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1 Whistle communication in mammal-eating killer whales (*Orcinus*
2 *orca*): further evidence for acoustic divergence between ecotypes

3

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18

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

43 **Keywords** Eavesdropping – Feeding ecology – Predation – Private signals – Public
44 signals – Social networks

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 matriline 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 matriline (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 (± 3 dB) 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 \pm 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: $\kappa = 0.88$,
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 matriline 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 delphinids (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

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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.

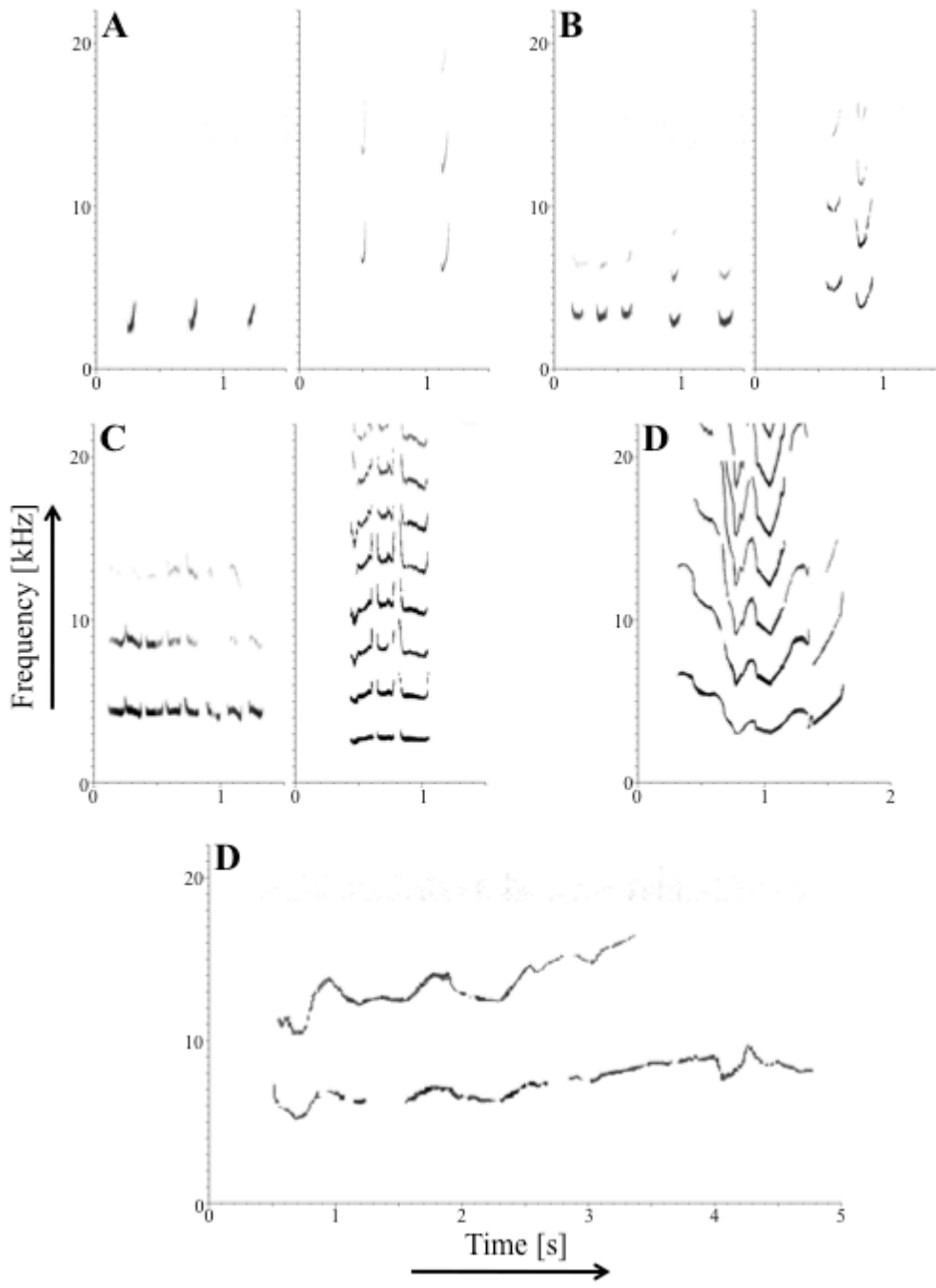
Whistle	<i>N</i>	Start frequency [kHz]	End frequency [kHz]	Minimum frequency [kHz]	Maximum frequency [kHz]	Frequency range [kHz]	Dominant frequency [kHz]	Whistle duration [s]	Frequency modulations
<i>(a)</i> within transients									
Variable	897	4.56±1.69	4.85±1.92	3.81±1.41	5.49±1.99	1.69±1.22	4.90±1.98	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
<i>(b)</i> 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)					

