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# The Social Signaling Behavior of Humpback Whales on the Hawaiian Breeding Grounds Investigated Using Acoustic Tags

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# The Social Signaling Behavior of Humpback Whales on the Hawaiian Breeding Grounds Investigated Using Acoustic Tags

**Mestrado em Biologia Marinha**

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# Declaração de autoria de trabalho

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Declaro ser o(a) autor(a) deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

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# Abstract

Humpback whales (*Megaptera novaeangliae*) are one of the most social of all baleen whale species. The song produced by males has captivated audiences, both scientific and public alike. Despite extensive research into humpback whale songs, gaps remain in the understanding of humpback whale communication. These gaps are particularly evident concerning humpback whale non-song social vocalizations. This study expands upon the current knowledge of non-song social call use and function by comparing call type, features, and temporal parameters across humpback whale groups of three different compositions: dyads, escorted mother-calf pairs, and competition groups (comprised of a single female and two or more competing males). Recordings were collected from 12 deployments of Acousonde$^{TM}$ acoustic and data logging tags on whales off Maui, Hawaii during the winter breeding seasons of 2019-2021. Individual social calls were selected based on visual and aural inspection of spectrograms using Raven Pro 1.6 software, with a total of 1,102 calls chosen throughout the 69.5 hours of acoustic recordings. Of these calls, 52.2% occurred in competition groups, 34.9% in escorted mother-calf pairs, and 12.9% in dyads, although the difference in call rate (calls/hr) was not statistically significant across groups (Chi-square, $p = 0.0671$). Commonly used call types varied across groups, but all group compositions often observed four call types (knock, squeak, bellow, moo). Though social calls were shared across groups, the temporal parameters and frequencies of the calls produced varied significantly (Kruskal-Wallis, $p<1e\text{-}07$). Our study provides new insights into humpback whale vocal communication behavior in the Hawaiian Islands breeding grounds, particularly concerning three main social groups whose non-song vocal communications have been understudied.

**Keywords:** humpback whale, social calls, vocal communication, group composition, acoustic tag, Hawaiian Islands

# Resumo em Português

Debaixo de água, a sinalização acústica é uma parte vital da vida dos organismos. O som encontra uma atenuação mínima na água, tornando a sinalização acústica o meio de comunicação mais eficiente entre a vida selvagem. Isto é especialmente verdade para as espécies de cetáceos. Sabe-se que os cetáceos utilizam a sinalização acústica para uma variedade de fins, incluindo a navegação, a prevenção de predadores, a localização de presas, e a facilitação de interacções sociais. Entre os cetáceos, o repertório vocal dos mysticetes (baleias de barbas) é relativamente pouco estudado, exceptuando no que diz respeito ao canto rítmico das baleias de bossa. Embora os cantos das baleias de bossasejam bem estudados, estas baleias também produzem uma variedade de vocalizações sociais que não são bem compreendidas. Estas vocalizações sociais são produzidas por todos os membros desta espécie e provavelmente desempenham um papel vital na facilitação das interacções sociais.

Recentemente, o interesse pelo comportamento de chamada social das baleias de bossa tem aumentado, com vários estudos documentando o repertório de chamadas sociais desta espécie. Apesar deste esforço acrescido, persistem lacunas críticas na compreensão do uso e função destas chamadas sociais. Isto é particularmente evidente com a variabilidade do comportamento de chamada social entre grupos sociais de diferentes composições (ou seja, grupos de competição, pares de crias escoltadas, e díades). Este estudo teve como objectivo desenvolver o conhecimento actual do comportamento de chamadas sociais das baleias de bossa através da 1) identificação dos tipos de chamadas sociais das baleias de bossa mais comummente utilizadas nos locais de reprodução das ilhas Havaianas, 2) comparação do padrão temporal do comportamento de chamadas sociais entre grupos e 3) avaliação da variabilidade do tipo, frequência e duração das chamadas sociais utilizadas em grupos de composições variáveis.

Para concretizar os objetivos deste estudo, analisámos o comportamento de vocação social das baleias de bossa nas ilhas do Havai, utilizando etiquetas acústicas e de registo de dados acústicos de Acousonde$^{TM}$ em baleias ao largo de Maui, no Havai, durante as épocas de reprodução de inverno de 2019-2021. As etiquetas foram implantadas em grupos de baleias de bossa com várias composições, incluindo díades (duas baleias de sexo desconhecido), grupos de competição (compostos por uma única fêmea e dois ou mais machos concorrentes), e

acompanhados pares de mãe-bezerro. No total, houve 12 desprendimentos bem sucedidos de tags que se registaram durante 69,5 horas. Estas gravações foram inspecionadas visualmente e oralmente na sua totalidade por um observador (JC). As inspecções visuais e auditivas foram realizadas utilizando espectrogramas produzidos no software acústico Raven Pro 1.6 com um DFT de 4096 pontos e 80% de sobreposição. A partir destes espectrogramas foram selecionadas individualmente as chamadas sociais com limites de selecção o mais próximo possível do sinal produzido. Para serem incluídas no processo de selecção, as chamadas tiveram de ter um ponto de início e fim distinguível, com pouca ou nenhuma sobreposição com conspecíficos, e uma relação sinal/ruído (SNR) de 10dB ou superior. As chamadas repetidas em episódios foram selecionadas individualmente e não foram incluídas se o padrão repetido se assemelhasse à canção do ano de estudo.

Após a selecção das chamadas sociais, foram utilizados algoritmos Matlab personalizados para obter medições das principais características acústicas de cada escolha, incluindo medições de duração e frequência. Estes guiões utilizaram a subtração do ruído para eliminá-lo do fluxo associado à energia das etiquetas acústicas e do ruído ambiente por parte do tráfego de embarcações e de conespecíficos próximos. Isto permitiu medições muito mais precisas dos sinais acústicos. Estas medições foram utilizadas para realizar uma análise do agrupamento hierárquico que reuniu chamadas com base na semelhança das suas medições acústicas. Foram selecionadas amostras de chamadas de cada um dos aglomerados em todos os grupos para estabelecer as mais frequentemente utilizadas de cada composição destes. Além disso, para avaliar a variabilidade do comportamento das chamadas sociais nos grupos, o padrão temporal da produção de chamadas foi comparado em todos os grupos e respetivas medições de frequência e duração foram testadas para estatísticas significativas, utilizando testes Kruskal-Wallis e Wilcox-pairwise.

