More of the same: Allopatric humpback whale populations share acoustic repertoire

Michelle EH Fournet Corresp., 1, 2, Lauren Jacobsen 3, Christine M Gabriele 4, David K Mellinger 2, Holger Klinck 3

1 Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, United States
2 Cooperative Institute of Marine Resource Studies, Oregon State University and NOAA Pacific Marine Environmental Laboratory, Newport, OR, United States of America
3 Bioacoustics Research Program, Cornell Lab of Ornithology, Cornell University, Ithaca, New York, United States
4 Humpback Whale Monitoring Program, Glacier Bay National Park and Preserve, Gustavus, Alaska, United States

Corresponding Author: Michelle EH Fournet
Email address: michelle.fournet@oregonstate.edu

Background. Humpback whales (Megaptera novaeangliae) are a widespread, vocal baleen whale best known for producing song, a complex, repetitive, geographically distinct acoustic signal sung by males, predominantly in a breeding context. Humpback whales worldwide also produce non-song vocalizations (“calls”) throughout their migratory range, some of which are stable across generations. Methods. We looked for evidence that temporally stable call types are shared by two allopatric humpback whale populations while on their northern hemisphere foraging grounds in order to test the hypothesis that some calls, in strong contrast to song, are innate within the humpback whale acoustic repertoire. Results. Despite being geographically and genetically distinct populations, humpback whales in Southeast Alaska (North Pacific Ocean) share at least five call types with conspecifics in Massachusetts Bay (North Atlantic Ocean). Discussion. This study is the first to identify call types shared by allopatric populations, and provides evidence that some call types may be innate.
More of the same: allopatric humpback whale populations share acoustic repertoire

Michelle E. H. Fournet\textsuperscript{1,2}, Lauren Jacobsen\textsuperscript{3}, Christine M. Gabriele\textsuperscript{4}, David K. Mellinger\textsuperscript{2}, Holger Klinck\textsuperscript{3}

\textsuperscript{1} Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331
\textsuperscript{2} Cooperative Institute for Marine Resources Studies, Oregon State University and NOAA Pacific Marine Environmental Laboratory, Newport, OR, 97365
\textsuperscript{3} Bioacoustics Research Program, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 14850
\textsuperscript{4} Humpback Whale Monitoring Program, Glacier Bay National Park and Preserve, Gustavus, AK 99826

Corresponding author:
Michelle E. H. Fournet\textsuperscript{1,2}

Email Address:
michelle.fournet@gmail.com
Abstract

**Background.** Humpback whales (*Megaptera novaeangliae*) are a widespread, vocal baleen whale best known for producing song, a complex, repetitive, geographically distinct acoustic signal sung by males, predominantly in a breeding context. Humpback whales worldwide also produce non-song vocalizations (“calls”) throughout their migratory range, some of which are stable across generations. **Methods.** We looked for evidence that temporally stable call types are shared by two allopatric humpback whale populations while on their northern hemisphere foraging grounds in order to test the hypothesis that some calls, in strong contrast to song, are innate within the humpback whale acoustic repertoire. **Results.** Despite being geographically and genetically distinct populations, humpback whales in Southeast Alaska (North Pacific Ocean) share at least five call types with conspecífics in Massachusetts Bay (North Atlantic Ocean). **Discussion.** This study is the first to identify call types shared by allopatric populations, and provides evidence that some call types may be innate.

Introduction

The study of acoustic signaling is a valuable tool for investigating animal behavior across a broad range of taxa (Brockelman & Schilling 1984, Gannon 2008, Pijanowski et al. 2011, Clink et al. 2018). Sounds produced by animals can be systematically measured and compared, as can patterns of vocal behavior made in association with critical activities such as breeding, foraging, or socializing. Acoustic monitoring allows for broad-scale observations of animals across space and time and between populations (Mann & Lobel 1998, Cerchio et al. 2001, Risch et al. 2007, Potvin et al. 2011). When coupled with what is known about genetics, population structure, and behavior, acoustic analyses become powerful tools for investigating the factors that shape communication signals.

Drivers of acoustic repertoires vary between taxa and species. While anatomy is a restricting force driving sound production, genetic, neurological, and environmental drivers also influence acoustic repertoires and vocal plasticity. For acoustic communication to be effective, a sound must be detectable within its acoustic habitat and sufficiently convey information to a receiver. As such, acoustic communicators have evolved adaptations to couple the acoustic properties of sounds to the environment in which they are produced in order to meet their signaling needs and
maximize fitness (Slater 1983, Boncoraglio & Saino 2006). As a result, within the repertoire of
most, if not all, sound-producing vertebrates are a collection of innate (i.e., unlearned) calls that
are exercised independently of vocal learning and persist across generations (e.g., Domestic
Fowl Gallus gallus and other species in the order Galliformes (Konishi 1963, Matsunaga &
Okanoya 2009), white-handed gibbons Hylobates lar (Brockelman & Schilling 1984), New
Zealand fur seals Arctocephalus forsteri (Page et al. 2001)). A smaller subset of taxa – most
notably passerine songbirds – exhibit a combination of learned and unlearned vocal signals,
which persist over time within a population (Baker & Jenkins 1987, Vicario 2004, Matsunaga &
Okanoya 2009, Zann 2010). Some mammals including pinnipeds (taxonomic group including
seals and sea lions), and cetacean species (taxonomic group including whales, dolphins, and
porpoises) are also capable of vocal learning as indicated by vocal imitation or improvisation
(Tyack & Sayigh 1997, Poole et al. 2005, Petkov & Jarvis 2012). What is less well described
among mammalian vocal learners, however, is the coupling of stable sound types, which may be
innate, with a dynamically changing repertoire of sound types whose variation appears to be
culturally driven. Cetaceans, and specifically humpback whales (Megaptera novaeangliae), may
be the best example of a taxon which exhibits this coupling of highly stable calls types and
dynamically shifting vocal behaviors (Payne & Payne 1985, Tyack & Sayigh 1997, Rekdahl et
al. 2013, Fournet et al. 2015a, Fournet 2018).

