

Differences in acoustic features of vocalizations produced by killer whales cross-socialized with bottlenose dolphins

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(Received 24 October 2013; revised 23 July 2014; accepted 4 August 2014)

Limited previous evidence suggests that killer whales (*Orcinus orca*) are capable of vocal production learning. However, vocal contextual learning has not been studied, nor the factors promoting learning. Vocalizations were collected from three killer whales with a history of exposure to bottlenose dolphins (*Tursiops truncatus*) and compared with data from seven killer whales held with conspecifics and nine bottlenose dolphins. The three whales' repertoires were distinguishable by a higher proportion of click trains and whistles. Time-domain features of click trains were intermediate between those of whales held with conspecifics and dolphins. These differences provided evidence for contextual learning. One killer whale spontaneously learned to produce artificial chirps taught to dolphins; acoustic features fell within the range of inter-individual differences among the dolphins. This whale also produced whistles similar to a stereotyped whistle produced by one dolphin. Thus, results provide further support for vocal production learning and show that killer whales are capable of contextual learning. That killer whales produce similar repertoires when associated with another species suggests substantial vocal plasticity and motivation for vocal conformity with social associates.

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PACS number(s): 43.80.Ka, 43.80.Lb, 43.66.Gf [ADP]

Pages: 1990–2002

I. INTRODUCTION

Vocal imitation is inferred when an animal perceives a sound and later produces a sound with similar acoustic features. If the two sounds are associated in time, the behavior is further defined as vocal matching. In social species, vocal imitation and matching are thought to facilitate cohesion among group members, promoting social relationships and cooperation to achieve adaptive goals (Janik and Slater, 1997, 1998; Tyack, 2008).

Vocal imitation requires an animal to perceive the acoustic features of a template sound, store them in memory, and control its vocal anatomy to produce one or more sounds with features similar to those of the original. Refinement can take time, with repeated tries shaped by auditory feedback. If the altered sound becomes a part of the animal's repertoire, the animal has learned. This is termed vocal production learning (Janik and Slater, 1997), which results in development of novel vocalizations or vocal features. Contextual learning (Janik and Slater,

2003) results in altered usage of vocalizations already in the animal's repertoire to conform to usage patterns of other individuals, the template for contextual learning.

Although historically considered rare in non-human mammals, there is mounting evidence that a range of mammalian taxa have at least some capacity for vocal learning and motivation to produce vocalizations similar to those of social partners, whether or not the vocalizations occur in matched exchanges (e.g., Sugiura, 1998; Boughman, 1998; Crockford *et al.*, 2004; Tyack, 2008; Arriaga and Jarvis, 2013). There is also evidence for varying usage in different social contexts (Crockford *et al.*, 2004; Hooper *et al.*, 2006; Bohn *et al.*, 2013).

Some of the best the evidence for vocal plasticity in non-human mammals comes from odontocetes, but the extent of their ability to learn, fidelity of their vocal imitations, and context for matching are still poorly understood. This report describes the results of adventitious cross-socialization experiments in learning created by maintaining killer whales (*Orcinus orca*) with another odontocete species, the bottlenose dolphin (*Tursiops truncatus*). Note that “vocal” and “vocalization” are be used here in the broad sense, to refer to sounds produced by any vibrating or resonating structure with air flow from the respiratory tract.

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There are several lines of evidence that bottlenose dolphins and other odontocetes are capable of imitating novel sounds outside their species-typical repertoire (Richards *et al.*, 1984; Caldwell *et al.*, 1990; Miksis *et al.*, 2002). A beluga (*Delphinapterus leucas*) spontaneously produced sounds similar to human speech (Ridgway *et al.*, 2012). Foote *et al.* (2006) recorded a socially isolated juvenile killer whale that produced barks similar to those of California sea lions (*Zalophus californianus*) in an area where the sea lions were common. Finally, two species of small social odontocetes significantly altered the frequency structure of their whistles in an apparent effort to imitate artificial mid-frequency sonar signals, although the fidelity of the imitations was poor (DeRuiter *et al.*, 2013).

In the killer whale, social organization is correlated with both genetic and vocal similarity (Deecke, 2010), ranging from clans sharing some calls (Yurk *et al.*, 2002) to pods composed of related matrilineal lines that share many or all of the elements in their repertoire (Ford, 1991). Matrilineal lines and pods are uniquely identified by their discrete, stereotyped pulsed call repertoires, leading to their characterization as “dialects” in the killer whale literature (Ford, 1989, 1991).

Whales match dialect elements (hereafter, call types) during social interactions within and between allied matrilineal lines and pods (Miller *et al.*, 2004; Deecke *et al.*, 2000; Filatova *et al.*, 2010). There is also evidence that free-ranging killer whales sometimes match call types at the level of the clan (Weiß *et al.*, 2011). It is not understood how killer whales maintain these stable, unique repertoires over the long term while still allowing qualitatively new call types to arise. Limited observations of individual repertoire use in the best studied populations suggest that change in call types is slow, potentially multi-generational (Miller *et al.*, 2004), and not always in the direction of greater similarity (Grebner *et al.*, 2011; Filatova *et al.*, 2013).

Evidence for learning of the species-typical repertoire is limited, but there are some direct observations from younger killer whales. During the first few months of life, a female calf gradually shaped unstereotyped pulsed calls to approximate the majority of the call types in her mother’s vocal repertoire (Bowles *et al.*, 1988). One young adult female learned call types from another dialect under controlled conditions (Bain, 1986). In a similar cross-socializing experiment, two juvenile to subadult male killer whales learned call types from a male whose dialect had untypical features (Crance *et al.*, 2014).

Killer whale repertoires are composed of three main types of vocalizations: Clicks, pulsed calls, and narrowband whistles (Ford, 1989, 1991). The clicks are short-duration broadband sounds that usually have bimodal distributions with both lower and higher peak frequencies present (Au *et al.*, 2004). Whistles are tonal, with peak frequencies usually ranging between 6 and 12 kHz (Ford, 1989) and variable durations on the order of seconds. They may be simple, with shallow frequency modulation, or a more complex series of deep modulations marked by rapid frequency transitions (Riesch *et al.*, 2008). Killer whale whistles are not stereotyped nor are they composed of rapid, repeated upsweeps and downsweeps of the type common in bottlenose dolphins,

although some have sinusoidal “loops.” Instead, the primary vocalization of killer whales is the pulsed call, composed of trains of pulses separated by short interpulse intervals (Watkins, 1967). When analyzed spectrographically with sampling windows of moderate length, these pulse trains appear variously as burst-pulses; modulated, harmonically related frequency bands characterized as “screams”; or chaotic sweeps.

Killer whale pulsed calls can be discrete and stereotyped, aberrant, or variable (Ford, 1991). Discrete stereotyped pulsed calls are composed of one or more segments called “components,” separated by rapid, perceptually salient changes in timbre and time-frequency contour (e.g., from a burst-pulse to a scream). Scream components may have two independently modulated sound sources operating simultaneously (low and high frequency components). Unique repertoires of 7–18 of these call types compose the killer whale dialect (Ford, 1991).

Aberrant calls are recognizable as call types but are distorted or modified, often by warbling the terminal scream, the “excitement calls” of Ford (1989). Variable pulsed calls are even less stereotyped and may not be composed of clearly differentiated components (Rehn *et al.*, 2007). Killer whales are also capable of producing short, unstereotyped burst-pulse sounds.