Ao longo das 69,5 horas de gravação acústica, foram selecionadas 1.102 chamadas sociais, com 52,2% das chamadas produzidas por grupos competitivos, 34,9% das chamadas produzidas por pares de mãe-cria acompanhados e 12,9% das chamadas produzidas pelas díades. Enquanto a produção de chamadas variou consideravelmente entre grupos, a taxa de chamadas (chamadas/hora) não foi significativamente diferente (Chi-squared, p = 0,067). A partir das chamadas em amostra na análise de agrupamento, foram estabelecidos um total de vinte e dois tipos de chamadas sociais comuns, com quatro destes partilhados em todos os grupos (knock, squeak, bellow, moo). Os tipos de chamadas foram frequentemente partilhados entre os grupos, mas os parâmetros temporais e medições de frequência variaram significativamente entre grupos (Kruskal-Wallis, p = 1,09e-07).

As chamadas foram produzidas com mais frequência em grupos competitivos com períodos de inter-chamadas significativamente mais curtos do que as díades (Wilcox-pairwise, p = 0,00062) e pares mãe-cria escoltados (p = 7,9e-07). Estes resultados coincidem com estudos anteriores que mostraram que as baleias de bossa aumentam a taxa de sinalização com a adição de novas baleias a um grupo. A adição de novas baleias a um grupo estabelecido também pode aumentar os níveis de excitação dos indivíduos e promover mudanças no comportamento da chamada. Para além de terem os períodos mais curtos entre chamadas, grupos competitivos também produziram chamadas com durações significativamente mais curtas do que ambas as díades (Wilcox-pairwise, p = 0,00091) e pares de mãe-cria escoltados (p = 0,00091). Isto foi um pouco inesperado, uma vez que muitos animais são conhecidos por produzirem chamadas mais longas em contextos de excitação mais elevados. No entanto, este padrão de duração da chamada foi documentado anteriormente em baleias de bossa, portanto, é possível que a duração das chamadas sociais da baleia de bossa seja influenciada por outros fatores que não o nível de excitação ou que as nossas suposições sobre o nível de excitação dos grupos nas amostras estavam incorretas.

Enquanto as durações de chamada observadas fossem inesperadas, as frequências de chamada observadas correspondiam aos padrões observados em estudos anteriores. As frequências medidas de chamadas variaram significativamente entre grupos, com pares de mãe-cria acompanhados produzindo a maior frequência de pico medido (p = 3,74e-06), frequência central (p = 4,68e-09), primeira frequência de quartil (p = 4.88e-08), terceira frequência de quartil (p = 4.13e-10) e 95 centésima frequência (p = 2,47e-06) de todos os grupos. A alta frequência de chamadas em pares de mãe-cria acompanhados é provavelmente devido à contribuição de chamadas das crias que são produzidas a uma frequência mais elevada que a dos adultos. Estas elevadas frequências podem ser devidas à produção de chamadas de aversão em contextos onde a escolta não foi desejada. Grupos competitivos produziram chamadas de média frequência, o que se deveu provavelmente ao uso combinado de chamadas de alta frequência de aversão e chamadas agressivas de baixa frequência.

Os resultados do nosso estudo fornecem fortes evidências de que o comportamento de vocação social das baleias de bossa muda dependendo da composição do grupo, o que apoia a evidência de complexidade do sistema de comunicação desta espécie. Numa época de crescente ruído antropogénico oceânico, é crucial compreender o comportamento de vocação social das baleias de bossa para conservar esta espécie. O nosso estudo aproxima-nos mais um passo para atingirmos este objectivo.

# General Introduction

## *Cetacean acoustic communication*

In the underwater world, sound is an essential aspect of life. Because sound faces minimal attenuation in water and can travel further than light, it is an ideal modality for mediating essential survival functions. Sound production is often used for communication, foraging, and even navigation (Stimpert et al. 2015). For many marine mammal species, particularly cetaceans, vocalizations are vital in communication, especially facilitating social interactions (Janik and Sayigh 2013, Janik 2014). Although baleen whales were long thought to be silent (Fournet 2014), it is now well known that both odontocetes and mysticetes produce a wide variety of vocalizations, although the methods by which they do so vary greatly.

Odontocetes (toothed whales) produce clicks for echolocation, which is utilized in prey detection, navigation, and predator avoidance (Au 2018). For many years the structures involved in this sound production remained a mystery. However, through extensive study, Cranford (2000) confirmed that sound production in odontocetes originates from the phonic lips. Sounds produced for echolocation are then focused by a structure called the melon to create an echolocation beam (McKenna et al. 2012). In addition to echolocation, many odontocete species produce vocalizations to communicate with individuals within their species. Dolphins have even been shown to produce signature whistles used to identify individuals within a population (Janik et al. 2006, Janik and Sayigh 2013). Compared to baleen whales, vocal communication has been well studied in toothed whale species, both in captivity and in the wild.

In contrast to odontocetes, sound production in baleen whales is not well understood. Still, several models have been proposed to explain the structures and mechanisms used by humpback whales and other baleen whale species to produce sound (Aroyan et al. 2000, Frazer and Mercado III 2000, Reidenberg and Laitman 2007, Adam et al. 2013). Studies have shown that mysticetes have laryngeal vocal folds that serve as the sound source (Reidenberg and Laitman 2007, Adam et al. 2013). Unlike humans, the mouth and tongue are not utilized to modify sound in mysticete whales; instead, sounds are produced by creating a circuit-like airflow back and forth between the lungs and laryngeal sac (Adam et al. 2013). However, sound production and modification may be limited by the physical features of the signaler, with smaller animals (like calves) unable to produce the same calls as their larger counterparts

(Indeck et al. 2020). Understanding the sound production systems in humpback whales and other mysticetes is essential for researchers to fully understand these animals' complex acoustic communication systems.

### ***Humpback whale song***

Historically, little was known about sound production in baleen whales and it was long believed that they did not produce sounds (Fournet 2014). However, this was not due to the lack of being heard. Historic whaling records describing whale songs (Aldrich 1889) existed long before the scientific community acknowledged that baleen whales vocalize. As early as 1952 humpback whale sounds were recorded by Schreiber (1952), but the species was not identified. During World War II, when naval sonar and anti-submarine research was being conducted, whale vocalizations were recorded for the first time (Payne and McVay 1971). During this time in the 1970s, humpback whale songs were studied in-depth (Payne and McVay 1971) for the first time and recordings were released to the broader public (Payne 1970).

