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7 Changing durations of southern resident killer whale (*Orcinus orca*)
8 discrete calls between two periods spanning 28 yr

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18 Killer whales vocalize in order to navigate, forage, communicate, and engage in
19 social behavior. The sounds made by killer whales are classified into three types of
20 vocalizations: clicks, whistles, and discrete calls. Discrete calls are pulsed calls that
21 have been categorized into stereotyped call types (Ford 1987). Discrete calls are easily
22 differentiated by the human ear and also provide a unique spectrographic structure.

23 Discrete call usage in killer whales of the eastern North Pacific represents one
24 case in which long-term studies of underwater acoustic communication are available.
25 There are several distinct populations of killer whales that use the inland waters of
26 British Columbia and Washington. This study focuses on the fish-eating Southern
27 Resident population that utilizes the waters off the southern end of Vancouver Island.
28 The Southern Residents comprise three pods (J-, K-, and L-Pods) that, as of July
29 2009, totaled 85 animals (Center for Whale Research 2009). The Southern Resident
30 population is currently listed as endangered under the Endangered Species Act in
31 the United States (as of 2005) and the Species at Risk Act in Canada (as of 2003).

32 A standard catalogue of the 25 discrete call types used by Southern Residents has
33 been developed (Ford 1987). Each call type has an alphanumeric designation made
34 up of a letter that denotes the community of whales that produce that call and an
35 arbitrary number that indicates the order in which the call was first identified. "S"
36 is the prefix for the 25 call types and their associated subtypes made by Southern
37 Residents (Ford 1987).

38 In general, vocalizations can vary in multiple parameters, such as call rate, fre-
39 quency, amplitude, or duration, and these parameters can change for many reasons.
40 The factors influencing vocalization parameters vary between species and between
41 vocalizations. For example, the calls of greater horseshoe bats (*Rhinolophus ferrume-*
42 *quinum*) are known to undergo maturational effects (Jones and Ransome 1993),
43 whereas the vocalizations of Weddell seals (*Leptonychotes weddellii*) vary with sea-
44 sonality (Rouget *et al.* 2007). On a more rapid timescale, changing behavioral contexts
45 are known to influence the parameters of vocalizations in species like bottlenose dol-
46 phins (*Tursiops truncatus*) (Janik and Slater 1998). On a more prolonged timescale,
47 factors in the social environment, such as group membership, will lead to changes in

call parameters as was seen for budgerigar flocks (*Melopsittacus undulatus*) (Barlett and Slater 1999) or marmoset (*Callithrix jacchus*) populations (Rukstalis *et al.* 2003). Genetic differences can affect call parameters as seen in populations of great tits (*Parus major*) (Kölliker *et al.* 2000), or call parameters may differ between geographic locations as demonstrated by studies of bowerbirds (*Ptilonorhynchus violaceus*) (Nicholas *et al.* 2007). In species with learned vocalizations such as marine mammals, cultural drift can lead to changes as has been shown for both killer whales (Deecke *et al.* 2000) and humpback whales (*Megaptera novaeangliae*) (Noad *et al.* 2000). In some cases, either learned or more innate vocalizations are also altered to overcome the masking effects of background noise as has been shown for killer whales (Foote *et al.* 2004, Holt *et al.* 2009) and belugas (*Delphinapterus leucas*) (Lesage *et al.* 1999) as well as great tits (Slabbekoorn and Peet 2003).

The above examples clearly show that discrete calls are not static. Specifically for killer whales, it has previously been demonstrated that the structure of individual discrete calls can vary over time (Deecke *et al.* 2000, Foote *et al.* 2004). While duration increases have been demonstrated for a single prominent call type in each of the three Southern Resident pods (Foote *et al.* 2004), this study takes a more comprehensive approach and is the first to look at the alteration of call durations across the repertoires of each pod by assessing the change of mean call duration for 19 different call types (76% of the repertoire) between two data sets spanning a period of 28 yr.

