, one could make the argument that TW3 potentially should have been split into

369   two different subcategories, or that some whistles that we incorporated into the category

370   TW3 (the right-hand spectrogram in Fig. 1; online supplementary Figure S2) should

371   rather be classified as aberrant TW3 (i.e., are signals that are based clearly on discrete

372   whistles, but were highly modified or distorted in structure; Ford 1989). Nonetheless, it is

373   also important to keep in mind that we did not include any bioacoustic measurements in

374   our statistical analysis that incorporate whistle contour. Therefore, we decided to stay

375   with our original classification that lumps all of these whistles into the same category

376   (TW3), but suggest that future work that incorporates more in-depth contour analysis

377   (e.g., neural network analyses; Deecke and Janik 2006) could attempt to better resolve

378   this issue. However, whether or not TW3 were actually split into two different categories,

379   would not change any of our general interpretations that we will discuss in the following

380   paragraphs.

381

382   Transient whistles versus resident whistles

383

384   Stereotyped whistles of mammal-eating killer whales are clearly different from those of

385   resident fish-eating killer whales: whistles of transient killer whales generally have lower

386   dominant frequencies, narrower frequency ranges, are shorter in duration, and have fewer

387   frequency modulations (Thomsen et al. 2001; Riesch et al. 2006, 2008). Contrary to our

388   first prediction, this means that transient whistles are actually moving away from the

389   characteristics that are usually ascribed to private signals (higher frequencies, wider

390   frequency range, and greater degree of frequency modulations; Holland et al. 1998;

391   Dabelsteen 2005). We did find support for our second prediction, however, as whistle

392   rates across behavior categories were lower in transients compared to whistle rates

393   published for resident killer whales (Thomsen et al. 2002). While stereotyped whistles of

394   resident killer whales (in particular northern resident whistles) show relatively high

395   variability in several bioacoustic parameters as well as in general spectrographic contour

396   between whistle types, transient whistle types all seem to be variations of a common U-

397   to W-shaped contour (see Riesch et al. 2006, 2008). Hence, in addition to having

398   repertoires of pulsed calls that are distinct from residents (Ford 1984; Deecke 2003),

399   transient killer whales also have a distinct, population-specific repertoire of whistles.

400

401   Vocal imitation/mimicry of resident whistles

402

403   We found two whistles that could have been imitations of stereotyped whistles of resident

404   killer whales. Both mimicked whistles were recorded within the range of the resident

405   killer whale population producing the template whistle types (i.e. the W6-like whistle

406   within the northern resident home range and the SW1-like whistle within the southern

407   resident home range), but killer whale whistles are relatively faint signals that have a

408   detection range of approximately 500 m (Thomsen et al. 2001). For this reason, we feel

409   that it is unlikely that these were produced by close-by matrilines of resident killer

410   whales. Given the complexity of killer whale whistles, it is also relatively unlikely that

411   these match resident killer whale whistle types by chance. Combined with the fact that

412   these were the only such examples in over 40 hrs of recordings this suggests that they

413   probably are not part of the normal repertoire of transient killer whales, but most likely

414   represent vocal imitation/mimicry, which has previously been described for killer whales

415   and other delpinids (Ford 1991; Janik 2009; Weiß et al. in press). However, future

416   research will have to investigate this further.

417

418   Possible function of transient whistles

419

420   In other delphinids, stereotyped whistles often serve as individual-specific signature

421   whistles thought to facilitate group cohesion (e.g., Caldwell and Caldwell 1971; Janik

422   and Slater 1998; Tyack 1998; Janik 2009). In the case of male alliances in bottlenose

423   dolphins (*Tursiops truncatus*), signature whistles are thought to additionally encode

424   social affiliation, as signature whistles within an alliance become more alike over time

425   (Watwood et al. 2004). However, Riesch et al. (2006) demonstrated that stereotyped

426   whistles in resident killer whales clearly do not serve as individual signatures. The

427   stereotyped whistles of transients are distinct from those of residents, but there is also no

428   indication that contour shape of whistles encodes individual identity: the transient killer

429   whale community comprises more than 250 individuals (Ellis et al. 2008) yet there are

430   only 3 stereotyped whistle types. Hence our results are further evidence against signature

431   whistle variation of the type described for bottlenose dolphins and other delphinids in

432   killer whales. It is, however, still possible that the observed variability between whistles

433   within the same type (Fig. 1) is a sign of individual variability. In this case, all mammal-

434   eating killer whales would use the same three whistle types but each individual would

435   have its own unique version of it, as has been suggested for resident killer whale pulsed

436   calls (Nousek et al. 2006).