In current times humpback whale song is well known, and extensive research has been conducted on this topic (Garland et al. 2011, Risch et al. 2012, Vu et al. 2012, Cholewiak et al. 2013). The song is produced by arranging individual sound units into distinct patterns, repeated in a predictable manner (Schneider and Mercado 2018). These songs are only produced by male humpback whales and occur predominantly in breeding grounds (Herman et al. 2013). The single-sex usage of song has also been found in closely related fin whales (Croll et al. 2002), and it is believed to be related to reproductive behavior (Parsons et al. 2008, Smith et al. 2008, Herman 2017). At any given time, all males within a population of humpbacks will sing the same song (Winn and Winn 1978, Parsons et al. 2008). Over time, whale song evolves and changes, and interestingly song patterns appear to be passed between populations (Garland et al. 2011, Janik 2014). These synchronous modifications of whale songs over time demonstrate that cetaceans are capable of vocal production learning (Janik 2014). Vocal production learning is the ability for animals to develop and change the signals that they produce based on the interactions that they experience (Janik 2014). This ability is rare in mammals and has only ever been recorded in cetaceans, bats, pinnipeds, elephants, and humans (Tyack 2008, Janik 2014). Humpback whales were first among the baleen whales discovered to display vocal production learning.

### *Humpback whale social group structure*

An essential factor to consider that may regulate humpback whale social calls is group composition and dynamics. Humpback whales, like most mysticetes, do not live in close-knit family pods, as seen in many odontocete species. However, they are known to form fluid social groups throughout their feeding and breeding grounds and along migration routes. In high latitude feeding grounds, it is well documented that humpback whales join in groups to perform cooperative feeding (Jurasz and Jurasz 1979, D'vincent et al. 1985, Fournet et al. 2018b). Social vocalizations are considered a vital cue to organize this feeding behavior, including a "feeding call" recorded in Alaskan waters (D'vincent et al. 1985, Cerchio and Dahlheim 2001, Fournet et al. 2018b). While most groupings are typically short-lived, some studies have shown that some of these associations can last for extended periods, and some individuals even rejoin intermittently over many years (Weinrich 1991, Ramp et al. 2010, von Ziegesar et al. 2020).

Although most social groups of humpback whales are fluid, one relationship within this species is not. That is the relationship between mother and calf. A humpback whale calf will remain with its mother for the first 10-11 months of its life (Chittleborough 1958, Baraff and Weinrich 1993, Sardi et al. 2005). Throughout this first year, the mother will rarely allow the calf to wander more than a body length away from her, and it has been found that mother-calf pairs will even dive synchronously during periods of foraging (Tyson et al. 2012). Additional whales (escorts) often join mother-calf pairs which can evoke varying reactions from the mother. On some occasions, the escorting male may have an affiliative relationship with the female on feeding grounds (von Ziegesar et al. 2020). However, it also has been documented that female whales often avoid males (Smultea 1994, Craig et al. 2014). It has been found that the mother may sometimes insert herself between the escort and the calf to prevent any type of interaction between them (Sardi et al. 2005).

### *Humpback whale social sounds*

Despite being most known for their song, the humpback whale vocalization repertoire is not limited to this rhythmic song. These whales also produce a wide array of social sounds, including non-song vocalizations and surface-generated sounds (e.g., breaching, pectoral, and tail slapping) (Silber 1986, Dunlop et al. 2007, Rekdahl et al. 2013). The study of these social sounds remains limited. However, several studies have been able to document the repertoire of social calls used by these animals in different populations (Dunlop et al. 2007, Stimpert et al.

2011, Fournet et al. 2015, Rekdahl et al. 2017). While individual calls vary between different populations, several of these studies from different locations have found similarly characterized calls like "wops," "whups," and "grunts" to be commonly used (Dunlop et al. 2007, Dunlop et al. 2008, Stimpert et al. 2011, Wild and Gabriele 2014, Dunlop 2017, Rekdahl et al. 2017), suggesting that certain calls may be of high importance to social interactions and may transcend cultural differences.

Unlike the continuously changing humpback whale song, social calls interestingly display temporal stability. This stability has been documented in both Australian (Rekdahl et al. 2013) and southeast Alaskan populations (Fournet et al. 2018a) of humpback whales. Rekdahl et al. (2013) revealed that twelve call types commonly used in the social call repertoire of east Australian humpback whales were stable across all years of their study. Furthermore, (Fournet et al. 2018a) found similarly in southeast Alaska that twelve common social calls showed temporal stability over 36-years. This display of temporal stability in social vocalizations demonstrates that humpback whale social calls likely play a crucial role in the complex communication system of these animals.

Humpback whale social vocalization rates have been shown to vary with group size and dynamic. Silber (1986) found that social call rate increased along with group size, although the individual vocalization rates were not significantly variable. Additional studies have shown that humpback whales may also alter their signaling behavior depending on the group dynamic (Rekdahl et al. 2015, Dunlop 2016). Social call bouts are produced significantly more when an outside whale joins an existing group (Rekdahl et al. 2015). Furthermore, it has been found that whales modified "wop" calls, emitting these calls at lower levels, in the presence of a nearby singing whale (bystander) (Dunlop 2016). These studies demonstrate that group dynamics may lead to changes in the quantity and frequency of social calls produced, particularly when involving joining groups. The intentional change in signaling behavior may make it more difficult for an individual whale to locate a group (Dunlop 2016). This behavioral modification would be of particular interest in the Hawaiian breeding grounds where mother-calf pairs are more likely to be pursued by males, which can incur an energetic cost (Cartwright and Sullivan 2009).

While it has been found that social calling behavior is sometimes naturally modified due to group dynamics, it has also been found that some cetacean species will modify their calls due to increased background noise (Dunlop et al. 2010), often related to anthropogenic activities (Miller et al. 2000, Foote et al. 2004). Anthropogenic noise can mask vocalizations, reducing the area over which animals can communicate. In some areas, humpback whale signals can experience masking levels of 80% or more, limiting their communication space significantly (Cholewiak et al. 2018). To compensate for the increase in background noise, cetaceans often change their signaling behavior. For example, orcas display longer call durations (Foote et al. 2004), North Atlantic and Southern right whales increase call frequency (Rekdahl et al. 2013), and humpback whales increase call length in response to sonar (Miller et al. 2000). The modification of call behavior is an essential factor to consider in this study, as the humpback whales' Hawaiian breeding ground in which this study took place is an area of extensive tourism boat traffic.