Recordings included in this study were collected from May to August of 2005 and 2006. All recordings of J-, K-, and L-Pods were made from shore *via* ground-mounted hydrophones located on the west side of San Juan Island, Washington, at Lime Kiln Lighthouse (48°31'N, 123°09'W). Recordings were included regardless of behavioral context (foraging, socializing, resting, *etc.*) but were only included if a single pod was present. This study included 31 recordings totaling 15 h 58 min (J-Pod: 12 recordings, K-Pod: 11 recordings, L-Pod: 8 recordings; range 10–71 min).

In 2005, two Cetacean Research Technology C304 hydrophones (sensitivity –169 dB re 1 V/ μ Pa, sampling rate 44.1 kHz) were used and data were recorded using Sound Forge (Sony Creative Software, Madison, WI). In 2006, an altered Navy Sonobuoy hydrophone (uncalibrated, sampling rate 44.1 kHz) was used and recordings were made using the custom Visual Basic program LightHouseVocalObserver (Val Veirs, Colorado College, Colorado Springs, CO). All recordings had bandwidths from 100 to 20,000 Hz and were analyzed using Raven Pro Sound Analysis Software 1.2.1 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY). Durations were measured manually in Raven's spectrogram window (window type: Hann, window size: 512 samples) and included the entire visible spectrograph. Calls were classified based on the conventional alphanumeric call type categories (Ford 1987). Call type identification occurred aurally and, when necessary, was confirmed spectrographically. A total of 3,472 discrete calls were counted, 2,765 (80%) of which were categorized into one of the conventional call categories. The other 20% of calls heard were either too faint to be identified or were aberrant discrete calls, which are defined as nonrepeated pulsed vocalizations (Ford 1987). The duration of

every categorized vocalization was recorded in Raven. The researcher remained blind to exact durations previously measured for each call type until the completion of data collection. Mean call durations were calculated in R 2.4.1 (R Development Core Team 2006).

Data from this study were compared to published data (Ford 1987) that utilized recordings made between 1978 and 1983 on cassette recorders. This comparison is justified in that both sets of recordings were of the Southern Resident population in the same general geographic area during the same season and over a variety of behavioral contexts, whether the pod was foraging, socializing, or traveling. The 1978–1983 recordings had a bandwidth of up to 8–14 kHz and this study's recordings had a bandwidth of up to 20 kHz; however, all major components of the discrete calls began and ended below 8 kHz so this difference in monitored frequency did not affect observed overall call duration; however, it should be noted that other differences in recording equipment have not been assessed.

All possible past (1979–1983) and present (2005–2006) call type durations were compared when both time periods included more than one instance of a call type for a specific pod. Some call types had to be excluded for not being recorded by a pod in both time periods. For instance, three call types recorded for a pod in the 1979–1983 time period were not heard by that pod in the 2005–2006 time period; similarly, several call types that are now known to be in a pod's repertoire (*i.e.*, Ford 1991) did not have duration data reported for that pod in the 1979–1983 study. Using these criteria, 21 call comparisons were made representing 19 call types. The only call type to be compared between the two studies for each of the three pods independently is S10; the other 18 call types were compared between the two studies only for a single pod. Mean durations were compared statistically in R 2.4.1 using two-tailed *t*-tests. Sample sizes in the 1978–1983 data set ranged from 3 to 52 and in the 2005–2006 data set ranged from 2 to 549, but *t*-tests account for variances in sample size and thus statistical rigor was maintained.

The mean durations for the 21 comparable calls are presented in Figure 1. Mean duration ranged from 0.08 s for call S5 (1978–1983) to 2.25 s for call S10 (K-Pod, 2005–2006), however, the important comparisons are within call type between studies. There was a statistically significant change (*t*-test, $P < 0.05$) in mean duration between the 1978–1983 study and the 2005–2006 study for 16 of 21 call types (10 of 21 at $P < 0.0001$). Of the 16 call types that showed a change in duration, 14 showed a statistically significant increase in duration (9 at $P < 0.0001$) and 2 showed a statistically significant decrease in duration (1 at $P < 0.0001$). Significant increases in duration ranged from 15% (S1) to 218% (S5) with a mean increase in duration of 54%, while significant decreases were by 11% (S37i) and 61% (S19).