437   If they are not signature whistles, what then is the function of stereotyped

438   whistles? In resident killer whales, whistles are thought to be important close-range

439   signals that facilitate and coordinate social interactions (Thomsen et al. 2001, 2002;

440   Riesch et al. 2006, 2008), and consequently they are the predominant acoustic signal

441   during close-range interactions, while pulsed calls dominate all other behavior states

442   (Thomsen et al. 2002; Riesch et al. 2008). Furthermore, their physical characteristics

443   (Table 1, reanalyzed from Riesch et al. 2006, 2008) suggest that they are signals designed

444   to prevent eavesdropping by unintended receivers, which in the case of residents are most

445   likely competitors/rivals (i.e. other resident killer whales; Riesch et al. 2008). The

446   function of transient whistles, on the other hand, is more difficult to identify, because

447   rather than being the predominant acoustic signal during social interactions, transients

448   generally do not vocalize at all except during 'milling after kill' and 'surface-active'

449   behaviors (Deecke et al. 2005; this study). However, once the animals start to get vocally

450   active both pulsed call and whistle rates increase simultaneously (Deecke et al. 2005; this

451   study). This is strong evidence against our third prediction, that transients should

452   preferentially use their less conspicuous signals (whistles) during behaviors correlated

453   with active search for prey, because they are less likely to be detected than calls. Since

454   transients do not appear to use whistles as a safe means of communication to avoid

455   alerting eavesdropping prey, why do they not attempt to at least restrict conspecific

456   eavesdropping (i.e., rival transient groups)? Compared to the resident killer whale

457   communities, the transient killer whale community is spread out over a much larger

458   geographic area (ranging from southern California to southeastern Alaska; Ford and Ellis

459   1999; Ford et al. 2000) so that chance-encounters with 'rival' transient groups are much

460   less likely. Furthermore, as Deecke et al. (2005) already argued, the noise created by an

461   attack on marine mammals (e.g., sounds generated during prey handling and prey

462   vocalizations) would have already alerted potential competitors to the scene, thus further

463   decreasing the need to make whistle communication private in this particular behavior

464   context.

465   Does this mean that transient whistles serve a different function than resident

466   killer whale whistles? We can currently only speculate, as direct data are lacking.

467   However, several indirect lines of evidence suggest that resident and transient killer

468   whale whistles could share a similar function. First, food-sharing is often observed in

469   mammal-eating killer whales (Jefferson et al. 1991), and Deecke et al. (2005) proposed

470   that transient pulsed calls may be important in delineating social relationships during

471   these and similar events. If whistles served a similar function in transients and residents,

472   we would expect the whistle rate to also increase under these circumstances, which is

473   exactly what we found in the present study. Additionally, prey carcasses often show

474   evidence of intricate manipulation (e.g., porpoise carcasses are often completely stripped

475   of skin and blubber; V. Deecke, pers. observation), which is bound to require a high

476   degree of coordination between individuals. Since whistles in fish-eating killer whales are

477   thought to coordinate behavior or social interactions (Riesch et al. 2006, 2008), whistles

478   in mammal-eating killer whales could also play an important role here. Hence, we

479   hypothesize that whistles in transient killer whales may also serve as signals that facilitate

480   and coordinate close-range interactions during surface-active behavior (similar to

481   socializing in resident killer whales) and prey handling during feeding. Future studies

482   will have to focus more on the specific function of whistles in transient killer whales to

483   unequivocally answer this question.

484   Why do transient killer whales have such a small whistle repertoire (3 stereotyped

485   whistle types with rather similar contours), when that of resident killer whales is so

486   elaborate (up to 11 stereotyped whistles of varying contour; Riesch et al. 2006, 2008)?

487   We propose two mutually not exclusive hypotheses. First, as we argued above, whistles

488   in transient killer whales may actually have the same function as pulsed calls during food

489   sharing (Deecke et al. 2005), so the actual acoustic repertoire for this behavior probably

490   encompasses the combined repertoires of pulsed calls and whistles. This decreases the

491   need for an extensive whistle repertoire. Second, transient social structure is much more

492   fluid than that of residents (Baird and Whitehead 2000; Baird and Dill 1996; Ford et al.