There is a growing understanding of the social call repertoire of humpback whales; however, little is known about the behavioral function of these calls except with feeding calls in southeast Alaska (D'vincent et al. 1985, Fournet et al. 2018b). Previous studies have established that motivational-structural rules exist in the signals of terrestrial animals, which allow the receiver to understand the motivational state of the signaler (Morton 1977). High-frequency signals are typically connected with fearful/appeasement contexts, whereas low-frequency signals are more often associated with aggressive contexts. Humpback whale social calls may also fit the motivational contexts mentioned above, with non-affiliating groups of whales producing more "low arousal" calls and joining groups using a more significant proportion of "aggressive" signals (Dunlop 2017). Additionally, it has been speculated that the commonly used "whup" may be used to maintain inter-group communication due to its usage pattern and resemblance to contact calls of other baleen whale species (Wild and Gabriele 2014). While these studies have made significant progress in the understanding of humpback whale social calls, gaps remain.

### *Research gaps*

In more recent years, there has been an increased effort to understand the social vocalizations of humpback whales; however, gaps remain. Most current studies have been restricted to migration routes (Dunlop et al. 2007, Dunlop et al. 2008, Rekdahl et al. 2015, Rekdahl et al. 2017) and feeding grounds (Stimpert et al. 2011, Fournet 2014, Fournet et al. 2015), which has left the breeding grounds of the Hawaiian Islands understudied in regards to this topic. Although some previous research has been conducted on humpback whale social calls in Hawaii, it was more specifically focused on the vocalizations produced by calves

(Zoidis et al. 2008), or lacked current technology, which allows for more nuanced and robust data collection (Silber 1986). In particular, there has been little work investigating the social call dynamics in escorted mother-calf pairs. This is an essential area of interest, as maternal care can be very energetically costly, and the presence of an escort can be either to the benefit or, if unwanted, to the detriment of the mother's energetic reserves.

Not only is previous research on humpback whale social calls limited in scope, but it is also limited by the methodology used. Nearly all the studies conducted on this topic have utilized either stationary or towed hydrophone arrays combined with visual observations. These methods can make it difficult to discern which calls are produced within a group. Using acoustic recording tags can enhance the ability to detect calls produced and heard within a group, although it remains nearly impossible to identify the specific individual producing the call.

This study aims to close a crucial knowledge gap in the usage of social calls across humpback whale groups of varying composition in the Hawaiian Islands Humpback Whale National Marine Sanctuary. This region serves as a critical habitat for humpback whales' breeding season and hosts various compositions, including large competitive groups, escorted mother-calf pairs, and dyads of varying compositions.

### *Research approach*

In this study, recordings from Acousonde$^{TM}$ acoustic tags were combined with field notes to compare the use of humpback whale social vocalizations in groups of varying composition in the critical breeding habitat of the Hawaiian Islands. My objectives in this study were to 1) identify the most commonly used humpback whale social call types produced in the Hawaiian Islands breeding grounds, 2) compare the temporal pattern of calling behavior across groups, and 3) assess the variability of the type, frequency, and duration of social calls used in groups of differing compositions, to better understand the importance that social calls play in facilitating social interactions.

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**TITLE**

# The social signaling behavior of humpback whales on the Hawaiian breeding grounds investigated using acoustic tags

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## Abstract

Humpback whales (*Megaptera novaeangliae*) are one of the most social of all baleen whale species. While extensive research has been conducted on humpback whale songs, gaps remain in understanding communication, particularly regarding humpback whale non-song social vocalizations. This study expands upon the current knowledge of non-song social call use and function by comparing call type, features, and temporal parameters across humpback whale groups of three different compositions: dyads, escorted mother-calf pairs, and competition groups. Recordings were collected from 12 deployments of Acousonde$^{TM}$ acoustic and data logging tags on whales off Maui, Hawaii, during the winter breeding seasons of 2019-2021. Individual social calls were selected based on visual and aural inspection of spectrograms using Raven Pro 1.6 software, with a total of 1,102 calls chosen throughout the 69.5 hours of acoustic recordings. Of these calls, 52.2% occurred in competition groups, 34.9% in escorted mother-calf pairs, and 12.9% in dyads, although the difference in call rate (calls/hr) was not statistically significant across groups (Chi-square, $p = 0.0671$). Commonly used call types varied across groups, but all group compositions often observed four call types (knock, squeak, bellow, moo). Though social calls were shared across groups, the temporal parameters and frequencies of calls produced varied significantly (Kruskal-Wallis, $p = 1.09e\text{-}07$). Our study provides new insights into humpback whale vocal communication behavior in the Hawaiian Islands breeding grounds, particularly for three principal social groups whose non-song vocal communications have been understudied.

## Introduction

Acoustic signals can serve a variety of purposes among different species, including navigation, predator avoidance (Au 2018), prey localization (Madsen et al. 2002, Miller et al. 2004, Samarra 2015) and facilitating social interactions (Janik and Sayigh 2013, Janik 2014). They help to maintain contact among group members (Clark 1983, Wild and Gabriele 2014) and can encode the physical characteristics (May-Collado et al. 2007, Martin et al. 2017), motivational context (Morton 1977, August and Anderson 1987, Dunlop 2017), and the arousal of the signaler (Cusano et al. 2020). In some animals, acoustic signals indicate fear, appeasement, or aggression from the signaler (Morton 1977, August and Anderson 1987, Dunlop 2017), which can influence the reactions from others within a group. While visual cues are commonly used for communication among many animals, marine species are often more reliant on acoustic signaling as the predominant means of communication. This is largely due to the ability of sound to transmit efficiently through water with little attenuation, making it more efficient than visual cues. Among marine species, cetaceans are well known for their utilization of acoustic signaling to facilitate many aspects of their lives. Odontocete acoustic communication has been well studied (Janik et al. 2006, Morisaka 2012, Janik and Sayigh 2013) and research has shown that baleen whales utilize acoustic signals to mediate reproductive behavior (Parsons et al. 2008, Smith et al. 2008, Herman 2017), cooperative feeding (D'vincent et al. 1985, Cerchio and Dahlheim 2001), and group contact (Clark 1983, Wild and Gabriele 2014); however, many aspects of cetacean acoustic communication remain a mystery.