As mentioned previously, there are many factors, both short and long term, which could lead to a change in the duration of a repertoire of calls. If maturational effects were the explanation, a uniform change of either an equal increase or decrease across all call types would be expected, and that is not observed here. Additionally, it has been demonstrated that separate groups with similar age/sex structure can produce distinct variants of the same vocalization, so changes in discrete calls are not due to maturational effects alone (Ford 1991).

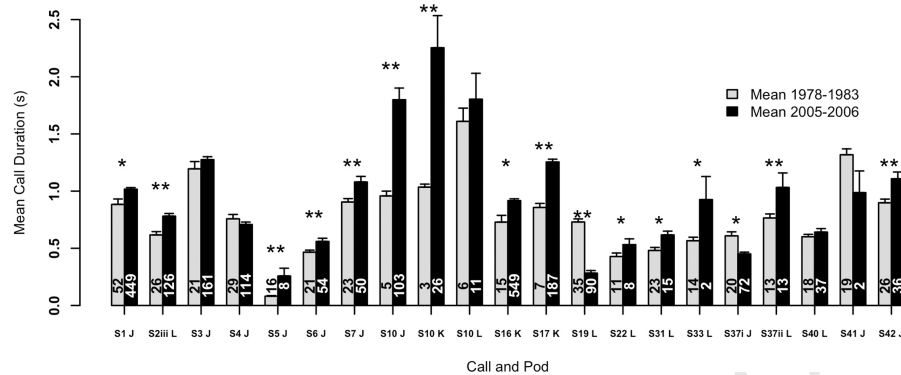


Figure 1. Comparison of mean call durations from 1978–1983 to 2005–2006. Mean durations for call types in the 1978–1983 time period (gray, from Ford 1987) compared to those from the 2005–2006 time period (black). * $P < 0.05$, ** $P < 0.0001$, by t -tests. Bars indicate standard error. Numbers within bars indicate sample size.

Seasonality is also ruled out as an explanation for the differences in duration between the calls in the two studies, as both were made during the same time period: June–September for 1987–1983, and late May–August for 2005–2006. Similarly, all recordings were made in the same general geographic area, and across a variety of behavioral contexts, so those are also unlikely explanations for the observed variation.

There have been births and deaths in the population between the two studies, so a change in group membership is a possible explanation for the observed vocalization changes. Group-related changes in vocalizations have been demonstrated in resident killer whales, but only when groups change at the pod level, with entire pods rather than matriline or individuals merging or splitting (Weiß *et al.* 2007). In this study, recordings were only included if a single pod was within acoustic range of the hydrophones. Additionally, there are multiple individuals in every pod that were alive for both time periods, so if changing group membership is the explanation, cultural drift would also have to be at play.

Cultural drift does occur in killer whales, because discrete calls are learned (Yurk *et al.* 2002), and this phenomenon has been observed before (Deecke *et al.* 2000). In Deecke *et al.*'s study, different rates of change occurred for different calls, demonstrating that when cultural drift occurs, it can have different mutation rates for different calls. However, if cultural drift were the explanation for this study, we would expect a nondirectional shift in call duration. Instead, we see 14 of 16 changed call types increasing in duration, and 5 call types not showing a significant change in duration at all. These ratios show a statistically significant bias toward increased duration (sign test $P < 0.05$) supporting the hypothesis that a factor other than nondirectional cultural drift is involved in the observed change.

An explanation that cannot be ruled out is an increase in duration due to overcoming the masking effects of background noise. Much work has been done to study the effect of vessel noise on cetaceans. Humpback whales increase the duration of their songs in the presence of low frequency active sonar playbacks (Miller *et al.* 2000).