Bottlenose dolphins produce broadly similar classes of vocalizations. Their clicks are a few cycles long, with bandwidths of 20–60 Hz and peak frequencies generally between 30 and 120 kHz (Au, 1993), usually emitted in a series or train. When echolocating, clicks with short interclick intervals (ICI) often terminate the train, sounding like a buzz to the human ear (terminal buzz). Although echolocation is one function of these click trains, others are possible. Their burst-pulse sounds are not stereotyped by individual or group or made up of components. Instead, the predominant vocalizations of bottlenose dolphins are click trains and whistles. A subset of the whistles have distinct, stereotyped contours (Caldwell *et al.*, 1990), here termed “stereotyped whistles.” They are composed of rapid upsweeps, downsweeps, and sinusoidal modulations, with individual contours as short as a few hundred milliseconds and sequences generally lasting 1–2 s.

For social communication, bottlenose dolphins predominantly produce whistles (Janik and Sayigh, 2013) while killer whales produce pulsed calls (Ford, 1989). The stereotyped whistles of bottlenose dolphins appear to function as cohesion calls exchanged among social associates (Janik and Slater, 1998). They are reported to be individual-specific (“signature whistles”) and characterized as stable for life (Sayigh *et al.*, 1990). However, the signature whistle hypothesis has been contentious (McCowan and Reiss, 1995a; Harley, 2008; Sayigh *et al.*, 2007). For the purposes of this report, the important points are that bottlenose dolphins produce high proportions of whistles, a subset are stereotyped, and these whistles are emitted frequently by individuals. In contrast, the prevailing characterization of killer whale call type use is of a common repertoire that encodes group information, hence the “dialect” terminology (Ford, 1989; Deecke *et al.*, 2000).

To date, the methods that have characterized individual killer whale use of the group dialect differ from those used to study individual bottlenose dolphin repertoires. They include experimental playback to groups of killer whales (Filatova *et al.*, 2011); observations of individual call usage (Miller *et al.*, 2004; Grebner *et al.*, 2011); and experimental studies under controlled conditions (Bain, 1986; Crance *et al.*, 2014). The experiments have been limited to within-species cross-socializing and there has been no experimental evidence obtained under semi-controlled conditions. In contrast, bottlenose dolphin learning has been studied in controlled (Caldwell *et al.*, 1990; Reiss and McCowan, 1993; McCowan and Reiss, 1995b; Miksis *et al.*, 2002), semi-controlled (Fripp *et al.*, 2005; Sayigh *et al.*, 2007; Janik and Sayigh, 2013), and free-ranging (King *et al.*, 2013) conditions. These studies have shown that individual bottlenose dolphins can learn to imitate stereotyped whistles and other sounds, add them to their repertoires, and use them in matching exchanges with conspecifics (McCowan *et al.*, 1998; Quick and Janik, 2012; King *et al.*, 2013).

The strongest evidence for learning in the bottlenose dolphin comes from studies using artificial sounds and cross-socializing experiments. They have learned spontaneously (Miksis *et al.*, 2002) and under stimulus control (Richards *et al.*, 1984) to make a variety of tonal and burst-pulse sounds, some with sufficient fidelity to fool human listeners. In cross-socializing experiments they have learned stereotyped whistles from other small delphinids (Caldwell *et al.*, 1990), although the new sounds differed little from those in their species-typical repertoire.

If killer whales learn and are motivated to match the vocalizations of social associates, then one strong measure of plasticity would be changes in repertoires of whales socializing with other species. They might acquire new calls, or change acoustic features or usage of existing ones, increasing similarity to vocalizations of their new social partners. Data were collected from three classes of subjects, killer whales housed only with conspecifics, killer whales that had been housed with bottlenose dolphins for prolonged periods, and bottlenose dolphins. The data were used to determine whether cross-socializing experience led to differences in call type usage or acoustic features by killer whales. If the whales acquired novel vocalizations from bottlenose dolphin social partners, they would provide evidence for vocal production learning (Janik and Slater, 1997). If whales shifted usage to emphasize vocalization types used more often by dolphins, the evidence would support vocal contextual learning (Janik and Slater, 2003).

II. METHODS

Three types of acoustic recordings were collected, (1) vocalizations broken into broad categories so that differing species-typical repertoires could be compared, (2) acoustic features of click trains, and (3) acoustic features of a human-conditioned chirp produced by bottlenose dolphins and one killer whale. Nineteen individuals were included in the study, subdivided into the three categories: KW—killer whales housed only with conspecifics (seven whales);

KW-BD—killer whales currently or previously housed with bottlenose dolphins (three whales); and BD—bottlenose dolphins (nine dolphins).

A. Subjects

The killer whales housed with conspecifics (KW) were recorded in two facilities, F1, F3, F4, F14, M4, and M6 in Facility 1; and F9 in Facility 2. Two of the three KW-BD whales were also studied in these facilities, M8 (Facility 1) and F2 (Facility 2). They had been exposed to bottlenose dolphins for 6–10 years prior to transfer, but no recordings were available for either from these periods. F13 was held concurrently with the 9 dolphins at Facility 3 during the study.

1. Killer whales, Facility 1

Seven whales were recorded in Facility 1. F1, the oldest, was a post-reproductive female from A-pod in British Columbia, housed at Facility 1 for 1.5 decades. The dominant female in the facility, F3, was an adult female from Icelandic waters who had been in the facility for nearly 2 decades. F4 had been born in there. She was an unrelated adult female of Icelandic origin and F3's closest social associate. M4 was F3's son, ranging from the calf through juvenile age classes during data collection. F14 was F3's daughter, a young adult at the start of data collection in 2001. M6 was a subadult male born in Facility 2 (the grandson of F2) and transferred to Facility 1 as a juvenile. M8 was an adult male at the start of the study, also originating from Icelandic waters. He had been housed with bottlenose dolphins for at least a decade prior to transfer and had been with killer whales at Facility 1 for 7 years.

2. Killer whales, Facility 2

The two subjects at Facility 2 were adult females. F2 was from Icelandic waters and had been housed with bottlenose dolphins intermittently over a 10 year period prior to transfer to Facility 2, where she had been for 2 years when recordings were first collected. F9 originated in Icelandic waters and had been held at Facility 2 with other killer whales since she was a juvenile. The period of recordings included the birth of three calves (two born to F9, and one to F2) in 1989 and 1993, during which period the females had an allomaternal relationship. Only the vocalizations of the adults were included in the analysis; vocalizations of young calves are quite distinctive (Bowles *et al.*, 1988), and were excluded.

3. Killer whale F13 and bottlenose dolphins, Facility 3

The subjects at Facility 3 were nine Atlantic bottlenose dolphins (BD1–9) and F13, an adult female killer whale of Icelandic origin born in an oceanarium in France. F13 had been housed with killer whales for nearly a decade before being transferred to Facility 3 as a subadult. She had been living with bottlenose dolphins for 5 to 7 years when recorded.

Two bottlenose dolphins were selected as subjects for the repertoire and click train measurements because they

were frequently social associates of F13. The first (BD1) was an adult male and had been at Facility 3 throughout F13's tenure. The second (BD2) was a subadult male that had been stranded and rehabilitated as a juvenile, and had been at Facility 3 for over 5 years when recorded.