Humpback whales are the most vocal of the baleen whale species. They are well-known for the complex songs that male humpback whales produce on breeding grounds. These songs are composed of a repeated pattern of sound units and are known to play an integral role in the reproductive behavior of this species (Parsons et al. 2008, Smith et al. 2008, Herman 2017). In addition to the whale song produced only by males, all humpback whales produce various non-song social vocalizations. Interest in understanding the use of non-song vocalizations of humpback whales has grown in recent years, and several studies have documented the repertoire of these calls in different locations (Dunlop et al. 2007, Stimpert et al. 2011, Fournet et al. 2015, Rekdahl et al. 2017). These repertoires have identified 46 social calls in Australia (Dunlop et al. 2007, Rekdahl et al. 2013) and 16 social calls in Alaska (Fournet et al. 2015). Both repertoires consist primarily of calls that have been previously recorded as units of whale song; however, 13 of the calls recorded in Australia were unique and were not recorded in the song of any of the studied years (Dunlop et al. 2007). Although the social vocalization repertoire of humpback whales utilizes calls from whale songs, it differs from song in that these calls continue to be used in the social call repertoire over long periods, even after the regional song has changed. Some social calls from these repertoires have shown temporal stability over decades (Rekdahl et al. 2013, Fournet et al. 2018). The continued use of social calls over many years suggests that they serve an important function in the social communication of this species and may help to relay the motivational context and arousal of the signaler to conspecifics.

While studies have been able to link the motivational context of humpback whale songs to reproductive behaviors (Parsons et al. 2008, Smith et al. 2008, Herman 2017), the function of social calls is only beginning to be understood. A recent study has shown the motivational context of humpback whale social calls (Dunlop 2017) bears resemblance to vocalizations of previously studied species (Morton 1977, August and Anderson 1987). Aversive or appeasement calls were high in frequency (Dunlop 2017). In contrast, aggressive whale calls were low frequency with wide bandwidths (Dunlop 2017), a trend noted previously with terrestrial species (e.g. elk, Feighny et al. 2006, e.g. white-faced capuchins, Gros-Louis et al. 2008). In addition to motivational context, arousal has been linked to changes in signaling behavior. Arousal has been defined in animal studies as the intensity of emotional states (Briefer 2012). High arousal situations have been linked with the production of higher frequency and longer duration signaling (Briefer 2012, Fischer and Price 2017). In aversive contexts, such as escorts joining a mother-calf pair, humpback whales have been documented to change their calling behavior, indicating that both motivational context and arousal impact the social signaling of this species (Cusano et al. 2020).

An important factor to consider when investigating the social calling behavior of humpback whales is the group's composition when calls are produced. While humpback whales do not travel in family pods, as is often seen with odontocete species (Connor et al. 1998, Parsons et al. 2009), they do engage in social interactions. Humpbacks are described to have a fission-fusion social structure where groups can remain together for short or very long periods (Mobley Jr and Herman 1985, Brown and Corkeron 1995). Furthermore, humpback whales have very close bonds between mother and calf pairs during the first 10-11 months of the calf's life (Sardi et al. 2005), and bonded relationships between adult whales have been documented on Alaskan feeding grounds (von Ziegesar et al. 2020). Humpback whale groups can vary largely in number, and commonly seen group compositions on the breeding grounds include competitive groups, escorted mother-calf pairs, and dyads. Group membership has been shown to impact calling behavior, with studies finding that humpback whales alter their calling depending on the number of whales in the group (Silber 1986, Cusano et al. 2020) or the affiliation between group members (Dunlop 2016). Call rates (calls/hr) have been shown to increase in conjunction with increasing group size, with competition groups displaying the highest call rates (Silber 1986, Cusano et al. 2020). Smaller social groups like dyads and escorted mother-calf pairs typically produce fewer vocalizations (Cusano et al. 2020); however, the affiliation between group members may be a factor that contributes to this. Several studies have shown that humpback whales increase their calling rate when unaffiliated whales join the group (Silber 1986, Rekdahl et al. 2015, Cusano et al. 2020). Some humpback whales even altered the levels at which they signaled in the presence of an unaffiliated singer, which is believed to be a method to avoid detection by the singer (Dunlop 2016).

As the aforementioned studies make clear, humpback whale group composition may significantly impact the type and use of social vocalizations; however, research in this area remains limited. This is especially true for comparing calling behavior across varying group compositions. Typically, studies have focused solely on a single group type, like mother and calf pairs (Zoidis et al. 2008, Indeck et al. 2020), and have not drawn comparisons with other known group compositions. Older studies that did compare signaling in varying group compositions lacked the current technology, which allows for more nuanced and robust data collection (Silber 1986). Additionally, most contemporary studies of humpback whale social calling behavior have been conducted along migration routes (Dunlop et al. 2007, Rekdahl et al. 2013, Rekdahl et al. 2015, Dunlop 2016, 2017, Indeck et al. 2020, Recalde-Salas et al. 2020) or on feeding grounds (Fournet 2014, Wild and Gabriele 2014, Fournet et al. 2015) which has left the social calling behavior of certain group types on breeding grounds understudied.

In a time of increasing oceanic anthropogenic noise, it is important to understand the vocalization behavior of humpback whales to help conserve this species. In this study, we use acoustic tags to compare social vocalizations of humpback whale groups of varying compositions. The aims of this work are to 1) identify the most commonly used humpback whale social call types produced on the Hawaiian Islands breeding grounds, 2) compare the temporal pattern of calling behavior across social group types and 3) assess the variability of the type, frequency, and duration of social calls used in groups of varying compositions.

## Methods

### *Data Collection*

The data for this study was collected off west Maui, Hawaii in the Hawaiian Islands Humpback Whale National Marine Sanctuary (Figure 1.) during the three winter breeding seasons between 2019 and 2021. Recordings were made using suction cup Acousonde$^{TM}$ tags temporarily deployed on humpback whales, with a total of 12 tag deployments from whale groups of three different compositions: competition groups, dyads, and escorted mother-calf pairs. Competition groups consisted of a leading female and two or more escorts competing for the primary escort position closest to the female. Escorted mother-calf pairs consisted of a mother whale with her calf and a single escorting whale of unknown gender and dyads consisted of pairs of two whales of unknown genders. Competition groups were classified as “high arousal” groups due to the aggressive nature of competition (Baker and Herman 1984, Herman et al. 2007) and its relationship with reproductive behavior (Parsons et al. 2008, Smith et al. 2008, Herman 2017). Escorted mother-calf pairs were classified as “moderate arousal” due to interactions within these groups being documented as both affiliative (von Ziegesar et al. 2020) and agonistic (Smultea 1994, Craig et al. 2014) in different contexts. Finally, dyads were classified as “low arousal” as pairs of whales have been documented to have extended, non-agonistic affiliations (Weinrich 1991, Andriolo et al. 2014), although relationships between adult pairs are not well understood.