493   1998; Ford and Ellis 1999), and transient individuals may form temporary hunting groups

494   with others they only encounter infrequently. In this scenario a less complex whistle

495   repertoire would be of great advantage in ensuring successful cooperation and temporary

496   bonding between infrequent social companions.

497

498   Costly communication and predator-prey coevolution

499

500   The stereotyped whistles of resident and transient killer whales are clearly distinct, and it

501   therefore seems reasonable to believe that potential prey species would be able to tell

502   them apart as has been shown for stereotyped pulsed calls (Deecke et al. 2002). However,

503   if this is the case, how can we explain that compared to residents, transient whistle

504   parameters are shifted back towards those characteristic for public signals (Holland et al.

505   1998; Dabelsteen 2005)?

506   A shift of communication to frequencies outside of the hearing range of their prey

507   has been proposed for echolocation in bats (e.g., Fullard and Dawson 1997; but see

508   Windmill et al. 2005). However, potential killer whale prey (pinnipeds and other

509   cetaceans) all have hearing ranges overlapping and sometimes even exceeding that of

510   killer whales making a shift of communication frequency not a feasible option for

511   mammal-eating killer whales (see discussion in Deecke et al. 2005). Hence the main

512   strategy of transients to minimize detection by potential prey is to limit vocal

513   communication to certain behavioral contexts, making detection based on whistle

514   recognition by prey impossible during foraging, regardless of a potential receiver's

515   hearing capabilities (Barrett-Lennard et al. 1996; Deecke et al. 2005). This in turn seems

516   to have relaxed the selection on making whistles acoustically private (i.e., higher

517   frequencies and more frequency modulations). Together with the differences in social

518   structure, this could explain the observed differences in acoustic parameters between

519   resident and transient whistles.

520

538

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680

681 **Table 1** Descriptive statistics (Mean±SD) for (**A**) transient killer whales whistles and (**B**) stereotyped whistles of T (transients), NR

682 (northern residents), and SR (southern residents). NR and SR values were reanalyzed from Riesch et al. 2006.

Whistle	N	Start frequency [kHz]	End frequency [kHz]	Minimum frequency [kHz]	Maximum frequency [kHz]	Frequency range [kHz]	Dominant frequency [kHz]	Whistle duration [s]	Frequency modulations
(*a*) within transients									
Variable	897	4.56±1.69	4.85±1.92	3.81±1.41	5.49±1.99	1.69±1.22	4.90±1.98	0.65±0.84	2.8±4.4
TW1	70	3.79±1.34	4.86±1.96	3.24±1.12	4.89±1.95	1.65±1.13	3.68±1.36	0.10±0.05	1.0±0.0
TW2	154	4.58±1.30	4.61±1.33	3.64±1.13	4.86±1.32	1.22±0.53	4.93±2.17	0.13±0.04	1.1±0.5
TW3	97	4.07±0.92	4.13±0.97	3.33±0.72	4.34±0.97	1.01±0.49	4.11±1.38	0.13±0.04	1.7±1.1
(*b*) between communities									
T	321	4.25±1.25	4.52±1.42	3.46±1.03	4.71±1.41	1.25±0.73	4.41±1.87	0.12±0.04	1.3±0.8
NR	395	8.42±2.81	4.63±1.11	4.23±0.84	9.56±2.75	5.31±2.68	8.60±3.23	1.19±0.46	21.2±26.5
SR	45	5.78±1.18	5.35±0.83	4.50±0.54	6.80±1.19	2.30±0.99	5.98±1.63	4.47±2.91	26.8±22.6

683   **Table 2** Categorization of whistles by mammal-eating killer whales according to three

684   naïve human observers. Numbers correspond to the internal identification number of the

685   whistle, while numbers in parentheses indicate how many of the three observers put the

686   corresponding whistle into one type. Identification numbers of stereotyped whistles are in

687   bold.

Whistle type						
Variable		TW1	TW2	TW3	Stereotyped X	Stereotyped Y
2 (3)	25 (3)	**4** (3)	**1** (3)	**13** (3)	**23** (2)	8 (1)
3 (3)	27 (3)	**10** (3)	**9** (3)	**16** (3)	**26** (2)	20 (1)
5 (3)	28 (3)	**30** (3)	**19** (3)	**23** (1)		
6 (3)	29 (3)	**39** (3)	**24** (3)	**26** (1)		
7 (3)	31 (3)	**40** (3)	**35** (3)	**34** (3)		
8 (2)	32 (3)					
11 (3)	33 (3)					
12 (3)	36 (3)					
14 (3)	37 (3)					
15 (3)	38 (3)					
17 (3)	41 (3)					
18 (3)	42 (3)					
20 (2)	43 (3)					
21 (3)	44 (3)					
22 (3)	45 (3)					