Seven additional dolphins (BD3-BD9) were subjects in the chirp series dataset (see below). They were three females and four males ranging from juvenile to adult age classes, five of which had been born in oceanaria (all but one at Facility 3). Two were adults collected in the early 1980s.

B. Datasets collected

1. Killer whales, Facility 1

Acoustic and video recordings were collected between 9/01 and 11/06 in a test pool at Facility 1 with underwater viewing and an eight-element array of ITC 6050H and ITC 8212 hull-mounted hydrophones (ITC, Santa Barbara, CA). The hydrophones were embedded in niches recessed within the rocks and sides of the pool. Eight channel recordings were collected using a custom system developed by BAE Systems in San Diego (custom software by D. McGehee and C. Greenlaw). Simultaneous behavioral recordings were collected on video, with signals multiplexed from two underwater and two overhead video cameras (Robot MV94 multiplexer, Sormatic Video Products, San Diego, CA) and recorded on a Panasonic SVHS or DMR-E95H digital video recorder (Panasonic Consumer Electronics, Secaucus, NJ) with system bandwidth 50 Hz to 16–22 kHz. The combined coverage of the pool was 90%, including an overhead camera view of the main body of the test pool, and a view covering the channel connecting it to other pools. The DVR recorded two channels of hydrophone data to allow events on video to be related to recorded signals. Water clarity in this facility was high, as was true of all three facilities, and the behaviors of interest were readily detected whenever the subjects were visible.

The pool dimensions were 24.7 m × 41.2 m × 6.1 m, and subjects were always within 10 m and line-of-sight of a recording hydrophone. Although the levels of some vocal components could vary depending on the orientation of the whale (e.g., click trains or the high frequency component of some call types), vocalizations were always detectable. However, when multiple whales were in the test pool, attributing calls to callers often presented challenges. Although the channel to the test pool could be closed off by a gate, its grating was wide and did not block acoustic signals from other pools. Thus, procedures were developed for attributing vocalizations to individuals, with emphasis on reliability.

First, the channel video and a hydrophone mounted in the channel were used to detect and eliminate vocalizations that might have been transmitted from other pools. Second, acoustic localization was used to attribute calls and check the reliability of attributions obtained using other methods. Multichannel recordings were entered into a custom program also developed by BAE Systems and implemented in MATLAB (The MathWorks, Inc., Natick, MA). The program displayed a diagram of all eight hydrophones and determined the sound exposure level (SEL), a measure of the

energy in the call, of each event at each hydrophone. Sample recordings were triggered by any sound exceeding a pre-set threshold and collected in 2-s segments. If calls lasted longer than 2 s, multiple samples could be collected from the same call. The program displayed oscillograms of the segments from all eight hydrophones and a spectrogram of the sample with the greatest energy. This display was compared with time-synchronized video recordings to identify whales in the pool, show locations when a call was detected, and determine behavior. The display was also used to eliminate spurious sounds, such as banging gates.

Data collected with the array were limited to calls with the highest possible attribution accuracy. Calls could be attributed to a whale with relative certainty when it was over the hydrophone receiving the highest SEL. The caller had to be within one body length (BL) of the hydrophone recording the greatest SEL, all other hydrophones had to have substantially lower SEL, and whales had to be separated by >3 BL from the caller. These strictures ensured reliable attributions, but many calls could not be attributed. In addition, the requirement for separation among the whales was a potential source of bias. Therefore, additional means of call attribution were used, as described below (Data Analysis).

2. Killer whales, Facility 2

Acoustic and video recordings were collected between 6/89 and 12/94 using a portable ITC 6050c hydrophone (ITC, Santa Barbara, CA) with built-in pre-amp (sensitivity: –157 dB re 1 V/μPa) suspended in the water column at least 1.3 m from any surface and in a gateway immediately adjacent to the pool holding one or both of the focal whales (F2 and F9). The flat frequency response (± 1 dB) of the hydrophone ranged from 50 Hz to 50 kHz. Sound traveled freely across the barrier between the hydrophone and the pool (a gate with apertures >20 cm). When subjects were relatively well-isolated from others and within 10 m of the hydrophone, proximity cues could be used to attribute calls. Only calls with high signal-to-noise ratio (SNR), low distortion due to reverberation, and high frequency energy characteristic of signals projected near and in the direction of the hydrophone were accepted. Otherwise, attribution was based on localization by ear at the surface and behaviors synchronous with calls.

The voice and hydrophone tracks were recorded with the signal from a CCD camera (Princeton Instruments, Trenton, NJ) onto an EVO9500 VHS video recorder (Sony Electronics Inc., Minato, Japan).

3. Killer whale F13 and bottlenose dolphins, Facility 3

Recordings of the individuals at Facility 3 were collected between 11/09 and 5/11 using the ITC 6050c hydrophone. Acoustic recordings were made with a four-channel Edirol R44 digital audio recorder (Roland, Los Angeles, CA) using a 96 kHz sampling frequency, or a two-channel Fostex FR-2 field memory recorder (Fostex Company, Akishima, Japan) using 48 kHz sampling and 16 bit analog-to-digital conversion. The hydrophone was placed in the gate channel of a pool with the gate closed to prevent

interference by the subjects. The hydrophone was submerged to a depth of 1.5 m and at least 1.5 m from all walls. Author Musser was present throughout all recording periods to collect behavioral observations and to identify the source of vocalizations.

All recordings of repertoires in Facility 3 were made while focal subjects F13, BD1, and BD2 could see, hear, and approach other individuals across alternate gateways. Proximity cues were not used for attribution unless the subject was within 10 m of the hydrophone and well-separated from potential confounding callers. Vocalizations were collected *ad libitum* in three-day blocks for as many daylight hours as possible given the normal activities in the facility.

The chirp dataset was collected after initial recordings and consultation with Facility 3 animal care staff showed that F13 could have been producing a sound learned at the facility from resident dolphins, a series of chirps that the dolphins produced under stimulus control in public shows. Chirp series used for statistical comparison were collected at Facility 3 4/11 and 5/11. To obtain samples of this sound, F13 and eight of the bottlenose dolphins (BD1, BD3-BD9) were signaled to produce trains of chirps. A target of ten chirp series with seven or more chirps per series was solicited from each of the nine subjects (8 BD and 1 KW-BD) over two sampling periods.

C. Data reduction and analysis

The study was designed to compare vocal repertoires of killer whales held with conspecifics (KW) to those that had been housed with bottlenose dolphins (KW-BD) and with the sample collected from bottlenose dolphins (BD) at Facility 3. Data reduction and processing compared individuals and the three classes of subjects using the three datasets, (1) repertoire composition; (2) acoustic features of click trains; and (3) acoustic features of chirp series.

1. Data extraction, call attribution and classification

Archival recordings from Facility 1 and 2 were digitized from video using Adobe Premiere software (Adobe Systems Inc., San Jose, CA). The audio track was extracted from digitized video and processed as for all other audio recordings. Digital audio recordings from Facility 2 and 3 were initially extracted using Sound Forge (V 6.0, Sony Creative Software, Inc., Minato, Japan). Oscillograms and spectrograms of vocalizations were prepared and quantified in Raven Pro, V1.3 or later (Cornell Laboratory of Ornithology, Cornell, NY).