Two Acousonde$^{TM}$ tags were used for this study (B010 and B046), with hydrophones recording 16-bit audio with the sampling rate set to 12,226 Hz, an 8th order elliptic anti-alias filter at 4646 Hz, a 4-stage cascaded high pass filter at 22 Hz, and a total path gain of +2.4 dB. The acoustic sensitivity of the B010 and B046 tags were -187.2 dB re 1 V/µPa and -187.9 dB re 1 V/µPa, respectively. In addition to acoustic recordings, field notes were compiled documenting the general group composition and behavior when the research vessel remained with the animals, although this typically did not account for the entire tag deployment.

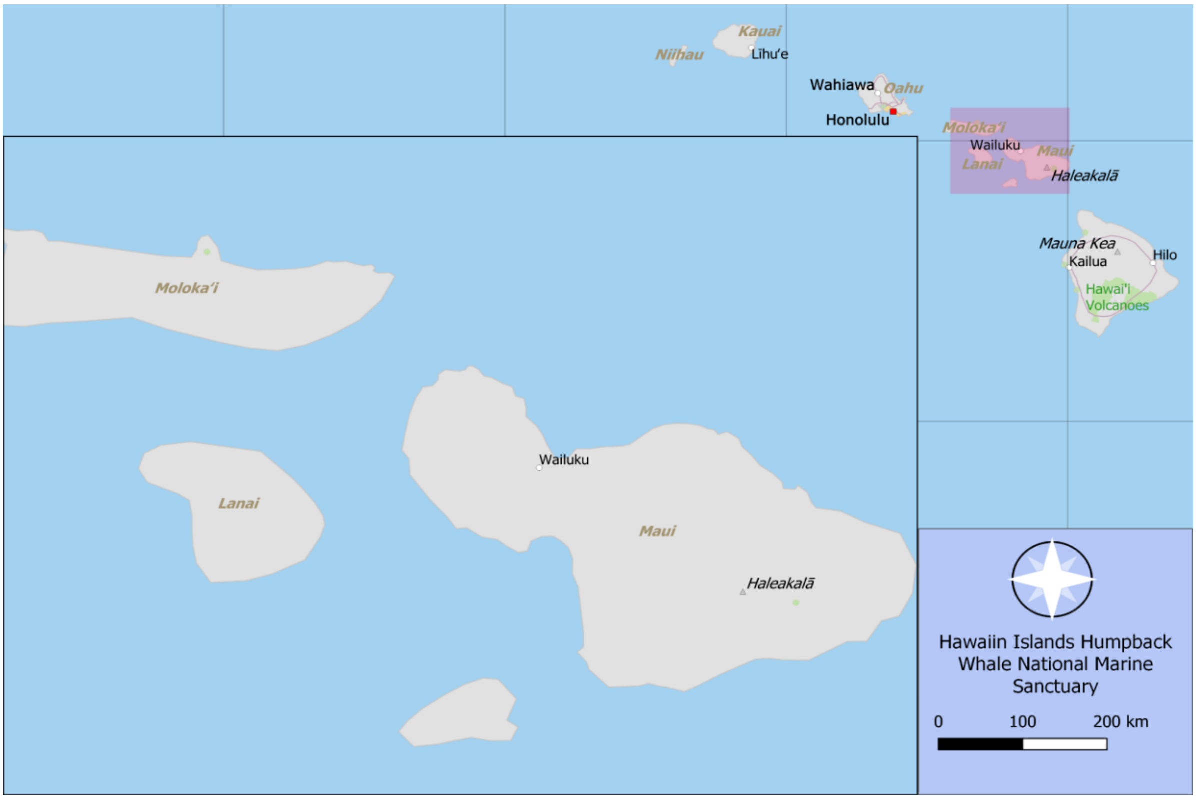

Figure 1. Map displaying the general area of study where tagging and field observations took place.

### *Call Detection*

Spectrograms were generated using Raven Pro 1.6 (The Cornell Laboratory of Ornithology 2019) with a 4096-point DFT and 80% overlap. All recordings were visually and aurally inspected in their entirety, and all selections were made by one observer (JC). All social calls were selected in Raven Pro, with selection boundaries set as tight as possible to the produced signal to ensure the highest accuracy for call measurements. For calls to be included in the selection process, it was necessary that there be a distinguishably clear start and endpoint and have little to no overlap with calls from conspecifics. For any social calls that were repeated in bouts, each call was selected individually. If any calls were repeated in a pattern resembling the whale song of the current season, they were not selected. To be included in quantitative analysis calls needed to have a signal-to-noise ratio of at least 10 dB or higher, which is the accepted threshold that has been established in previous studies (Dunlop et al. 2007, Dunlop et al. 2008, Stimpert et al. 2011, Rekdahl et al. 2013, Fournet 2014).

### *Call Measurement*

Due to the nature of acoustic tag recording, most files contained some flow noise in the 0-200Hz range. Furthermore, with high rates of tourism traffic in the study area, vessel traffic was occasionally disruptive in the recordings. To account for the disturbances from ambient and flow noise, social calls from all group compositions were measured using custom-written noise subtraction Matlab algorithms (Indeck et al. 2020). For every call selection, a corresponding noise selection (between 1-3 seconds long) was made in the time either preceding or following the call selection to capture the ambient noise at the time of signaling. Occasionally, during call bouts, one noise file was used for more than one signal file to ensure that noise selections corresponded as closely as possible to the respective signal. The spectrum from noise selections was subtracted from the corresponding signal file to remove most of the energy from flow noise, vessel traffic, and song from nearby conspecifics.

Once most noise energy was removed from the call files, acoustic characteristics were measured from the observer-selected bounds of the call files. The temporal boundaries of call selections were made as close to the visible start and endpoint of the call as possible, and frequency boundaries were selected as close to the lowest and highest frequency possible. This ensured that the call was captured while also attempting to reduce as much background noise as possible. The measured acoustic characteristics of the calls seen in Table 1, included both temporal and frequency measurements as used previously by Indeck et al. (2020). For analysis, frequency measurements were log-transformed to better reflect the mammalian perception of pitch (Richardson et al. 1995).