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3 Similarly, beluga whales have been shown to alter the sound frequency of their calls
4 in response to engine noise interference (Lesage *et al.* 1999), and bottlenose dolphins
5 whistle at a higher rate in the presence of vessels (Buckstaff 2004). Most recently, it
6 has been demonstrated that killer whales will increase the amplitude of at least their
7 most common call types in the presence of vessel noise (Holt *et al.* 2009).

8 It has been estimated that underwater noise from boats can mask killer whale calls
9 at distances up to 14 km (Erbe 2002). A recent study found that all three Southern
10 Resident pods increase the duration of their most common call type (S1 for J-Pod,
11 S16 for K-Pod, and S19 for L-Pod) in the presence of an increased number of boats
12 (Foote *et al.* 2004). This study finds an increase in duration for S1 and S16, however,
13 a decrease in S19 was found. S19 call duration has been shown to be variable over time
14 (Foote *et al.* 2004); therefore, while the current observation of decreased call duration
15 does not match the previous trend, this particular call type may be more labile than
16 others. In fact, while S19 used to be the primary call type of L-Pod (Foote *et al.*
17 2004), call S2iii was observed more frequently in this study, suggesting that other
18 changes in the usage of S19 are occurring as well. What this study demonstrates is
19 that the trend of increased mean call duration is occurring on a broader scale than
20 previously appreciated, with a statistically significant increase in 14 of the 21 call
21 types compared here.

22 The number of active commercial whale-watching vessels on scene with Southern
23 Resident killer whales during the summer months increased five-fold between 1990
24 and 2000 (Foote *et al.* 2004), perhaps crossing a disturbance threshold in terms of
25 underwater engine noise and leading to the increased length of discrete calls. The
26 28-yr time period covered by this study correlates with a substantial increase in
27 active commercial whale-watching vessels. From 1978 to 1983, there was an average
28 of five boats in the active commercial whale-watching fleet, compared to an average
29 of 75 boats in 2005–2006.¹ In this study, either commercial or private motorized
30 boats were on scene with the whales in 30 of 31 included recordings. Motorized boat
31 numbers ranged from 1 to 23, with a mean of eight boats present.

32 Foote *et al.* suggest a dynamic short-term compensation mechanism for call dura-
33 tions, while this study supports a long-term compensation mechanism since increased
34 mean durations were observed regardless of the number of boats present. However,
35 since motorized boats were present in nearly all of the recordings in this study, it
36 is not possible to conclude whether the observed change in mean call duration is
37 an extension of short-term behavioral plasticity occurring only in the presence of
38 boats or a long-term behavioral adaptation to the overall increase of boats. The next
39 necessary step would be to obtain recordings in the absence of boats, but this is
40 logistically difficult because the ubiquitous presence of boats around the whales has
41 them accompanied by motorized vessels during almost all daylight hours in the
42 summer season.

43 With the endangered listing of the Southern Resident population, the National
44 Marine Fisheries Service has identified three primary potential risk factors: prey

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46 ¹Soundwatch Boater Education Program 2006 Final Report, The Whale Museum, P. O. Box 945,
47 Friday Harbor, WA 98250.

availability, pollution and noise, and stress associated with marine vessels (NMFS 2005). With vessel effects listed as one of the three primary potential risk factors, it is especially important to consider the implication of the current results. The increase of mean durations of discrete calls demonstrated here indicates that the Southern Residents are making a behavioral adjustment as a result of vessel noise. Because they are adjusting their vocal behavior, we must consider the very real possibility that engine noise is hindering their ability to communicate, and may well impact their efficiency at using acoustics to forage and navigate, as well. The results presented here underscore the importance of future research concerning the impact of vessel noise on Southern Resident killer whales and should be considered in the development of new conservation and management plans.

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Queries

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