688

689   **Fig. 1** Representative spectrograms of multilooped transient whistle types (**A**) TW1, (**B**)

690   TW2, and (**C**) TW3, as well as (**D**) two variable whistles (fast Fourier transformation

691   size: 4096 samples, frame length: 512 samples, overlap between frames: 75%,

692   normalization: Hamming)

693
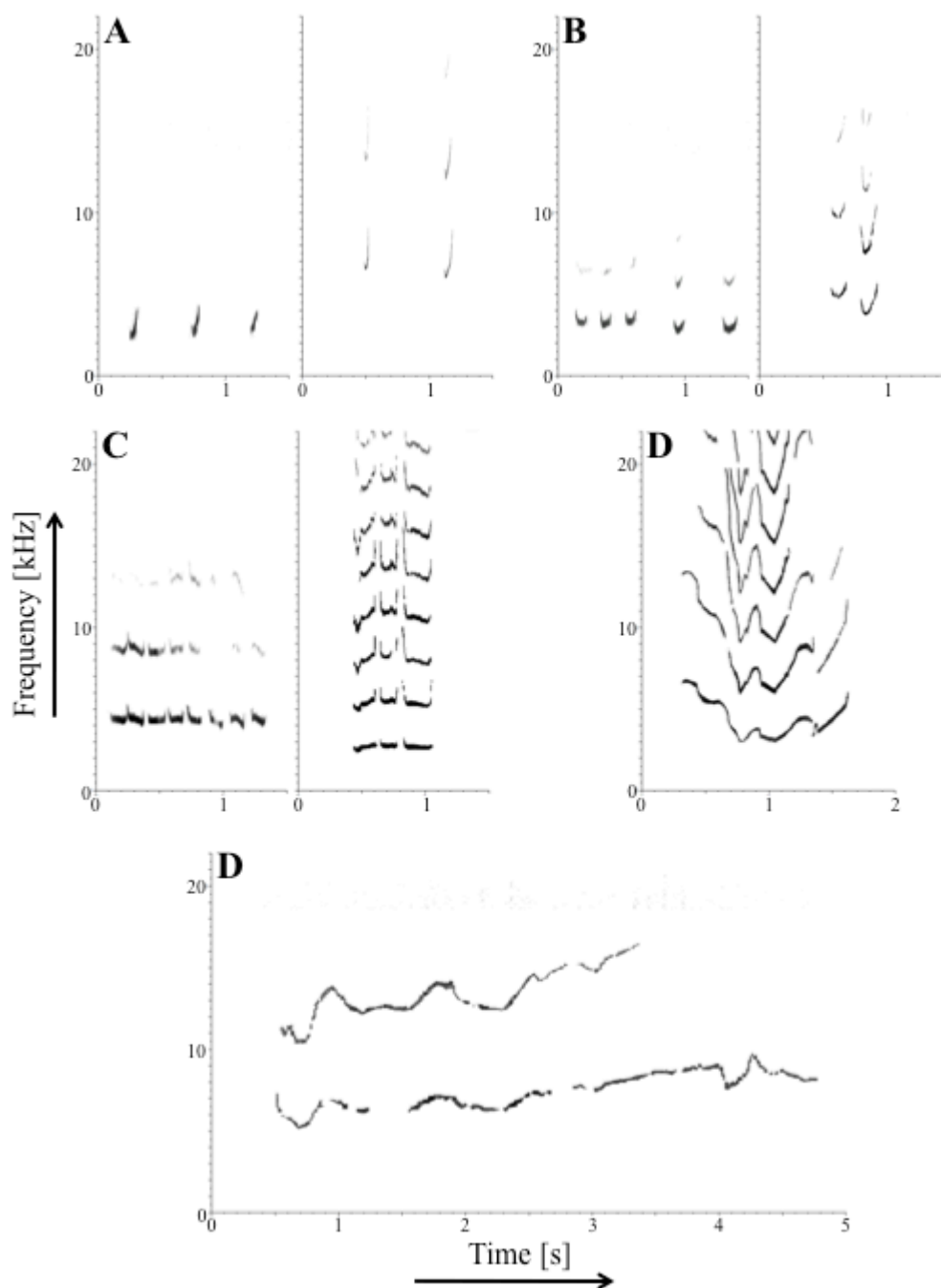
694   **Fig. 2** Discriminant function analyses (Group centroids ± SDs) for separation of