Table 1. Description of acoustic measurements used for agglomerative hierarchical clustering. All frequency measurements were log-transformed for analysis except frequency ratio.

| Measurement | Abbreviation | Description |
|---|---|---|
| Duration | Dur | The period of time between 1% and 99% of the call's energy |
| Centre Time | CT | The time dividing the call's energy in half |
| First Quartile Time | Q1T | The period of time of the first 25% of the call's energy |
| Third Quartile Time | Q3T | The period of time of the first 75% of the call's energy |
| Inter-Quartile Time | IQT | The difference in time between the third quartile and the first quartile time |
| Fifth Centile time | C05T | The period of time of the first 5% of the call's energy |
| Ninety-Fifth Centile Time | C95T | The period of time of the first 95% of the call's energy |
| Inter-Centile Time (90) | ICT90 | The difference in time between the ninety-fifth centile and the fifth centile |
| Peak Frequency | PF | The point at which the maximum energy level in the call occurs |
| Centre Frequency | CF | The frequency which divides the call's energy level in half |
| First Quartile Frequency | Q1F | The frequency separating of the first 25% of the call's energy from the remaining 75% |
| Third Quartile Frequency | Q3F | The frequency separating of the first 75% of the call's energy from the remaining 25% |
| Inter-Quartile Frequency | IQF | The difference in time between the third quartile and the first quartile frequency |
| Fifth Centile Frequency | C05F | The frequency separating of the first 5% of the call's energy from the remaining 95% |
| Ninety-Fifth Centile Frequency | C95F | The frequency separating of the first 95% of the call's energy from the remaining 5% |
| Inter-Centile Frequency (90) | ICF90 | The difference in time between the ninety-fifth centile and the fifth centile frequency |
| Frequency Ratio | FR | Calculated as C99F/C01F |

### *Call Types*

Social calls which met all the initial requirements for inclusion were analyzed using agglomerative hierarchical clustering (agnes) in R (R Core Team 2020) (package: factoextra). Clusters were produced using the "ward" method, and calls were grouped based on the similarity of the measurements gathered from the initial sound processing in Matlab (Table 1). Dendrograms were produced for each group composition, and the cutoff point was decided subjectively, based on the distance measure, as has been previously established (Stimpert et al. 2011, Fournet 2014). A secondary principal component analysis was performed to increase the certainty of cluster selections, and clusters were cross-checked across both methods.

Once call clusters were established for each group composition, several calls were randomly selected from each cluster and reviewed by one observer (JC), with a minimum of four calls reviewed for each cluster. This method was used to establish the most common call types recorded within each cluster of each group composition. However, some call types may not have been captured as not all calls were reviewed individually. The most common call types were then compared across all group compositions.

### *Temporal Patterns*

To investigate the temporal differences in calling behavior, we looked at the time periods between calls. For this analysis, all calls were used, including those eliminated from other analyses due to poor SNR. This was done so as not to skew the period between calls. Every call selection made in Raven measured the beginning and end time of the call based on the time boundaries of the selection. These time measurements were then used to calculate the time between social calls, where no signaling was recorded. This was calculated by subtracting the end time of a call from the beginning time of the proceeding call. This yielded a measurement of the number of seconds between calls. Because tag deployments lasted multiple hours but were viewed in 1-hour long wav files, the beginning of each file was recorded as though that file was the start of the tag deployment. Therefore, the time measurements needed to be adjusted to account for the time that elapsed from one 1-hour long file to the next. To accomplish this, the number of seconds within an hour (3,600 s) was added to the original measured time from recording and then multiplied by the number of hours that had elapsed from the start of the tag deployment.

### *Statistical Analysis*

The frequency measurements from all calls (Table 1) were compared across all group compositions and checked for statistical significance. A Kruskal-Wallis test was used to check for significant differences between all groups as a whole. Then to better understand the relationships within groups, a Wilcox-Pairwise test was used to test the differences between each group.

## Results

A total of 69.5 hours of acoustic recordings were collected from 12 deployments (Table 2) of Acousonde$^{TM}$ tags with 31.5 hours recorded in competitive groups, 22.1 hours recorded in escorted mother-calf pairs, and 15.9 hours recorded in dyads. A total of 1,102 individual social calls were selected throughout the entirety of recordings, with 736 calls meeting the requirements to be included in the analysis. Of the total calls, 52.2% were produced by competitive groups, escorted mother-calf pairs produced 34.9%, and dyads produced 12.9%. However, due to the differences in recording hours for each group, the call rate (calls/hour) was not significantly different between group compositions (Chi-square, p = 0.0671).

Table 2. Records of all 12 tags, including date of deployment, group composition, number of whales in the group, the role of the tagged whale, and tag on/off times. Names of group compositions have been abbreviated with comp representing competition groups, and MCE representing escorted mother-calf pairs.

| Date | Group Composition | Whales | Tagged Whale | Tag On | Tag Off |
|---|---|---|---|---|---|
| 2/26/2019 | Comp | 5-8 | n/a | 8:51:00 | 15:24:00 |
| 1/22/2020 | Comp | 4 | primary escort | 9:25:00 | 21:14:00 |
| 2/24/2021 | Comp | 3-4 | primary escort | 13:57:30 | 18:19:30 |
| 3/10/2021 | Comp | 6-7 | primary escort | 8:27:00 | 10:49:00 |
| 3/10/2021 | Comp | 6-7 | female lead | 11:20:00 | 17:48:00 |
| 2/25/2019 | Dyad | 2 | n/a | 9:57:30 | 13:49:30 |
| 1/24/2020 | Dyad | 2 | n/a | 10:32:00 | 19:37:00 |
| 1/27/2020 | Dyad | 2 | n/a | 9:23:00 | 12:18:00 |
| 1/21/2020 | MCE | 3 | mom | 9:56:00 | 13:42:00 |
| 2/3/2020 | MCE | 3 | mom | 15:04:00 | 17:12:00 |
| 2/3/2020 | MCE | 3 | mom | 15:59:00 | 2:11:00 |
| 2/8/2021 | MCE | 3 | mom | 10:37:30 | 16:35:50 |

### *Call Types*

Calls from each group composition were separated into clusters, with calls grouped based on the similarity of the measurements from Table 1. Calls from competitive groups and dyads could be separated into six distinct clusters, while calls from escorted mother-calf pairs were separated into seven clusters (Figure 2). Clusters were not matched across group compositions and were therefore displayed in different color palettes.