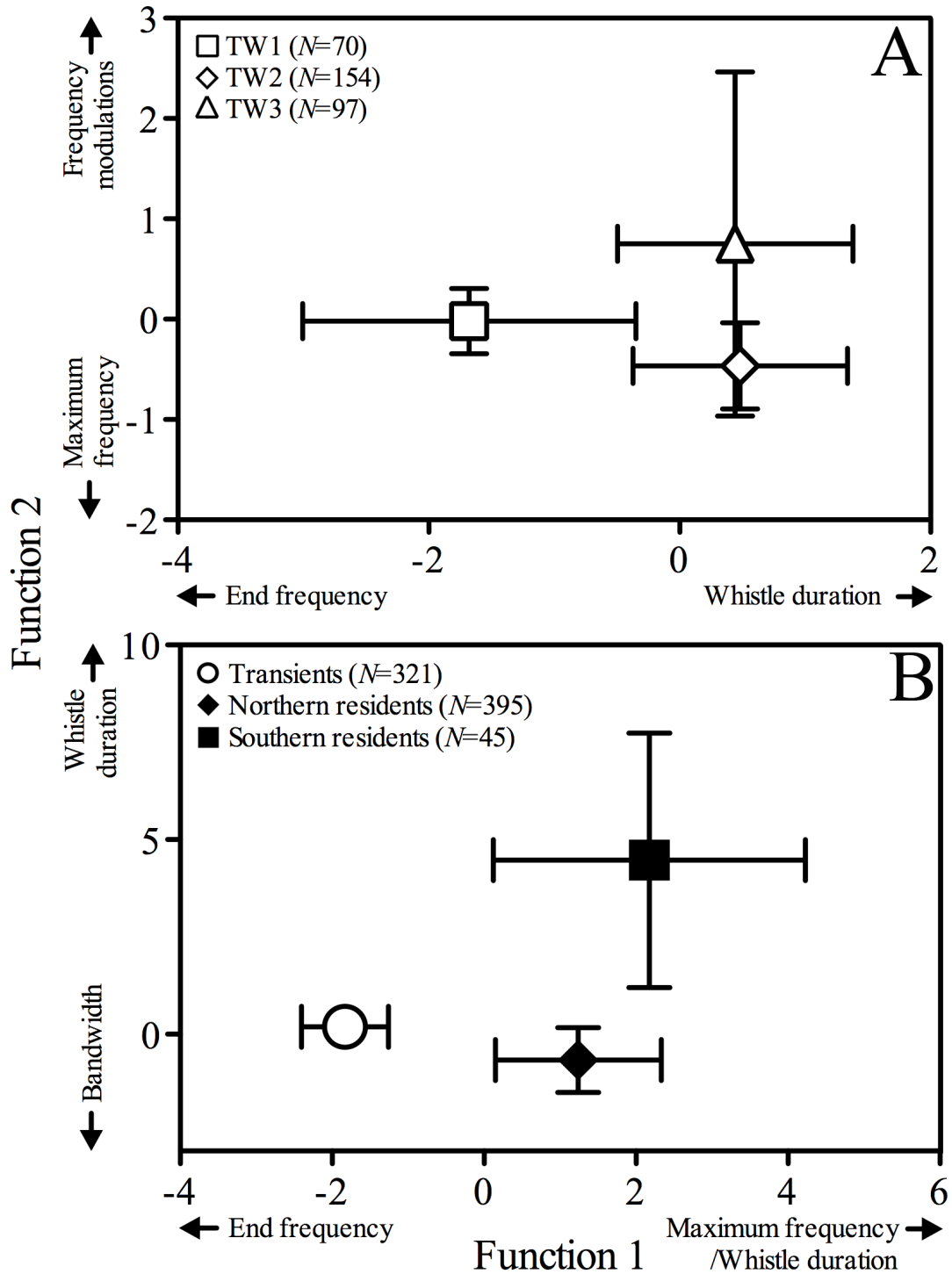
688

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 \pm 