Humpback whales are a migratory baleen whale with a cosmopolitan distribution. Generally,
humpback whales migrate between low-latitude breeding and calving grounds and high-latitude
foraging grounds (Clapham et al. 1999). Their vocal behaviors are geographically and seasonally
stratified. Primarily on breeding grounds and migratory corridors, but also to a lesser extent on
foraging grounds, male humpback whales produce a long elaborate, and repetitive vocal display
known as ‘song’, (Payne & McVay, 1971; Gabriele & Frankel, 2002; Stimpert et al., 2012;
Dunlop & Noad, 2016; Herman, 2017). Songs are highly structured and acoustically complex,
and are culturally transmitted between males within a single breeding region (Cerchio et al.
2001, Mercado et al. 2005, Herman et al. 2013, Herman 2017). Song structure changes rapidly
over time (1-2 years) (Payne & Payne 1985, Noad et al. 2000, Parsonset al. 2008). Further,
geographic variation in song between regions is typical (Winn et al. 1981, Cerchio et al. 2001,
Parsons et al. 2008), with song sharing only occurring between regions that share individuals (Cerchio et al. 2001, Mercado et al. 2005, Garland et al. 2015b, Herman 2017).

Humpback whales of both sexes and across the migratory range also produce a series of vocalizations (“calls”) independently of song (Silber 1986, Dunlop et al. 2008, Stimpert et al. 2011). Calls occur in isolation or in short bouts and occasionally appear as song units (Rekdahl et al. 2013, 2015). Call use varies based on social and behavioral context; some calls facilitate intra-group interactions, while other calls are specific to foraging contexts (Stimpert et al. 2007, Dunlop et al. 2008, Wild & Gabriele 2014, Fournet et al. 2018). Unlike song, many calls are stable over time. The most commonly produced call types in the east Australian migratory corridor, making up 64% of the call detected in one study, are stable over 7-11 year time periods (Rekdahl et al. 2013), while in Southeast Alaska, at least 16 call types, including all described call types to date, persist in the call repertoire for decades and across generations (Fournet et al. 2015a, Fournet 2018).

Call longevity across generations is an indication that some call types may be fixed within the humpback whale repertoire. Identifying the same stable call types in other, unrelated populations would provide further evidence that humpback whales may be anatomically or behaviorally predisposed toward the production of certain sounds. Qualitative comparisons have been made of calls produced in the North Pacific (Southeast Alaska, USA), South Pacific (East Australia), North Atlantic (Massachusetts Bay, USA) and South Atlantic (Coastal Angola, Africa) with the general agreement that global humpback whale populations produce some similar call types (Dunlop et al. 2007, Stimpert et al. 2011, Fournet, et al. 2015, Rekdahl et al. 2016), but no formal comparison of call types between populations has been thus far attempted.

To test the hypothesis that some calls types are inherent to humpback whales, we looked for evidence of shared call types in the call repertoire of two allopatric humpback whale populations on their northern latitude foraging grounds, one in the North Atlantic and one in the North Pacific. Based on genetic analyses it is estimated that global humpback whale populations last shared a maternal ancestor in the Miocene, approximately 5 Mya, and that discrete lineages split 2-3 Mya (Baker et al. 1993). In the northern hemisphere, humpback whales in the Atlantic and
Pacific Ocean are geographically separated by the North American continent and are genetically isolated from one another (Valsecchi et al. 1997, McComb et al. 2003). Cultural exchange of acoustic signals between the two populations is extremely unlikely based on this geographic barrier and known migratory patterns. Thus, a shared acoustic repertoire would indicate that individual signals may be fixed within the species and conserved with time, rather than socially learned. We hypothesized that call types that are stable across multiple generations on a North Pacific foraging ground would also be present in the humpback whale call repertoire on a North Atlantic foraging ground.

Methods

Data collection

We compiled acoustic datasets from two humpback whale foraging grounds in the North Pacific and North Atlantic. Acoustic data from Southeast Alaska (SEAK: North Pacific) were collected using passive acoustic recording devices during summer months (June-August) in Frederick Sound in 1976 and Glacier Bay National Park and Preserve (GBNPP) in 2007, and 2008. Acoustic recordings were also collected using passive acoustic recording devices deployed during summer months in Massachusetts Bay (MB; North Atlantic) in 2008 (Figure 1, Table 1). Acoustic recordings from Frederick Sound, SEAK were opportunistically collected with a dip hydrophone from a drifting vessel and were of variable duration (32-94 minutes). Acoustic recordings from GBNPP made in 2007 and 2008 were collected from a cabled hydrophone in Bartlett Cove (Figure 1) with a 30-seconds-per-hour recording cycle (Wild & Gabriele 2014). Data from GBNPP were reviewed by U.S. Navy acousticians to characterize the content of each sound sample. Data from MB were collected as part of a long-term monitoring project in that region (see also Hatch et al. 2012). Recordings were made using an array of marine autonomous recording units (MARUs; Calupca et al. 2000; Table 1). Research analysts from the Bioacoustics Research Program at Cornell Laboratory of Ornithology reviewed array recordings and noted the presence or absence of humpback whale calls on each element. We randomly subset 60 hours of two-channel acoustic data from the array for analysis (Figure 1). Sound samples from both regions were analyzed only if they were known to contain humpback whale calls.

Data Processing and Analysis
Recordings from SEAK were originally sampled at 44.1 kHz and were resampled at a rate of 2 kHz for consistency with data from MB (Table 1); all recordings were made with 16 bit resolution. Once resampled, recordings were comparable, though not completely equivalent. Differences in recording equipment and conditions may manifest in extracted feature values; however when paired with robust call inclusion criteria and our choice of feature extraction methodology (see below) call classification is robust to these differences. Spectrograms of acoustic recordings were created with Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY) using an FFT length of 1046, a 30 s window length, Hann window, 75% overlap, for a frequency resolution of 2.75 Hz and constrained to the 10 Hz to 1 kHz frequency range to facilitate analysis. Recordings were manually reviewed by experienced observers familiar with the humpback whale call repertoire. All calls were annotated in the time-frequency domain and salient acoustic features were extracted for quantitative classification in Raven Pro (Table 1). Aggregate entropy was also extracted for each sound (Table 1). In some cases differences in aggregate entropy reflect variation in recording conditions; however, where considerable differences in acoustic structure exist (e.g. between call types) aggregate entropy is one of the few acoustic measurements capable of discriminating between structurally ‘simple’ calls (see droplets in Figure 2b) and structurally ‘complex’ calls (see whups Figure 2d). For this reason when recording conditions vary, aggregate entropy is still relevant for discriminating between-call type differences, which are generally more contrasting. In this study data exploration did not reveal any significant differences in aggregate entropy related to recording location or year. For harmonic sounds, measurements of the start- and end-frequencies were made on the fundamental frequency. For amplitude-modulated sounds containing a broadband component, measurements were made on the lowest-frequency component of the call (Dunlop et al. 2007, Rekdahl et al. 2013). Frequency parameters were log-transformed to account for the mammalian perception of pitch (Table 2) (Richardson et al., 1995; Dunlop et al., 2007; Fournet et al., 2015b); although humpback pitch perception has not been studied experimentally, humpback ear morphology suggests that their sound reception is, like other mammals, approximately logarithmic (Southall et al., 2007). Time-frequency parameters were input into a Principal Component Analysis (PCA) in order to aggregate correlated variables for classification and comparative analyses (R, psych package). A varimax rotation was applied (Table 2) to maximize loading and facilitate variable interpretation.
By pairing PCA values with traditional acoustic measurements during classification analyses we account for the broad structure of the call (e.g. broadband and high frequency vs. narrowband and high frequency) as well as the fine-scale acoustic features. Boxplots (median, first, and third quartile PCA values) were generated in R using the ggplot2 package (Wickam, 2016) to qualitatively compare differences in call structure between ocean basins.