All attributed vocalizations were grouped into broad categories to make comparisons across species possible. For killer whales, discrete pulsed calls (pulsed calls) were categorized and pooled. Aberrant calls (also called “excitement calls”) were pooled with stereotyped pulsed calls since only the terminal components were aberrant and the differences were the result of easily recognized modulations. Unstereotyped variable pulsed calls were placed in their own category (variable calls). Click trains were categorized as any series of broadband pulsive transients lasting a few cycles, while whistles were defined as narrowband tonal sounds. Unstereotyped burst-pulse sounds were categorized as “Other.”

Localization using the hydrophone array in Facility 1 has been described. Because many calls could not be attributed by this method, particularly when subjects were socializing actively, and because the method could not be used in Facility 2 and 3, other forms of attribution were used as well.

First, behavioral cues indicated a vocalizing subject (bubbling, nodding). These were potentially biased with respect to call type and behavioral state (Fripp, 2005). However, when present, they were reliable methods of attribution.

Second, when a subject was close to and oriented on a hydrophone, its vocalizations could be attributed reliably. Cues included substantially greater SNR, minimal reverberation, and presence of higher frequency components. This method of attribution was unbiased with respect to vocalization types, but required the subject to be near the hydrophone (within 10 m) and well separated.

Third, vocalizations could be localized by ear at the surface or at an underwater viewing panel when the subject was close to an observer. This method of attribution required the subject to be well separated from other animals (>3 BL) unless the observer was close enough to observe movement in the muscles surrounding the blowhole (e.g., from a walkway over a gate).

Overlapping calls were eliminated. When calls were delivered in a bout (sequences of 2–7 vocalizations separated by at least 5 s), behavioral attributions could be assigned only for those vocalizations synchronous with the associated behavior, usually the first 1–2 calls in a bout. However, observers were often able to attribute longer sequences by ear if the subject was close to the gate channel.

All attribution methods had limitations, but they had the advantage of being usable over long periods without interfering with subject behavior or interrupting facility operations. Flexibility was important because data had to be collected from multiple facilities to eliminate the possibility of location bias. The methods were applied the same way at all three locations.

Pooling across attribution methods and collecting samples across multiple days yielded a sample of calls from each individual that was stable in composition and included the expected repertoire given their dialect (Crance *et al.*, 2014). There were no unexpected variances in relative proportions of vocalization categories from individual to individual and between facilities. Based on the limited sample of independent attributions made using the Facility 1 array and the distribution of vocalization categories from the sample of unattributed calls, the procedure was sufficiently unbiased to permit comparisons among individuals when vocalizations were encoded in broad categories for cross-species comparison (burst-pulses, pulsed calls, whistles, and click trains).

2. Acoustic measurements

Extraction of acoustic data was performed using Raven. Repertoire data were classified by experienced observers using both audio and a spectrographic display, and confirmed by authors Bowles (killer whales) and Musser (bottlenose dolphins).

KW subjects produced click trains that sounded to the human ear like echolocation when exposed to novel

equipment, such as a free-floating hydrophone (Bowles *et al.*, 1988), but rarely produced them spontaneously in the familiar test pools (Table I). The killer whales were well-habituated to the hydrophones used during data collection. However, both KW-BD and BD subjects produced click trains frequently (Tables II and III) in the test pools regardless of novelty. Because the sample of click trains from KW subjects was so small, all those with sufficient quality were pooled for analysis. For comparison, 20 click trains of good quality were selected at random for each KW-BD and BD subject.

Echolocation could not be distinguished reliably from other types of click trains in unconstrained study subjects. In addition, the subjects could be in any orientation and individual clicks were likely to be contaminated to some degree by reflections from surfaces. Therefore, spectral data were of limited use. However, when emitted close to the hydrophone, click trains with clear peaks could be collected. Basic time-domain characteristics of the click trains were measured as follows. The click train was the sampling unit, drawn at random from the total sample of click trains for each subject. Total duration was measured as the interval between the point that the first click exceeded the background by ~3 dB and the point where the last dropped back within ~3 dB. Interclick interval (ICI) could be measured at intervals exceeding 7 ms, but not at higher rates. For each click train, the five shortest and five longest ICI values (ICI > 7 ms) were averaged to obtain mean minimum and maximum ICI. If a sample ended in a series of clicks having ICI < 7 ms, it was classed as having a terminal buzz. The buzzes usually had sufficiently high click rates that they could also have been burst-pulses with a social function.

For the chirp dataset, five chirps were extracted from the center of each series and measured spectrographically (48 kHz sampling rate, 1024-point sampling window, 50% overlap). Measured features were chirp duration, inter-chirp interval, and frequency maximum, minimum, and range of the first spectral band. The five measurements for each series were averaged for input to the statistical analyses, making the chirp series the sampling unit.

3. Statistical analyses

Statistical analyses were conducted in the R statistical programming environment (R Development Core Team, 2013). Repertoire distance was assessed using hierarchical

cluster analysis in the R package *pvclust* (Suzuki and Shimodaira, 2006) using arcsin-transformed within-whale proportions of call categories as input measurements (Manhattan distance, single clustering). For each split in the resulting dendrogram, *pvclust* calculated an autonomous unbiased (AU) estimate of the probability that the split occurred using multi-scale bootstrap resampling (1000 iterations).

Preliminary graphical examinations indicated that acoustic features of click trains differed among classes of whales and individuals, but the combination of features that differed was not consistent among individuals. As a further exploratory analysis, the continuous acoustic features of click trains were compared with multifactor analysis of variance (between groups MANOVA) using Statistica 6.1 (Statsoft, Inc., Tulsa, OK), followed by a Bonferroni *post hoc* comparison. This analysis helped select acoustic measures likely to discriminate individuals or classes reliably. The observed proportion of terminal buzzes was compared across individuals using a deviance test (G-test). The mean proportion of terminal buzzes for the two subject dolphins was used to estimate expected counts.

Based on initial evaluation, the click train dataset was winnowed down to four variables, duration, click count, and minimum and maximum ICI. A linear discriminant analysis was conducted in R using the routine *lda* in the MASS package V 7.3–29, Rev: 3344 (Venables and Ripley, 2002). The probability of correct discrimination was assessed using the first two linear discriminant functions (LD1, LD2), and statistical validity was determined using MANOVA and a jack-knifing resampling procedure integrated with the package.

A similar approach discriminated chirp series produced by F13 and eight of the bottlenose dolphins (BD1, BD3–9). Highly correlated acoustic features were eliminated and LDA conducted on the remaining features (duration, minimum ICI, and range of ICI). The first two linear discriminant functions were used to calculate the probability of correct discrimination and evaluate significance.

III. RESULTS

A. Repertoire comparison

A total of 2861 attributed vocalizations (Tables I–III) were collected from the 12 subjects (ten killer whales and two bottlenose dolphins). Preliminary examinations of the data

TABLE I. Count of vocalizations attributed to killer whale subjects held with conspecifics (KW).