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

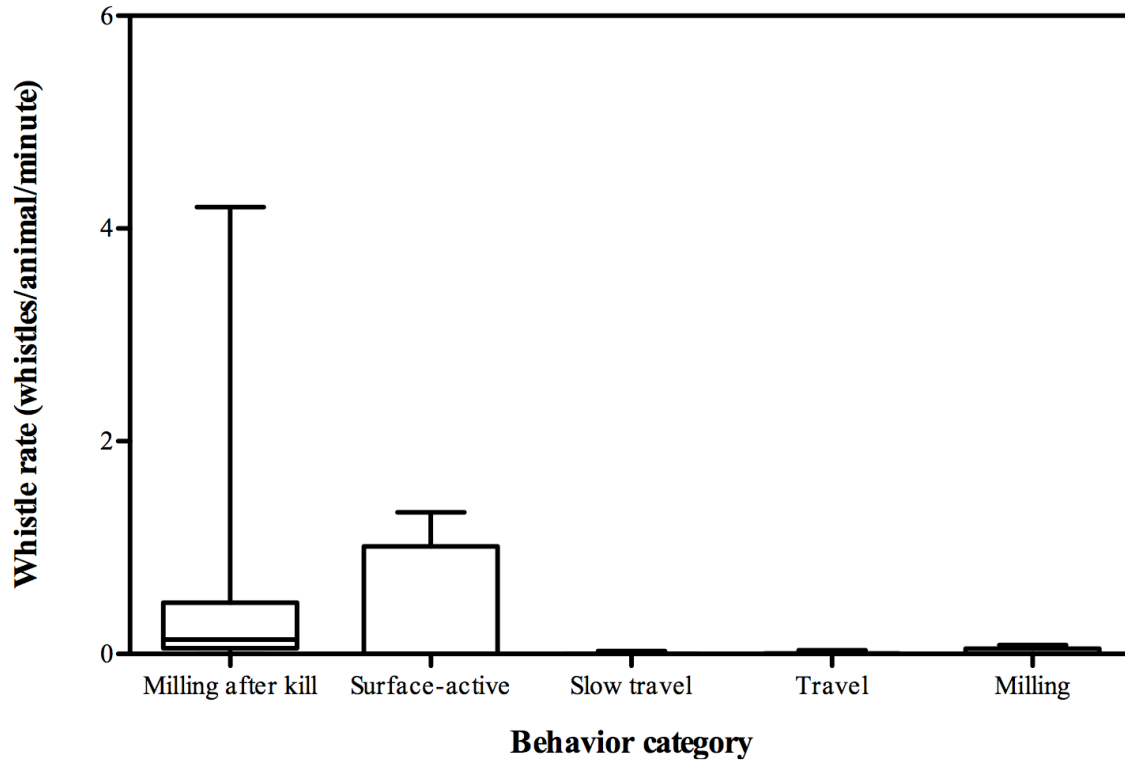


697

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