Signal-to-noise ratios (SNRs) were calculated for each acoustic sample by measuring the in-band power contained in a one-second sound sample directly preceding each call; this value was then subtracted from the in-band power measured of the call of interest to get the band-limited SNR value. Calls in this study were only included if they had a SNR of 10 dB or higher (Dunlop et al. 2007, Rekdahl et al. 2016).

Using the existing SEAK call catalog as a reference, each acoustic sample was assigned an *a priori* call type based on aural and visual call features. Because the goal of this study was to investigate the potential for call types to be fixed within this species, only call types that persist across generational timescales that could be detected given a 2 kHz sampling rate were included in this study; this included droplet, growl, swop, teepee, whup, and feeding calls (Fournet et al. 2015a, Fournet 2018). Droplets, swops, and teepees are short-duration pulsed calls that typically occur in short repeated sequences. Growls and whups, by contrast, are harmonic and amplitude-modulated calls that are generally not repeated (Wild and Gabriele, 2014, Fournet et al. 2015a, Fournet 2018). Feeding calls are stereotyped highly-tonal, low-complexity calls that have been closely associated with herring foraging in SEAK humpback whales (Cerchio and Dalheim 2001, Fournet et al. 2018b). Acoustic samples that were qualitatively different than previously described call types were classified as ‘unknown’ and no further attempts for classification were made. Initial data exploration found no significant differences in acoustic parameters of calls recorded in GBNPP and calls recorded in Frederick Sound; calls from SEAK were pooled for analysis.

Quantitative classification methods were identical to those used by Fournet (2018a), with the exception that all predictor variables were extracted in Raven Pro. For consistency with other
humpback whale call classification studies, calls were classified through the use of a Classification and Regression Tree analysis (CART, rPart package; R Core Development Team, 2012) and a random forest analysis (randomForest package; Liaw and Weiner, 2002) using the methodologies described by Rekdahl et al. (2013, 2016). The combination of CART and random forest analyses to validate human call type assignment has emerged as the preferable method for classification of humpback calls (as well as other cetaceans; Garland et al. 2015a). CART analyses are robust to outliers, non-normal and non-independent data, and random forest analyses improves accuracy using a bootstrapping method to generate a level of uncertainty for each classification tree, rather than a single classification tree (Breiman et al. 1984, Rekdahl et al. 2013, 2016). In the CART analysis the Gini index was used to assess the “goodness-of-split” for each node in the tree. All variables were considered independently and ranked, and the splitting variable that minimized splitting error was selected (Beiman et al. 1984, Rekdahl et al. 2013, 2016). Terminal nodes were set to have a minimum sample size of ten. Trees were overgrown and then pruned upward until reaching the tree with the lowest misclassification rate (Breiman et al. 1984). A total of 1,000 trees were grown for the random forest analysis. Predictor variables included salient acoustic features as well as two rotated principal components (PC) that aggregated correlated acoustic variables (Dunlop et al. 2007); a detailed description of predictor variables can be found in Table 2. Quantitative classification assignments were compared to a priori call type assignments to validate observer classification. Major discrepancies in call type assignment were re-reviewed by at least two observers. Calls were excluded if observers were not in agreement. If observers were in agreement about call type assignment than the a priori classification was deemed ‘correct’. All analyses were conducted in R version 3.3.3 (R, 2013).

To assess differences in acoustic parameters between calls from MB and SEAK populations, we summarized and compared PC values for all call types that exhibited stability between regions. Comparative analyses were made based on a priori classification. Humpback whales in both SEAK and MB exhibit seasonal movements throughout foraging grounds during summer months (Baker, 1985, Straley et al. 1993, Weinrich, 1998, Payne et al., 1986, Schilling et al., 1992), reducing the likelihood of their repeated acoustic capture on hydrophones, which have a finite listening range. Additionally, a random subset of acoustic data spanning summer months in MB was selected for analysis in order to reduce the likelihood of repeated capture of individuals.
Also, the temporal breadth of recordings made in in SEAK (Table 1) make the probability of
documenting only a small subset of individuals from this region unlikely. However, because data
were collected passively without concomitant visual observations the number of vocalizing
individuals is unknown. For this reason the independence of each data point cannot be confirmed
and statistical tests pertaining to population level differences are inappropriate.

Results
A total of 411 sounds fitting the inclusion criteria were classified to one of six known call types
(droplets, growls, feeding calls, swops, teepees, whups; Fournet et al. 2015b); 191 calls were
collected across 10 recording days from Massachusetts Bay (MB), and 220 calls were collected
across 76 sample days from Southeast Alaska (SEAK; Table 1, Table 3). Drops, growls, swops,
teepees, and whups were found in both populations (Figure 2, Table 3); feeding calls were
detected only in SEAK. A Bartlett’s Test of Sphericity
indicated that data was suitable for factorial analysis ($\chi^2 = 18106.78$, d.f. = 55, p < 0.00001); this
was confirmed by a Kaiser-Meyer-Olkin value of 0.61. The first rotated component (PC1)
corresponded most closely to aggregate entropy, bandwidth, and upper frequency (proportion
variance explained = 0.51), meaning that as PC1 increases, the calls grow more complex, grow
broader-band, and extend to higher frequencies. The second rotated component (PC2)
corresponded most closely to lower frequency, start frequency, and peak frequency (proportion
variance explained = 0.49), meaning that as PC2 increases, calls grow higher in pitch overall, but
not necessarily more broadband or complex. Neither component was strongly affiliated with
duration or bout in this analysis, meaning that the PC variables in this analysis do not represent
temporal variability.