Subject	Attributed vocalizations (N)	Proportion by vocalization category				
		Discrete pulsed calls	Variable pulsed calls	Whistles	Click trains	Other
F1	237	210 (89%)	17 (7%)	0	10 (4%)	0
F3	112	106 (95%)	5 (4%)	1 (1%)	0	0
F4	199	197 (99%)	2 (1%)	0	0	0
F9	202	186 (92%)	14 (7%)	0	2 (1%)	0
F14	124	118 (95%)	3 (2%)	2 (2%)	1 (1%)	0
M4	313	280 (89%)	25 (8%)	0	8 (3%)	0
M6	364	322 (88%)	41 (11%)	1 (<1%)	0	0
Total	1551	1419 (91%)	107 (7%)	4 (<1%)	21 (1%)	0

TABLE II. Count of vocalizations attributed to killer whale subjects held with bottlenose dolphins (KW-BD).

Subjects	Attributed vocalizations (N)	Proportion by vocalization category				
		Discrete pulsed calls	Variable pulsed calls	Whistles	Click trains ^a	Other
F2	261	195 (75%)	21 (8%)	6 (2%)	39 (15%)	0
F13 ^b	239	144 (60%)	5 (2%)	10 (4%)	74 (31%)	6 (3%)
M8	474	386 (81%)	10 (2%)	21 (4%)	57 (12%)	0
Total	974	725 (74%)	36 (4%)	37 (4%)	170 (17%)	6 (1%)

^aSubsample of 20 extracted for click train analysis.

^bF13 also produced 9 chirp trains that were included in analysis.

showed differences between the KW and KW-BD whales. KW whales produced a higher proportion of stereotyped pulsed calls. In contrast, KW-BD whales produced a higher proportion of whistles and substantially more click trains. KW whales produced so few click trains that the analyzable sample had to be pooled across subjects. They produced no click trains that were likely to be echolocation or having terminal buzzes. In contrast KW-BD whales produced 12%–33% of their repertoire as click trains; in the subsample used for statistical comparison, 15%–35% of these had terminal buzzes.

A total of 1551 vocalizations were attributed to KW subjects, >95% of which were pulsed calls, either stereotyped or variable (Table I). They produced few attributed whistles and click trains, averaging just 1% of the samples. Proportions of KW vocalization types were comparable across facilities, despite the different subjects and recording methods.

The two dolphins in Facility 3 predominantly clicked and whistled, with click trains comprising 56%–70% of the repertoire and whistles 22%–41% (Table III). They produced clicks trains with 30%–40% terminal buzzes (Table IV).

KW-BD subjects produced proportions of call categories more like those of the dolphins. F13 was living with dolphins at the time of recording, and her repertoire was the most similar (Table II). Of 239 attributed vocalizations, 60% were pulsed calls, 31% were click trains, and 4% were whistles. She was the only killer whale that produced isolated burst-pulses of the type attributed to dolphins (3% of her sample).

M8 produced 81% pulsed calls, 12% click trains (57 of 474 vocalizations) and nearly all of the whistles in the Facility 1 dataset (21 of 25, 4% of his sample). F2 had lived with dolphins for an unknown period before arriving at Facility 2 and shared an allomaternal relationship with F9. Her repertoire was the least like that of the dolphins. She

TABLE III. Count of vocalizations attributed to bottlenose dolphins (BD) by category.

Subjects	Attributed vocalizations (N)	Proportion by vocalization category		
		Whistles	Click trains ^a	Other
BD1	175	38 (22%)	123 (70%)	14 (8%)
BD2	161	66 (41%)	90 (56%)	5 (3%)
Totals	338	104 (31%)	213 (63%)	19 (6%)

^aSubsample of 20 extracted for click train analysis.

produced 83% pulsed calls, 15% click trains, and 2% whistles.

Hierarchical cluster analysis successfully separated the subjects by category (Fig. 1), discriminating the bottlenose dolphins and killer whales with high accuracy (BD vs KW and KW-BD), and within the killer whales sorted the KW-BD whales into two clusters, of which one (M8 and F2) was not separated from the KW whales at the highest level, but did form a sub-cluster separate from the KW whales. F13, housed concurrently with dolphins, was distinguished from all other killer whales. The remaining KW whales were clustered together.

B. Click train comparison

A total of 114 samples were used in the analysis of click train acoustic features. Only four KW produced attributed click trains (21 trains), of which only 14 from three whales had low distortion and sufficient SNR for analysis. They were pooled into a single category because the sample was not sufficient to treat them separately. They were compared with 20 trains subsampled from the attributed click trains from each of the three KW-BD and two BD subjects.

Duration and count of clicks per train, and minimum and maximum ICI were compared among the classes of subjects (Table IV). They differed significantly (MANOVA, Wilks' $\lambda = 0.7186$, $F = 2.4375$, $df = 15$, $p = 0.0023$). The Bonferroni *post hoc* procedure showed that click trains of the KW subjects differed significantly from those of BD subjects in click count ($p < 0.05$), duration ($p < 0.05$), and minimum ICI ($p < 0.001$). However, the KW-BD subjects showed a gradient of similarity, ranging from F13 (most) to F2 (least). Click trains of F13 did not differ from those of the dolphins in any acoustic feature. Compared to the BD subjects, the count and duration of the click trains from F2 differed ($p < 0.05$), while only minimum ICI differed for M8 ($p < 0.0001$). Thus, the KW-BD whales emitted click trains differing from those of BD based on individually distinctive sets of acoustic features.

The proportion of terminal buzzes (column 6, Table IV) was compared across subjects using the G-test. The expected count was calculated using the mean proportion of terminal buzzes for the two BD subjects, 0.35. While BD and KW-BD subjects produced click trains with terminal buzzes, KWs did not ($G = 13.1741$, $df = 1$, $p = 0.0002$). F2 produced a significantly smaller proportion of terminal buzzes (15% terminal buzzes, $G = 4.5321$, $df = 1$, $p = 0.0166$), but

TABLE IV. Comparison of click train features among the subjects of the three group types, KW, KW-BD and BD. Mean count, duration and ICI for the KW and KW-BD classes were compared to equivalent values of the two BD subjects.^a

Subject	Attributed click trains (N)	Mean count pulses/train mean (SE)	Mean duration, s (SE)	ICI min—max, s (min SE—max SE)	% Buzzes
Killer whales housed with conspecifics (KW)					
seven whales, pooled	14	56.1 (16.0)*	4.1 (1.0)*	0.058***—0.165 (0.0086—0.024)	0***
Killer whales housed with bottlenose dolphins (KW-BD)					
F2	20	70.9 (10.7)*	4.3 (0.6)*	0.021—0.146 (0.0030—0.022)	15*
F13	20	147.0 (33.0)	7.9 (1.1)	0.023—0.179 (0.0044—0.020)	35
M8	20	125.4 (31.9)	7.8 (1.6)	0.047***—0.167 (0.0072—0.035)	25
Bottlenose dolphins (BD)					
BD1	20	156.8 (24.2)	8.6 (1.2)	0.016—0.214 (0.0027—0.030)	40
BD2	20	190.8 (26.4)	10.0 (1.2)	0.017—0.222 (0.0020—0.025)	30

^aShaded, starred numbers indicate significance when compared with the bottlenose dolphin values, * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

proportions for both F13 and M8 were indistinguishable from expectation ($p > 0.05$).

The pattern of results in the MANOVA was supported by linear discriminant analysis (LDA). Duration, click count, and maximum and minimum ICI were entered into the LDA by class (KW, KW-BD, BD). The LDA for group types resulted in an overall correct classification of 0.607 (Fig. 2), above chance expectation (0.33). Click trains of KW and BD subjects could be discriminated, but neither could be distinguished reliably from KW-BD click trains (Table V).