695   stereotyped whistles of (**A**) transient killer whales, and (**B**) three different populations of

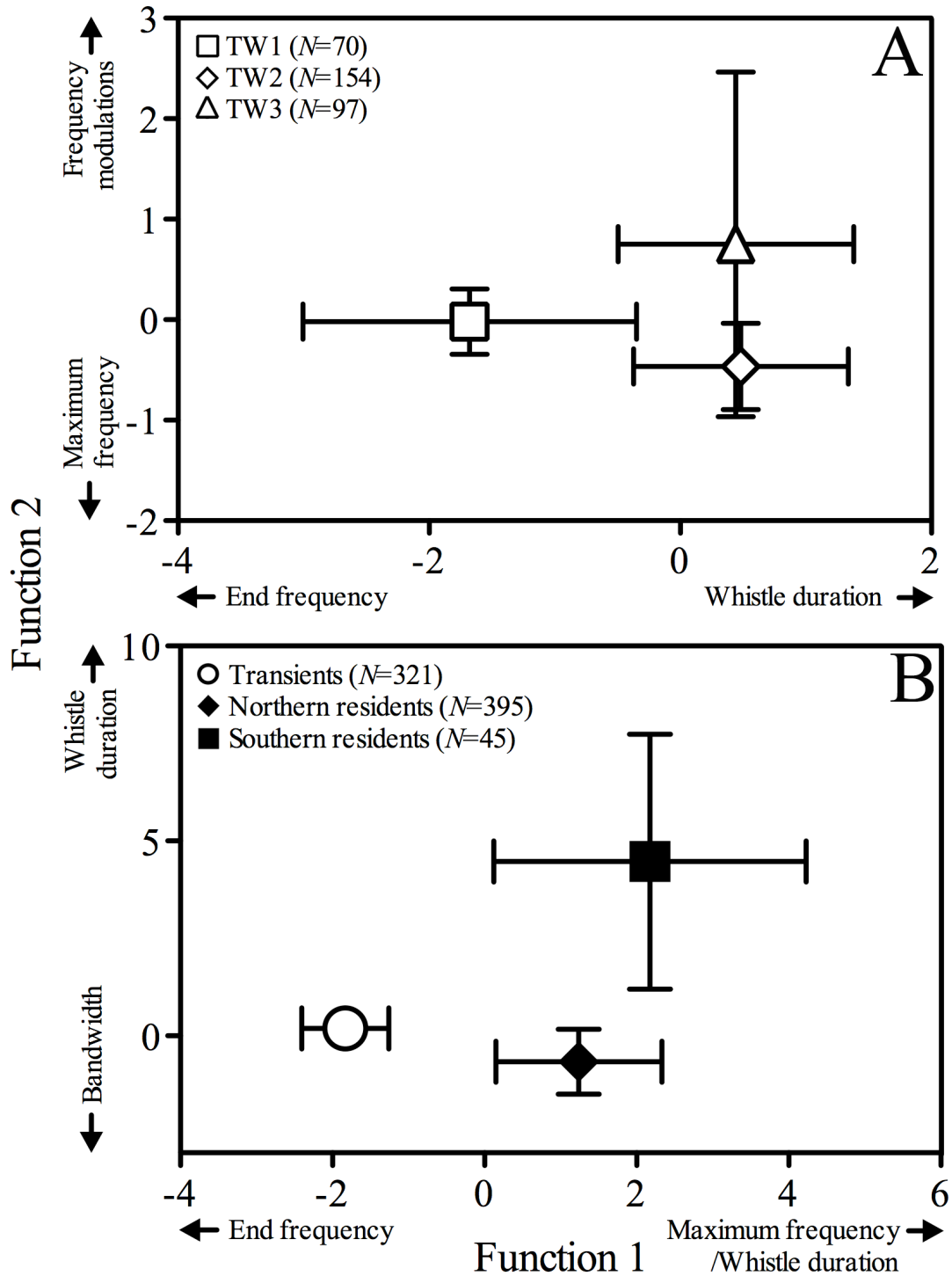696   killer whales from the Pacific Northwest

697

698   **Fig. 3** Rates of whistle production across behavior categories in transient killer whales.

699   Milling after kill: $N = 12$, surface-active: $N = 5$, slow travel: $N = 11$, travel: $N = 18$, and

700   milling: $N = 5$

701

702