CART call type assignment and \textit{a priori} call type assignment were in agreement 82% of the time
(n = 335/411, Table 4). In descending order of importance, splitting variables for CART
classification were bandwidth, bout, center frequency, duration, end frequency, aggregate
entropy, lower frequency, and PC1. The random forest analysis correctly classified most of the
calls (out-of-bag error rate = 23%). The variables most important for splitting decisions in the
random forest analysis in were bout, end frequency, duration, aggregate entropy, lower
frequency, PC1, PC2, and frequency trend, in descending order of importance. Whups were the
most commonly misclassified calls (Table 4); in the CART analysis whups were mistaken for
growls 38% of the time (n = 22). Observers validated call type assignment for most whup calls
(95%, n = 57); three calls were omitted due to classification incongruity.

PC1 values were higher in SEAK than MB for all call types except for growls, indicating that
calls from SEAK were generally broader band and exhibited higher levels of complexity (Table
3, Figure 3). PC2 values were higher in SEAK than MB for droplet and teepee calls (Table 3,
Figure 4), indicating that calls from SEAK were generally higher pitched than calls from MB.

Discussion
This is the first study to describe call types shared by allopatric humpback whale populations.
Evidence that temporally stable call types are shared between Southeast Alaska (SEAK) and
Massachusetts Bay (MB) humpback whale populations supports the hypothesis that a portion of
the call repertoire may be fixed in this species.

In SEAK there are six call types that are stable over generational time (Fournet 2015b) that have
average bandwidths between 10 - 1,000 Hz: droplets, growls, swops, teepees, whups, and
feeding calls. Misclassification was low for all call types, except for whups, which were
commonly classified as growls. Misclassification of these call types is unsurprising, as the only
distinguishing acoustic feature between growls and whups is a terminal upsweep, which
attenuates with distance and is not adequately encompassed by traditional acoustic parameters
(Figure 2) (Fournet et al. 2015b). The humpback whale call repertoire has been described as an
acoustic continuum, where graded signals are common (Rekdahl et al. 2013, Fournet et al.
2015b). The delineation between growls and whups is not discrete, and it is currently unknown
whether whups and growls are functionally interchangeable. Methods for either classifying
graded signals or more broadly aggregating them according to their functional roles merits future
investigation.

Within-call variation, related to individual anatomy, behavioral or environmental context can be
found within most if not all vertebrate vocalizers, and does not contradict placement into call
classes or types (Ford 1991, Tyack et al. 1997, Deecke et al. 2000, Tibbets et al. 2007, Rekdahl
et al. 2013). In this study, despite otherwise high classification agreement, there were some differences in call type parameters between populations. The increased PC1 values found in SEAK versus MB may be recording artifacts. The ambient sound conditions in SEAK are significantly different than MB (Kipple & Gabriele 2003, Hatch et al. 2008, Haver et al. 2018). Recordings from Frederick Sound were made in the absence of vessel noise, and recordings made in GBNPP were made in the presence of limited vessel traffic. By contrast, the hydrophones in MB were located within a shipping lane that services Boston Harbor, which is among the busiest harbors on the North American east coast. For this reason, vessel noise was recorded simultaneously with almost all calls recorded in MB (Figure 2). Overlapping ambient sounds – including vessel noise, which is common throughout the 10 – 1,000 Hz band (Wenz 1962) – may have masked fine-scale acoustic features, resulting in decreased aggregate entropy measurements in MB calls. Similarly, vessel noise in MB may have masked upper-frequency portions of calls, which contain less energy and attenuate faster and are thus more easily obscured by overlapping ambient sound. Systematic differences in frequency between droplets and teepees in SEAK vs. MB (Table 3) may be related to factors such as motivational state (Rehn et al. 2011, Dunlop 2017), body size (May-Collado et al. 2007), and/or ambient noise (Parks et al. 2007, Di’Iorio & Clark 2010, Parks et al. 2016), but a dedicated research effort that includes direct observation and identification of individuals would be required to address this question.

With one exception, call types of interest from SEAK were also found in MB. The notable exception was the SEAK feeding call. Feeding calls are highly stereotyped, tonal calls, with a fundamental frequency of ~500 Hz that occur when humpback whales in Southeast Alaska forage on Pacific herring (Clupea palisii) (D’Vincent et al. 1985, Sharpe 2001, Fournet et al. 2018). Herring are a primary food source for humpback whales in Southeast Alaska (Krieger & Wing 1984, D’Vincent et al. 1985, Dolphin 1988), whereas in MB humpback whales feed primarily on sand lance (Ammodytes spp.), a calorie-dense prey species that burrows in the sandy substrate (Overholtz & Nicolas 1979, Hain et al. 1995, Friedlaender et al. 2009). The absence of feeding calls in MB may be attributed to their focus on forage species other than herring.
Droplets, growls, swops, teepees, and whups were present in the call repertoire of both humpback whale populations. Evidence of the same calls in allopatric populations supports the hypothesis that a portion of the humpback whale call repertoire is innate. Many non-passerine bird species such as doves (Streptopelia sp.) produce highly stereotyped calls instinctively (Lade & Thorpe 1964), and as a result allopatric dove populations of the same species, even those separated by great distances, show no significant difference in call types (de Kort et al. 2002). Ornate chorus frogs (Microhyla fissipes) produce advertisement calls independently of vocal learning that are aurally indistinguishable between geographic regions, and that vary only minutely with genetic distance (Lee et al. 2016). Genetic predetermination of calls is common across taxa, including zebra finches (Taeniopygia guttata; Forstmeier et al. 2009), fur seals (Antarctic, Arctocephalus gazella, subantarctic, A. tropicalis, and New Zealand, A. forsteri; Page et al. 2001), and Spheniscus penguins (Thumser & Ficken 1998). Call type stereotypy in these species is generally multi-generational and geographically widespread. In humpback whales, identifying call types that are multi-generational, and persist in geographically and genetically discrete populations provides strong evidence that these call types are innate.

If the call types described in this study are innate to humpback whale worldwide, as we hypothesize, then it should be possible to build an automated acoustic detector that could be run on datasets from across ocean basins and years to confirm the presence of humpback whales at previously unknown regions or times. The ability to confidently credit particular vocalizations to humpback whales in the absence of visual confirmation allows for broader spatial and temporal monitoring with significantly lower effort and cost (see also Stimpert et al. 2011).