C. Chirp series and whistles

All the dolphins at Facility 3 produced a series of chirps conditioned by staff trainers for use in public shows. These chirps were not typical of the unconditioned repertoires of either bottlenose dolphins or killer whales. The training staff reported that F13 did not produce chirp series spontaneously when transferred to Facility 3, but after transfer they noticed that she began producing sounds that resembled it while she was observing training sessions with the dolphins. She was

not under trainer control during these sessions. After she initiated the behavior, the trainers brought it under stimulus control, but they did not shape it as they had for the dolphins.

In each series, subjects were cued to initiate the behavior and produced chirps until bridged. For study recordings, F13 and eight bottlenose dolphins (BD1, BD3-BD9) were asked to produce trains of chirps in 2 recording sessions, for a total of 9–12 high-quality sample series with 7 or more chirps per subject (89 samples total).

Example chirp series are shown from a BD subject [Fig. 3(a)] and F13 [Fig. 3(b)]. Exploratory analysis indicated significant differences among individuals (MANOVA, Wilks' $\lambda = 0.0031$, $F = 33.799$, $df = 8$, $p < 0.0001$), with the *post hoc* Bonferroni analysis indicating differences in mean chirp duration, interval, minimum frequency, and maximum frequency ($p < 0.0001$) among all animals.

LDA successfully discriminated 91% of the samples (Table VI). Data for all individuals were tightly clustered, including F13 (Fig. 4). The greatest deviation was in F13's maximum frequency (mean 2100 vs 2600 Hz), which resulted in chirps with approximately half the frequency range (mean 750 vs 1400 Hz) of those produced by BD subjects. Her series also began with variable chirps [Fig. 3(b)] that became more uniform as the series progressed. Dolphins, in contrast, produced uniform chirps throughout [Fig. 3(a)].

F13 also produced four examples of a whistle contour similar to the stereotyped whistle produced often by her most frequent dolphin social associate, BD1 [Fig. 5(a)]. This whistle was a short upsweep, untypical of her whistles and those of

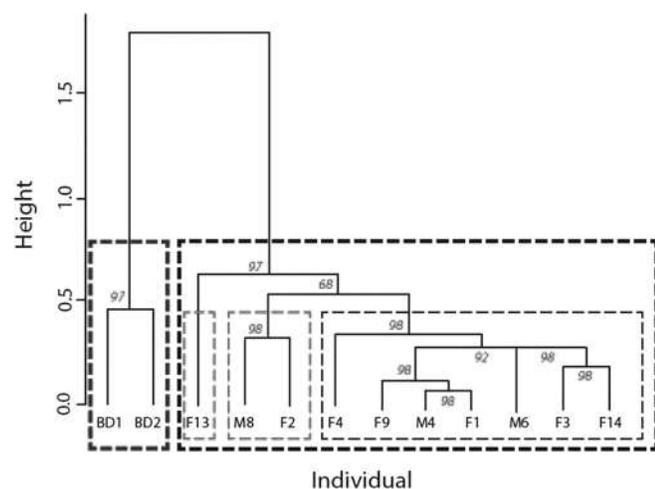


FIG. 1. Dendrogram resulting from the hierarchical cluster analysis of repertoire composition. Input data were the proportions of each call categories in the repertoire (Manhattan distance estimate). Clusters with the KW-BD whales are circled. Values in italics indicate the autonomous unbiased estimates of correct classification based on 1000 resampling iterations.

TABLE V. Counts and proportions of samples from the three classes of whales correctly classified by linear discrimination analysis (LDA) of click train acoustic features. Proportion of correct classifications determined by a jack-knifed resampling procedure is given in the right column (1000 iterations).

Subject/class	KW	KW-BD	BD	Total (percent correct)
KW	5	9	0	14 (36%)
KW-BD	3	44	11	58 (76%)
BD	0	21	19	40 (48%)
Total	8	74	30	112 (61%)

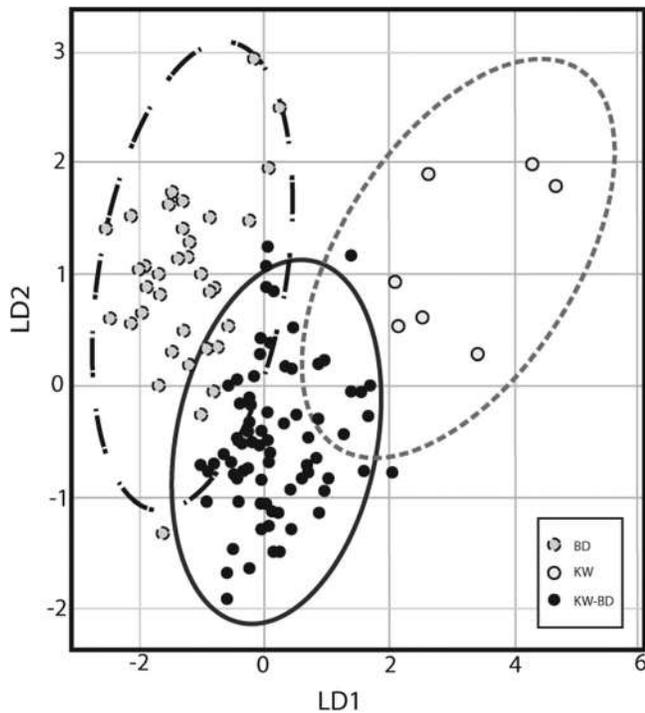


FIG. 2. Results of linear discriminant analysis (LDA) of click train data by subject class for the first two linear discriminant functions (LD1, LD2). Overall correct classification was 0.607 (1000 resampled iterations). Ellipses indicate 95% confidence limits by subject class.

other killer whales in frequency contour, timbre, and duration. F13's whistles [Fig. 5(b)] showed abrupt frequency transitions untypical of the dolphin.

IV. DISCUSSION

This study provided evidence that killer whales altered use of species-typical vocalizations in a new social context and learned novel, atypical sounds when cross-socialized with bottlenose dolphins (KW-BD). In contrast to killer whale subjects that had been housed only with other killer whales (KW), KW-BD whales produced 17 times as many click trains and up to four times as many whistles, making their relative usage of vocalization categories more similar to those of dolphin social partners. Acoustic features of their click trains were also less distinguishable from those of bottlenose dolphins (BD). One KW-BD subject learned to