For calls to be conserved within the call repertoire of genetically and geographically discrete populations is an indication that they play an important role in humpback whale life history by increasing individual fitness in some capacity. It has been proposed that in Southeast Alaska the whup call serves a contact function (Wild & Gabriele 2014), and the analogous “wop” call of east Australia may facilitate communication between cows and calves (Dunlop et al. 2008). There is also evidence that droplets, swops, and teepees are used for close range communication on foraging grounds (Fournet 2014), and similar pulsed calls may facilitate affiliation or disaffiliation in groups during migration (Dunlop et al, 2008). These broad contextual
descriptions, suggest that these calls serve a vital function or functions. The fixed nature of calls stands in marked contrast to humpback whale song, which is geographically discrete, changes rapidly, and is culturally transmitted rather than innate (Payne & Payne 1985, Noad et al. 2000, Cerchio et al. 2001). Thus it seems that the humpback whale vocal repertoire is composed of both fixed and adaptable calls. Dedicated research pairing the call types described in this study with behaviors and social context will further the understanding the role of calls in the acoustic ecology of humpback whales.

Conclusions

This study demonstrates that some humpback whale call types are shared between geographically discrete northern latitude foraging grounds. This feature lend support to the hypothesis that some calls may be innate, and in strong contrast to song, are not culturally transmitted. Natural next steps include a global comparison of call repertoires between allopatric populations and across the migratory range, with particular attention paid to change or stability at various temporal and geographic scales.

Acknowledgements

The authors wish to acknowledge Dr. Roger Payne for the use of the recordings from Southeast Alaska in 1976. We thank David Culp for data processing support, and Katherine Indeck for statistical support. We also wish to thank the National Park Service for its long term commitment to acoustic monitoring in Glacier Bay National Park, and to the Cornell Bioacoustics Research Program for use of the data from Massachusetts Bay. This is PMEL contribution number 4784.
Works Cited

Baker AJ, Jenkins PF (1987) Founder effect and cultural evolution of songs in an isolated population of chaffinches, *Fringilla coelebs*, in the Chatham Islands. Anim Behav 35:1793–1803

Baker CS, Herman LM, Perry A, Lawton WS, Straley JM, Straley JH (1985) Population Characteristics and Migration of Summer and Late-Season Humpback Whales *Megaptera novaeangliae* in Southeastern Alaska. Mar Mammal Sci 1:304–323

Baker CS, Perry a, Bannister JL, Weinrich MT, Abernethy RB, Calambokidis J, Lien J, Lambertsen RH, Ramírez JU, Vasquez O (1993) Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. Proc Natl Acad Sci U S A 90:8239–8243

Boncoraglio G, Saino N. (2007) Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Func Ecol 21:134-42.

Breiman L, Friedman JH, Olshen RA, and Stone CJ (1984) *Classification and regression trees.* Wadsworth International Group, Belmont, CA

Brockelman WY, Schilling D (1984) Inheritance of stereotyped gibbon calls. Nature 312:634–636

Calupca TA, Fristrup KM, Clark CW (2000) A compact digital recording system for autonomous bioacoustic monitoring. J Acoust Soc Am 108:2582–2582

Cerchio S, Dahlheim M (2001) Variation in feeding vocalizations of humpback whales *Megaptera novaeangliae* from Southeast Alaska. Bioacoustics 11:277–295

Cerchio S, Jacobsen JK, Norris TF (2001) Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. Anim Behav 62:313–329

Clapham PJ, Mead JG, Gray M (1999) *Megaptera novaeangliae.* Mamm Species:1–9

Clink DJ, Crofoot MC, Marshall AJ (2018) Application of a semi-automated vocal fingerprinting approach to monitor Bornean gibbon females in an experimentally fragmented landscape in Sabah, Malaysia. Bioacoustics DOI: [10.1080/09524622.2018.1426042](10.1080/09524622.2018.1426042)

D’Vincent CG, Nilson RN, Hanna RE (1985) Vocalization and coordinated feeding behavior of the humpback whale in Southeastern Alaska. Sci Reports Whales Res Inst 36:41–47
DeeckeVB, Ford JKB, and Spong P. (2000) Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. Anim. Behav. 40: 629–638.

Di’Orio L Clark CW (2010) Exposure to seismic survey alters blue whale acoustic communication. Biol Lett 6:334–335

Dolphin WF (1988) Foraging dive patterns of humpback whales, *Megaptera novaeangliae*, in southeast Alaska: a cost-benefit analysis. Can J Zool 66:2432–2441

Doyle LR, McCowan B, Hanser SF, Chyba C, Bucci T, Blue JE (2008) Applicability of Information Theory to the Quantification of Responses to Anthropogenic Noise by Southeast Alaskan Humpback Whales. Entropy 10:33–46

Dunlop RA (2016) The effect of vessel noise on humpback whale, *Megaptera novaeangliae*, communication behaviour. Anim Behav 111:13–21

Dunlop RA (2017) Potential motivational information encoded within humpback whale non-song vocal sounds. J Acoust Soc Am 141:2204-2213

Dunlop RA, Cato DH, Noad MJ (2008) Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*). Mar Mammal Sci 24:613–629

Dunlop RA, Noad MJ (2016) The “risky” business of singing: tactical use of song during joining by male humpback whales. Behav Ecol Sociobiol 70:2149–2160

Dunlop RA, Noad MJ, Cato DH, Stokes D (2007) The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*). J Acoust Soc Am 122:2893–2905

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can. J. Zool. 69, 1454–1483

Forstmeier W, Burger C, Temnow K, Derégnaucourt S (2009) The genetic basis of zebra finch vocalizations. Evolution 63:2114–2130

Fournet M (2014) Social calling behavior of Southeast Alaskan humpback whales (*Megaptera novaeangliae*): classification and context. Master's Thesis, Oregon State University

Fournet MEH (2018a) Humpback whale (*Megaptera novaeangliae*) calling behavior in Southeast Alaska: a study in acoustic ecology and noise. PhD Dissertation, Oregon State University. DOI: 10.13140/RG.2.2.35810.43200

Fournet MEH, Culp D, Gabriele CM, Sharpe FA, Payne RS, Mellinger DK, Klinck H (2015a) Temporal stability of non-song vocalizations in North Pacific humpback whales (*Megaptera novaeangliae*) at the decadal scale. 21st Biennial Conference on the Biology of Marine
Mammals, San Francisco. San Francisco, CA

Fournet MEH, Gabriele CM, Sharpe F, Strailey JM, Szabo A (2018b) Feeding calls produced by solitary humpback whales. Mar Mammal Sci 1–15

Fournet MEH, Szabo A, Mellinger DK (2015b) Repertoire and classification of non-song calls in Southeast Alaskan humpback whales (Megaptera novaeangliae). J Acoust Soc Am 137:1–10

Friedlaender AS, Hazen EL, Nowacek DP, Halpin PN, Ware C, Weinrich MT, Hurst T, Wiley D (2009) Diel changes in humpback whale Megaptera novaeangliae feeding behavior in response to sand lance Ammodytes spp. behavior and distribution. Mar Ecol Prog Ser 395:91–100

Gabriele C, Frankel A (2002) The Occurrence and Significance of Humpback Whale Songs in Glacier Bay, Southeastern Alaska. Arct Res United States 16:42–47

Gannon DP (2008) Passive Acoustic Techniques in Fisheries Science: A Review and Prospectus. Trans Am Fish Soc 137:638–656

Garland EC, Castellote M, and Berchok CL (2015a) Beluga whale (Delphinapterus leucas) vocalizations and call classification from the eastern Beaufort Sea population. J. Acoust. Soc. Am. 137: 3054–3067

Garland EC, Goldizen AW, Lilley MS, Rekdahl ML, Garrigue C, Constantine R, Hauser ND, Poole MM, Robbins J, Noad MJ (2015b) Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. Conserv Biol 29:1198–1207

Hain JHW, Ellis SL, Kenney RD, Clapham PJ, Gray BK, Weinrich MT, Babb IG (1995) Apparent Bottom Feeding by Humpback-Whales on Stellwagen Bank. Mar Mammal Sci 11:464–479

Hatch LT, Clark CW, Van Parijs SM, Frankel AS, Ponirakis D (2012) Quantifying loss of acoustic communication space for right whales in and around a U. S. National Marine Sanctuary. Conserv Biol 26:983-994

Hatch L, Clark C, Merrick R, Parijs S Van, Ponirakis D, Schwehr K, Thompson M, Wiley D (2008) Characterizing the Relative Contributions of Large Vessels to Total Ocean Noise Fields: A Case Study Using the Gerry E. Studds Stellwagen Bank National Marine Sanctuary. Environ Manage 42:735–752
Haver SM, Gedamke J, Hatch LT, Dziak RP, Parijs S Van, McKenna MF, Barlow J, Berchok C, DiDonato E, Hanson B, Haxel J, Holt M, Lipski D, Matsumoto H, Meinig C, Mellinger DK, Moore SE, Oleson EM, Soldevilla MS, Klinck H (2018) Monitoring long-term soundscape trends in U.S. Waters: The NOAA/NPS Ocean Noise Reference Station Network. Mar Policy 90:6–13

Herman LM (2017) The multiple functions of male song within the humpback whale (Megaptera novaeangliae) mating system: review, evaluation, and synthesis. Biol Rev 92:1795–1818

Herman LM, Pack AA, Spitz SS, Herman EYK, Rose K, Hakala S, Deakos MH (2013) Humpback whale song: Who sings? Behav Ecol Sociobiol 67:1653–1663

Konishi M (1963) The Role of Auditory Feedback in the Vocal Behavior of the Domestic Fowl. Ethology 20:349–367

Kipple B, Gabriele C (2003) Glacier Bay underwater noise—2000 through 2002: Report to Glacier Bay National Park Tech Rep NSWCCD-71-TR-2004/521, Naval Surface Warfare Center, Bremerton, WA

Kort SR de, Hartog PM den, Cate C ten (2002) Diverge or merge? The effect of sympatric occurrence on the territorial vocalizations of the vinaceous dove Streptopelia vinacea and the ring-necked dove S. capicola. J Avian Biol 33:150–158

Krieger KJ, Wing BL (1984) Hydroacoustic surveys and identification of humpback whale forage in Glacier Bay, Stephens Passage, and Frederick Sound, southeastern Alaska, summer 1983. NOAA Tech Memo NMFS-F/NWC-66 60p 1984:66

Lade BI, Thorpe WH (1964) Dove songs as innately coded patterns of specific behaviour. Nature 202:366–368

Lee KH, Shaner PJL, Lin YP, Lin SM (2016) Geographic variation in advertisement calls of a Microhylid frog - testing the role of drift and ecology. Ecol Evol 6:3289–3298

Mann DA, Lobel PS (1998) Acoustic behavior of the damselfish Dascyllus albisella: Behavioral and geographic variation. Environ Biol Fishes 51:421–428

Mann DA, Popper AN, Wilson B (2005) Pacific herring hearing does not include ultrasound. Biol Lett 1:158–161

Matsunaga E, Okanoya K (2009) Evolution and diversity in avian vocal system: An Evo-Devo model from the morphological and behavioral perspectives. Dev Growth Differ 51:355–367

May-Collado LJ, Agnarsson I, Wartzok D (2007) Reexamining the relationship between body
size and tonal signals frequency in whales: A comparative approach using a novel phylogeny. Mar Mammal Sci 23:524–552

McComb K, Reby D, Baker L, Moss C, Sayialel S (2003) Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav 65:317–329

Mercado E, Herman LM, Pack AA (2005) Song copying by humpback whales: Themes and variations. Anim Cogn 8:93–102

Noad MJ, Cato DH, Bryden MM, Jenner M-N, Jenner KCS (2000) Cultural revolution in whale songs. Nature 408:537–537

Overholtz WJ, Nicolas JR (1979) Apparent feeding by the fin whale, Balaenoptera physalus, and humpback whale, Megaptera novaeangliae, on the American sand lance, Ammodytes americanus, in the northwest Atlantic. Fish Bull 77:285–287

Page B, Goldsworthy SD, Hindell MA (2001) Vocal traits of hybrid fur seals: intermediate to their parental species. Anim Behav 61:959–967

Parks SE, Clark CW, Tyack PL (2007) Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. J Acoust Soc Am 122:3725–3731

Parks SE, Cusano DA, Bocconcelli A, Friedlaender AS, and Wiley DN (2016). Noise impacts on social sound production by foraging humpback whales. Proc of Meet on Acoust 27: 010009

Parsons ECM, Wright AJ, Gore MA (2008) The nature of humpback whale (Megaptera novaeangliae) song. J Mar Anim Their Ecol 1:22–31

Payne RS, McVay S (1971) Songs of humpback whales. Science 173:585–97

Payne K, Payne R (1985) Large Scale Changes over 19 Years in Songs of Humpback Whales in Bermuda. Ethology 68:89–114

Payne PM, Nicolas JR, O'brien L, and Powers KD (1986) The distribution of the humpback whale, Megaptera novaeangliae, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, Ammodytes americanu. Fish Bul 84:271-277

Petkov CI, Jarvis ED (2012) Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. Front Evol Neurosci 4:12

Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A, Krause BL, Napoletano BM, Gage SH, Pieretti N (2011) Soundscape Ecology: The Science of Sound in the Landscape.
Poole JH, Tyack PL, Stoeger-Horwath AS, Watwood S (2005) Animal behaviour: Elephants are capable of vocal learning. Nature 434:455–456