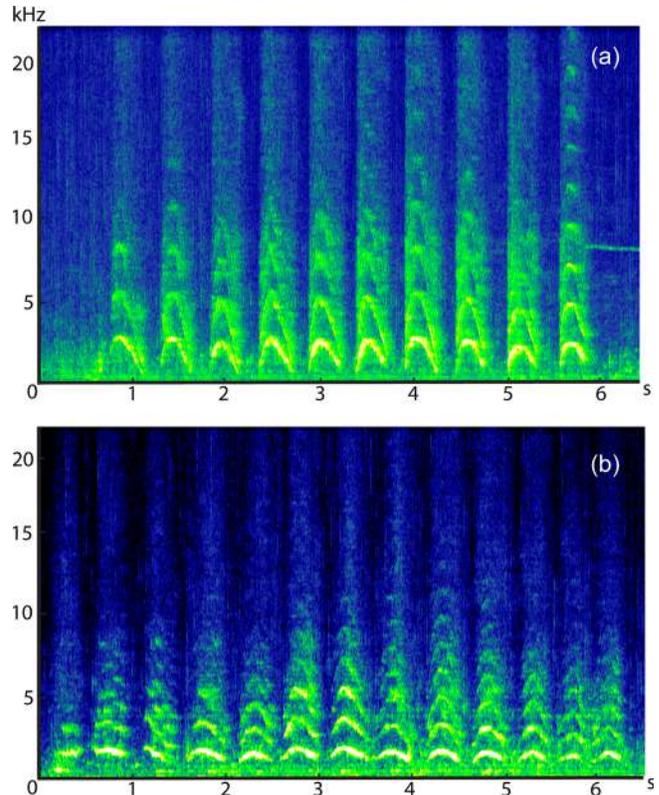


FIG. 3. (Color online) Spectrograms of chirp series emitted by (a) BD1 and (b) F13 under stimulus control. The tonal at the end of (a) is a reinforcing bridging whistle.

produce two novel call types, consistent with evidence from earlier work (Bain, 1986; Foote *et al.*, 2006; Crance *et al.*, 2014) that young killer whales (juveniles to young adults) are capable of production learning.

The sample of KW-BD whales was small and the genesis of the experiments adventitious—there were no “pre-treatment” measurements from the whales held with dolphins. Nevertheless, this evidence is some of the best available for an influence of odontocete cross-species socialization on vocal behavior. Previous experiments of this type have involved species that were similar in repertoire, and few quantitative measurements were made (Caldwell *et al.*, 1990). More systematic experimental manipulation, i.e., deliberately moving a larger sample of animals to

TABLE VI. Counts and proportions of individual chirp series correctly classified by linear discrimination analysis (LDA). Proportion of correct classifications determined by a jack-knifed resampling procedure is shown in the right column (1000 iterations).

Subject	F13	BD1	BD3	BD4	BD5	BD6	BD7	BD8	BD9	Total (percent correct)
F13	8		1							9 (78%)
BD1		9	1							10 (100%)
BD3			7	1			1			9 (78%)
BD4				8		1	1			10 (80%)
BD5					8			1		9 (89%)
BD6						9				9 (100%)
BD7				1			9	1		11 (91%)
BD8								11	1	12 (100%)
BD9									10	10 (100%)
Total										89 (91%)

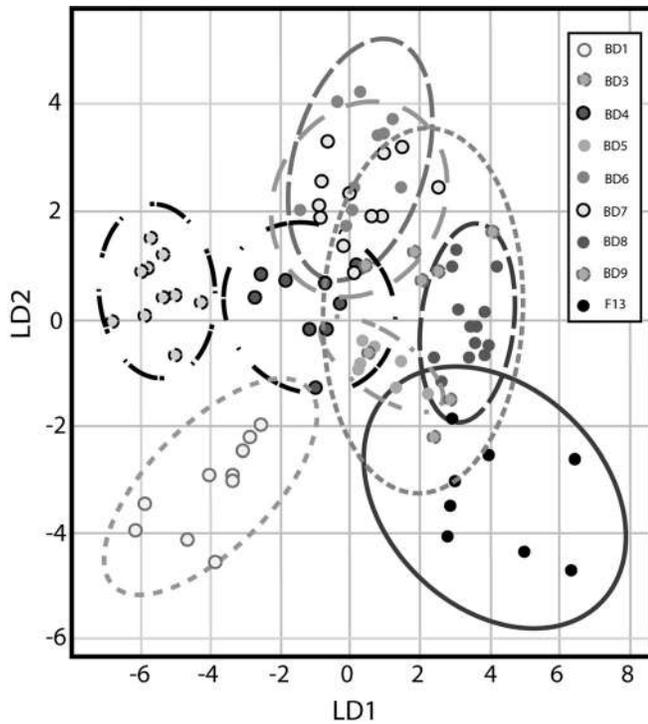


FIG. 4. Results of linear discriminant analysis (LDA) of the acoustic features of chirp series by individual subject. Values returned by the first two linear discriminant functions (LD1, LD2) are plotted. Ellipses indicate 95% confidence limits by individual.

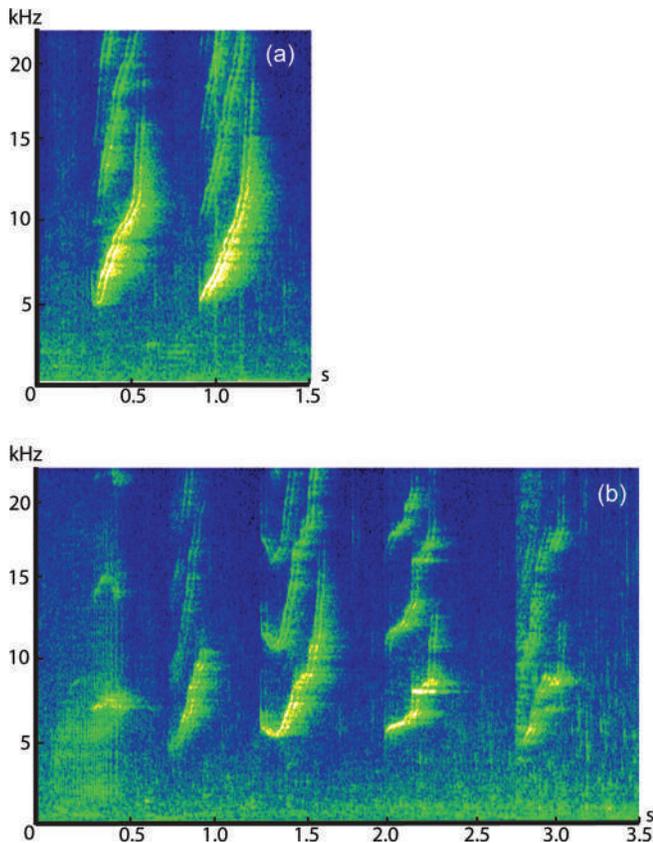


FIG. 5. (Color online) Spectrograms of (a) the stereotyped whistle of BD1 and (b) F13's imitation. BD1 emitted the whistle in pairs stereotypically, but F13 produced variable numbers of whistles in the four sequences collected during the study.

produce cross-socialization, would have been impractical and counter to prevailing guidelines for maintaining cetaceans.

Facility differences did not explain the differences observed. Two of the KW-BD whales were paired with KW whales in the same facility but still showed statistically distinguishable differences, even though they had been held with KW whales for years. There was a gradient across the three KW-BD whales that might have been interpreted as an effect of facility, but this explanation was less plausible than the effects of social association. The gradient ranged from F13, the only KW-BD whale concurrently housed with dolphins, to F2, a whale with a strong allomaternal relationship with another killer whale. Differences in vocalization usage and acoustic features were consistent with the gradient in association.

Previous evidence of call type learning across dialects in juvenile male killer whales suggested an influence of social association (Crance *et al.*, 2014). In addition, motivation for social contact was the most parsimonious explanation for the sea lion-like barks of the orphaned killer whale of Foote *et al.* (2006).