Potvin DA, Parris KM, Mulder RA (2011) Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (Zosterops lateralis). Proc Biol Sci 278:2464–9

Rehn N, Filatova O, Durban J, Foote A (2011) Cross-cultural and cross-ecotype production of a killer whale “excitement” call suggests universality. Naturwissenschaften 98:1–6

Rekdahl ML, Dunlop RA, Goldizen AW, Garland EC, Biassoni N, Miller P, Noad MJ (2015) Non-song social call bouts of migrating humpback whales. J Acoust Soc Am 137:3042–3053

Rekdahl ML, Dunlop RA, Noad MJ, Goldizen AW (2013) Temporal stability and change in the social call repertoire of migrating humpback whales. J Acoust Soc Am 133:1785–95

Rekdahl M, Tisch C, Cerchio S, Rosenbaum H (2016) Common nonsong social calls of humpback whales (Megaptera novaeangliae) recorded off northern Angola, southern Africa. Mar Mammal Sci 33:365–375

Richardson WJ, Greene CRJ, Malme CI, Thompson DH (1995) Marine Mammals and Noise. Academic Press, New York

Risch D, Clark CW, Corkeron PJ, Elepfandt A, Kovacs KM, Lydersen C, Stirling I, Parijs SM Van (2007) Vocalizations of male bearded seals, Erignathus barbatus: Classification And Geographical Variation. Anim Behav 73:747–762

Schilling MR, Seipt I, Weinrich MT, Frohock SE, Kuhlberg AK, and Clapham PJ. (1992) Behavior of individually identified sei whales (Balaenoptera borealis) during an episodic influx into the southern Gulf of Maine in 1986. Fish Bull 90:749-755

Sharpe FA (2001) Social foraging of the southeast Alaskan humpback whale, Megaptera novaeangliae. PhD dissertation, Simon Fraser University

Silber GK (1986) The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (Megaptera novaeangliae). Can J Zool 64:2075–2080

Slater PJB. (1983) The study of communication. Animal Behaviour, 2:9-43

Southall BL, Bowles A E, Ellison WT, Finneran JJ, Gentry RL, Greene Jr CR, Kastak, D, Ketten DR, Miller JH, Nachtigall PE and Richardson WJ (2007) Overview. Aquatic
mammals, 33: 411-414.

Stimpert AK, Au WWL, Parks SE, Hurst T, Wiley DN (2011) Common humpback whale
(Megaptera novaeangliae) sound types for passive acoustic monitoring. J Acoust Soc Am
129:476–482

Stimpert AK, Peavey LE, Friedlaender AS, Nowacek DP (2012) Humpback Whale Song and
Foraging Behavior on an Antarctic Feeding Ground. PLoS One 7:e51214

Stimpert AK, Wiley DN, Au WWL, Johnson MP, Arsenault R (2007) “Megapclicks”: acoustic
click trains and buzzes produced during night-time foraging of humpback whales
(Megaptera novaeangliae). Biol Lett 3:467–470

Straley JM, Gabriele C, Baker C (1993) Seasonal Characteristics of Humpback Whales
(Megaptera novaeangliae) in Southeastern Alaska. Proceeding Third Glacier Bay Sci
Symp. 229–238

Tibbets EA, Dale J (2007) Individual recognition: it is good to be different. Trends in Ecol. Evo.
22:525–537

Thumser NN, Ficken MS (1998) A comparison of the vocal repertoires of captive Spheniscus
penguins. Mar Ornithol 26:40–48

Tyack P, Sayigh L (1997) Vocal learning in cetaceans. In: Social influences on vocal
development. Elsevier , New York

Valsecchi E, Palsboll P, Hale P, Glockner-Ferrari D, Ferrari M, Clapham P, Larsen F, Mattila D,
Sears R, Sigurjónsson J, Brown M, Corkeron P, Amos B (1997) Microsatellite genetic
disrances between oceanic populations of the humpback whale (Megaptera novaeangliae).
14:355–362

Vicario DS (2004) Using learned calls to study sensory-motor integration in songbirds. Ann N Y
Acad Sci 1016:246–262

Weinrich M. (1998) Early experience in habitat choice by humpback whales (Megaptera
novaeangliae). J of Mamm 79:163-70

Wenz GM (1962) Acoustic Ambient Noise in the Ocean: Spectra and Sources. J Acoust Soc Am
34:1936

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer

Verlag New York

Wild LA, Gabriele CM (2014) Putative contact calls made by humpback whales (Megaptera
novaeangliae) in southeastern Alaska. Can Acoust 42:23–31
Winn HE, Thompson TJ, Cummings WC, Hain J, Hudnall J, Hays H, Steiner WW, (1981) Song
of the Humpback Whale: Population Comparisons. Behav Ecol Sociobiol 8:41–46
Zann R (2010) Ontogeny of the Zebra Finch Distance Call: I. Effects of Cross-fostering to
Bengalese Finches. Z Tierpsychol 68:1–23
Figure 1

Map of (A) Southeast Alaska, North Pacific recording locations and (B) Massachusetts Bay, North Atlantic recording locations. (Map data ©2016 Google)

Red area indicates sampling region for hydrophone recordings made in 1976. Stars in both maps indicate moored hydrophone locations.
Manuscript to be reviewed
Figure 2

Spectrograms of call types by ocean basin (FFT 256, Hann window, 90% overlap).

Call types: (A) swops, (B) whups and growls, (C) teepees, (D) droplets. The horizontal lines at ~500 and 800 Hz in spectrograms from the Atlantic indicate vessel noise.
Figure 3

Boxplots of PC1 values (indicative of entropy, bandwidth, and upper frequency components) between call types and ocean basins.

Calls recorded in the Atlantic Ocean are indicated by coral, and the Pacific ocean by teal. Call types: (A) Droplet (B) Growl (C) Swop (D) Teepee (E) Whup. Boxplots illustrate median, first, and third quartile PC1 values; dots indicate outliers.
Manuscript to be reviewed
Figure 4

Boxplot of PC2 values (indicative of lower frequency, start frequency, and peak frequency components) between call types and ocean basins.

Calls from the Atlantic are indicated by coral, calls from the Pacific are indicated by teal. Call types: (A) Droplet (B) Growl (C) Swop (D) Teepee (E) Whup. Boxplots illustrate median, first, and third quartile PC2 values; dots indicate outliers.
Table 1 (on next page)

Recordings specifications for data collection protocols from North Pacific and North Atlantic foraging grounds.
Table 1—Recordings specifications for data collection protocols from North Pacific and North Atlantic foraging grounds.

| Year          | 1976                  | 2007 & 2008                  | 2008                  |
|--------------|-----------------------|------------------------------|-----------------------|
| Hydrophone model | Unknown               | ITC 8215A                  | HTI-94-SSQ           |
| Sampling rate      | 44.1 kHz              | 44.1 kHz                     | 2 kHz                |
| System sensitivity | Unavailable           | -174 dB ± 2 dB re 1 V/μPa | -168 dB ± 1 dB re 1 V/μPa |
| Deployment method | Dipping (20 m)        | Bottom-mounted (52 m)       | Bottom-mounted (~60 m) |
| Location       | Frederick Sound       | Glacier Bay                 | Stellwagen Bank National Marine Sanctuary |
| Recording cycle | Non-standardized      | 30 seconds from every hour  | Continuous           |
| Data format    | Continuous            | 30-second recordings        | 5-minute recordings   |
| Recording Days | 4                     | 72                           | 10                    |
| Date Range     | July 1976             | June-September 2007         | June-August 2008      |
| Date Range     |                       | June-September 2008         |                       |
Table 2 (on next page)

Acoustic parameters used in Classification and Regression Tree (CART) analysis.

Log transformed parameters are indicated with an asterisk (*).
| Metric                                    | Description                                                                 |
|------------------------------------------|-----------------------------------------------------------------------------|
| Duration (90%) (s)                       | 90% of the duration of the annotated call                                  |
| Bout                                     | Number of repetitions of the same call type                                |
| Low Frequency (Hz)*                      | Lowest frequency component of the call                                      |
| High Frequency (Hz)*                     | Highest frequency component of the call                                     |
| Bandwidth (90%) (Hz)                     | 90% of the difference in frequency between high and low frequency          |
| Start Frequency (Hz)*                    | Starting frequency of fundamental                                           |
| End Frequency (Hz)*                      | Ending frequency of fundamental                                            |
| Peak Frequency (Hz)*                     | Frequency of the spectral peak                                             |
| Center Frequency (Hz)*                   | The frequency that divides the sound equally into two intervals of equal energy |
| Frequency Trend*                         | Start $F_0$ / End $F_0$                                                    |
| Aggregate Entropy (bits)                 | A measure of total disorder in the call (RavenPro, 1.5)                    |
Table 3 (on next page)

Summary statistics (mean in bold, standard deviation) for call parameters by call type and location.
Table 3- Summary statistics (mean in bold, standard deviation) for call parameters by call type and location.

| Type       | Variable     | Atlantic | Pacific |
|------------|--------------|----------|---------|
| Low Frequency Harmonic Growl | N | 41 | 78 |
| | Low Freq (Hz) | 41.5 | 35.8 |
| | Peak Freq (Hz) | 87.4 | 116 |
| | Duration (s) | 0.8 | 0.7 |
| | Low Freq (Hz) | 12.2 | 21.8 |
| | Peak Freq (Hz) | 15.1 | 62.6 |
| | Duration (s) | 0.24 | 0.3 |
| Low Frequency Harmonic Whup | N | 21 | 36 |
| | Low Freq (Hz) | 49.9 | 47.4 |
| | Peak Freq (Hz) | 94.9 | 128 |
| | Duration (s) | 0.6 | 0.7 |
| | Low Freq (Hz) | 15.8 | 25.1 |
| | Peak Freq (Hz) | 26.2 | 70.3 |
| | Duration (s) | 0.18 | 0.2 |
| | Low Freq (Hz) | 47.4 | 99.8 |
| | Peak Freq (Hz) | 148 | 120 |
| | Duration (s) | 0.3 | 0.16 |
| | Low Freq (Hz) | 99.8 | 148 |
| | Peak Freq (Hz) | 252 | 120 |
| | Duration (s) | 0.3 | 0.16 |
| Pulsed Droplet | N | 44 | 29 |
| | Low Freq (Hz) | 99.4 | 148 |
| | Peak Freq (Hz) | 187 | 252 |
| | Duration (s) | 0.4 | 0.3 |
| | Low Freq (Hz) | 49 | 99.8 |
| | Peak Freq (Hz) | 62.6 | 120 |
| | Duration (s) | 0.2 | 0.16 |
| | Low Freq (Hz) | 148 | 120 |
| | Peak Freq (Hz) | 252 | 120 |
| | Duration (s) | 0.3 | 0.16 |
| | Low Freq (Hz) | 99.8 | 148 |
| | Peak Freq (Hz) | 252 | 120 |
| | Duration (s) | 0.3 | 0.16 |
| Pulsed Swop | N | 45 | 16 |
| | Low Freq (Hz) | 76.5 | 70 |
| | Peak Freq (Hz) | 159 | 214 |
| | Duration (s) | 3.9 | 0.3 |
| | Low Freq (Hz) | 31.4 | 30 |
| | Peak Freq (Hz) | 54.3 | 85.6 |
| | Duration (s) | 4.2 | 0.2 |
| | Low Freq (Hz) | 70 | 30 |
| | Peak Freq (Hz) | 214 | 85.6 |
| | Duration (s) | 0.3 | 0.2 |
| | Low Freq (Hz) | 70 | 30 |
| | Peak Freq (Hz) | 214 | 85.6 |
| | Duration (s) | 0.3 | 0.2 |
| Pulsed Teepee | N | 40 | 51 |
| | Low Freq (Hz) | 79.2 | 214 |
| | Peak Freq (Hz) | 28.8 | 154 |
| | Duration (s) | 1.1 | 0.4 |
| | Low Freq (Hz) | 17 | 25.1 |
| | Peak Freq (Hz) | 214 | 70.3 |
| | Duration (s) | 1.77 | 0.23 |
**Table 4 (on next page)**

Confusion matrix indicating agreement between (vertical) Classification and Regression Tree call type assignment versus (horizontal) human call type assignment.
Table 4- Confusion matrix indicating agreement between (vertical) Classification and Regression Tree call type assignment versus (horizontal) human call type assignment.

|       | Droplet | Feed | Growl | Teepee | Whup | Agreement |
|-------|---------|------|-------|--------|------|-----------|
| Droplet | 58      | 0    | 3     | 5      | 4    | 3         | 79%    |
| Feed   | 0       | 10   | 0     | 0      | 0    | 0         | 100%   |
| Growl  | 0       | 0    | 111   | 1      | 3    | 4         | 93%    |
| Swops  | 5       | 0    | 1     | 44     | 9    | 2         | 72%    |
| Teepee | 3       | 0    | 3     | 4      | 81   | 0         | 89%    |
| Whup   | 2       | 0    | 22    | 2      | 0    | 31        | 54%    |

**Total Agreement** 82%