The differences between KW-BD and KW whales were also great enough that idiosyncratic differences among individuals were not a persuasive explanation. KW whales produced few to no click trains and never emitted terminal buzzes, whereas all three of the KW-BD whales produced dolphin-like click trains and terminal buzzes. In addition, all three produced at least twice as many whistles as the KW whales. If usage had simply been a matter of ongoing interactions with dolphins, these behaviors should have disappeared from the repertoires of the two KW-BD whales housed with KW whales. Instead, the trend was most consistent with the hypothesis that KW-BD whales shaped the incidence of clicking and whistling behaviors to be more similar to those of bottlenose dolphin social associates and then retained the behavior to at least some degree over long periods.

Ongoing exposure to dolphins did appear to have an influence, however. F13's whistle rate was highest among the KW-BD subjects, and she produced the lowest proportion of pulsed calls of any whale studied (60%), well below the lowest for any KW subject (88%). She was the only killer whale to produce isolated burst-pulse sounds similar to those of dolphins and the only subject to attempt a dolphin-like stereotyped whistle.

Neither the evidence of shift in click usage nor the evidence of convergence in acoustic features of clicks should be taken to imply presence or absence of functional echolocation in KW or KW-BD subjects. The data collected during the study were not appropriate for this purpose. Under free-ranging conditions, killer whales click frequently while foraging for fish (Ford, 1989; Au *et al.*, 2004). However, clicking can be rare under other conditions (Barrett-Lennard *et al.*, 1996). The data presented here suggest that killer whale clicking is sensitive to social context, irrespective of functional echolocation. More broadly, the proportionate production of click trains and whistles, vocalization categories common to both species, and changes in the statistical properties of click trains were consistent with vocal contextual learning (Janik and Slater, 1997, 2003).

The evidence for vocal contextual learning in odontocetes has been limited and difficult to interpret. Janik and Slater (2003) concluded that sperm whales were capable of contextual vocal learning because temporal features of click trains converged to match group specific-codas (Weilgart and Whitehead, 1997) and because they could match arbitrary human sonar pulse rates (Backus and Schevill, 1966). This conclusion hinges on the argument that sperm whales naturally produce clicks, so changes that made them more similar to codas and sonar pulses did not constitute learning a novel vocalization. However, all sperm whale vocalizations are made up of clicks, and the codas and sonar-like trains in these studies represented a specific temporal template that the sperm whales imitated, which could be interpreted as production rather than contextual learning. A comparable logic would explain F13's development of frequency contours similar to those of bottlenose dolphins as contextual learning because killer whales naturally produce frequency contours. However, this interpretation would not be consistent with other literature that treats the acquisition of new time-frequency contours and temporal patterns as procedural (Richards *et al.*, 1984; Caldwell *et al.*, 1990; Miksis *et al.*, 2002; Foote *et al.*, 2006; Ridgway *et al.*, 2012; DeRuiter *et al.*, 2013; Crance *et al.*, 2014).

Contextual learning should be defined by changes with context in statistical rates of vocalizations recognizably within an animal's repertoire. By this criterion, the KW-BD subjects showed contextual learning because they produced species-typical whistles at rates more similar to those of dolphins. The evidence for contextual use of click trains was less persuasive because KW whales rarely produced click trains unless they encountered unexpected changes in their environment. However, they were capable of producing click trains, and in the same facilities, KW-BD whales produced click trains frequently. Thus, the click train data provided evidence for contextual learning.

F13 provided the best evidence of production learning. After she transferred to Facility 3, she spontaneously imitated a chirp series that facility dolphins had been conditioned to produce. Differences between her chirps and those of the dolphins were of roughly the same magnitude as differences among the dolphins. This similarity could not have emerged from species-typical repertoires because the chirp series were artificially conditioned in the dolphins and not present in F13's spontaneous repertoire at transfer. In addition, F13 produced a few whistle contours that resembled a stereotyped dolphin whistle used by her most common social partner. These results were consistent with previous reports that odontocetes, including young killer whales, can imitate novel heterospecific or artificial signals (Richards *et al.*, 1984; Caldwell *et al.*, 1990; Miksis *et al.*, 2002; Foote *et al.*, 2006; Ridgway *et al.*, 2012; DeRuiter *et al.*, 2013).

Learning did not result from accurate imitation of fine-scale details, particularly in the frequency domain. The evidence from the study was consistent with two possibilities: (1) social or psychological factors made KW-BD whales less likely to produce certain sounds; or (2) whales had difficulty producing some sounds produced by dolphins. For example, it was unclear why KW-BD whistle rates were low (4% at

most), given that dolphins whistled at a rate nearly an order of magnitude higher. Most of the whistles of KW-BD subjects were species-typical killer whale whistles, which differ in timbre, spectral characteristics, and time-frequency pattern from those of bottlenose dolphins. The only exceptions were recorded from F13, who on four occasions produced a whistle similar to the stereotyped whistle used frequently by her most common dolphin companion. F13's imitations provided evidence for difficulty or lack of precision in imitations—they contained abrupt steps in frequency that were not typical of the dolphin's stereotyped whistle.

Other evidence suggested difficulty in producing accurate imitations. F13's chirp series had frequency ranges that were half that of the dolphins' chirps. Click trains of KW-BD whales were distinguished statistically from dolphin click trains on the basis of time-domain features, but only in the whales held with KW, and only in a subset of features.

The strongest tests of vocal plasticity in social animals come from cross-fostering and cross-socializing experiments (e.g., Owren *et al.*, 1992). Salinas-Melgoza and Wright (2012) showed that red-lore Amazon parrots (*Amazona aurocollaris*) made the greatest acoustic changes during the earliest stages of interaction with a new group. Cross-fostering experiments of the type conducted on parrots would not be practical for killer whales under free-ranging conditions, nor would semi-controlled experiments of the type conducted with bottlenose dolphins (Wells, 2003), but adventitious experiments under controlled conditions or when associations change by chance (e.g., Foote *et al.*, 2006) can help determine how social association and vocal plasticity interact to shape killer whale dialects. The question is important because the fates of killer whales in populations reduced or displaced by environmental change will be determined in part by their ability to socialize with new groups, and thus by the factors that control vocal plasticity.

ACKNOWLEDGMENTS

We would like to dedicate this paper to Mike Owren, whose sad death prevented him from seeing the improvements in this paper based on his editorial advice. SeaWorld Animal Training and electronic services personnel assisted with data collection and facilitated audio and video recordings, as did Mike Muraco and his staff at Six Flags Discovery Kingdom. We are grateful to Duncan McGehee and Charles Greenlaw at BAE Systems for inventing an economical and effective method for localizing callers over long periods. Sam Denes prepared the statistical analyses in R. Dr. Judy St. Leger and Dr. Pam Yochem provided valuable comments. We thank our dedicated HSWRI staff and interns, particularly Jennifer Keating, Eri Suzuki, and Caitlin Scully. Study procedures were authorized by SeaWorld and Six Flags Discovery Kingdom. The Hubbs-SeaWorld Research Institute (HSWRI) Animal Care and Use Committee reviewed and approved the research protocols. J.L.C. and W.B.M. received support from the University of San Diego (USD), the Hannon Foundation (J.L.C.), and the Stephen Sullivan Memorial Scholarship Fund (W.B.M.). Both were graduate students in the Department of Marine

and Environmental Studies at USD. The study was also supported by HSWRI and SeaWorld Entertainment.

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