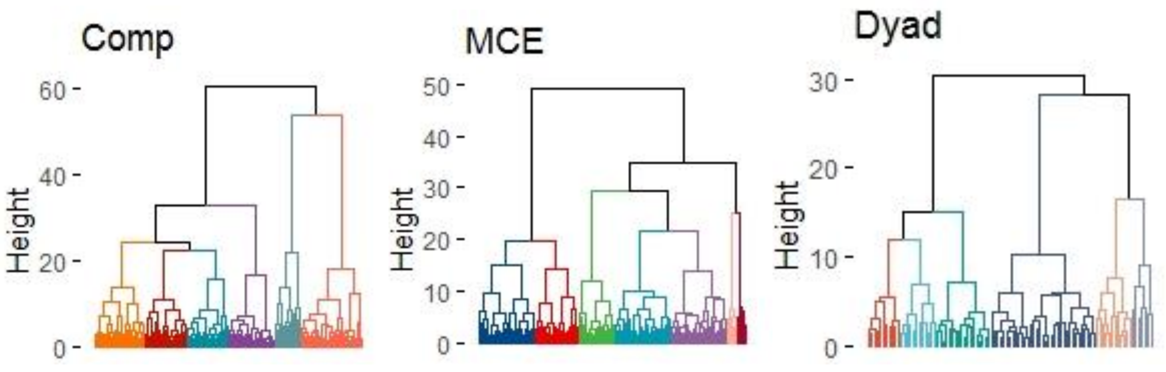

Figure 2. Cluster dendrograms for each group composition, showing the clusters into which calls were grouped. The colors used for each group composition differ to make clear the clusters within each group composition do not coincide with the clusters in the other groups and comparisons of the clusters themselves were not made across all groups.

From the review of calls within each cluster twenty-two of the most common social call types were established across all group compositions (Figure 3). Spectrograms for all twenty-two of these calls can be found in the appendix. Of these, four common call types including 'knocks,' 'squeaks,' 'bellows,' and 'moos,' were recorded across all group compositions (Figure 4). Escorted mother-calf pairs had the most call types shared across the groups, with three call types in common with competitive groups and five call types in common with dyads. Competitive groups only shared one call type (bark) in common with Dyads. Competitive groups had four unique call types, dyads had three, and escorted mother-calf pairs had two.

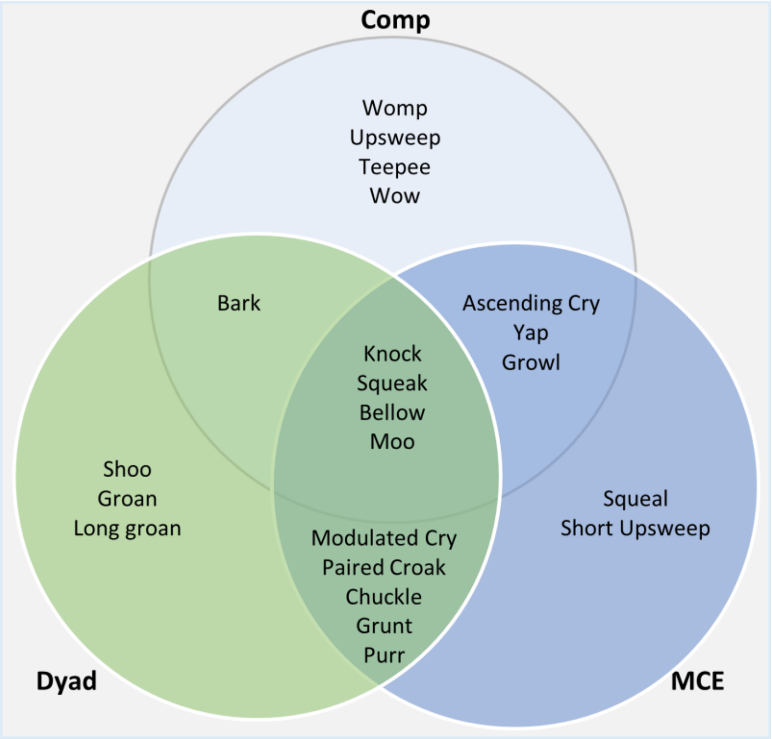

Figure 3. Venn diagram showing the most common calls recorded between three group compositions of humpback whales: competitive groups (comp), dyads, and escorted mother-calf pairs (mce). For spectrograms of each call see Appendix.

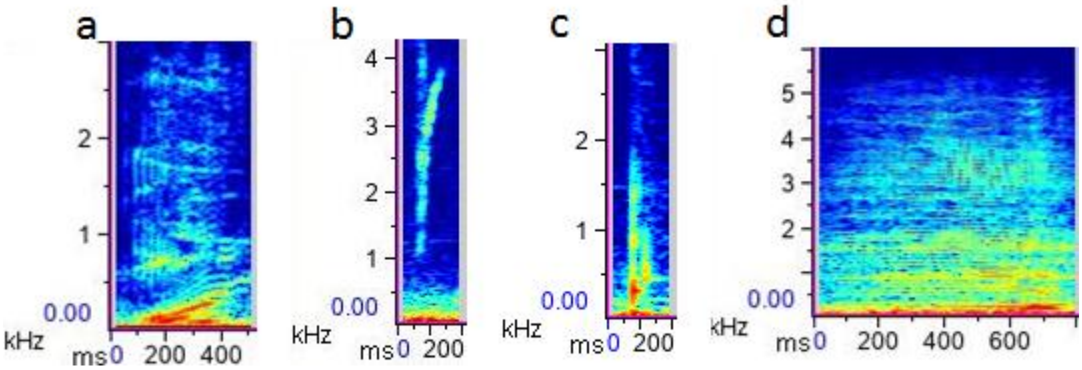

Figure 4. Spectrograms of the four common call types that were recorded across all group compositions: (a) bellow, (b) squeak, (c) knock, (d) moo.

*Time between calls*

The period between social calls where no social signals were recorded varied significantly across group compositions as a whole (Kruskal-Wallis, p = 1.09e-07) (Figure 5); however, the difference between escorted mother-calf pairs and dyads was not significant (Wilcox pairwise, p = 0.88955). The time between social calls ranged from 0 seconds (comp and mce) to 223 minutes (comp). The range of these values can be seen in figure 5 where the shape of the violin plots represents the probability of distribution of values throughout the data set. The median inter-call period was 0.548 seconds in competitive groups, 0.838 seconds in dyads, and 2.240 seconds in escorted mother-calf pairs. Dyads and escorted mother-calf pairs had long (> 10 s) inter-call time gaps more frequently than competitive groups. Competitive groups typically had shorter inter-call periods (mean = 135 s) than dyads (mean = 328 s) (p = 0.00062) and escorted mother-calf pairs (mean = 178 s) (p = 7.9e-07); however, the longest inter-call period was also recorded in this group composition (223 m).

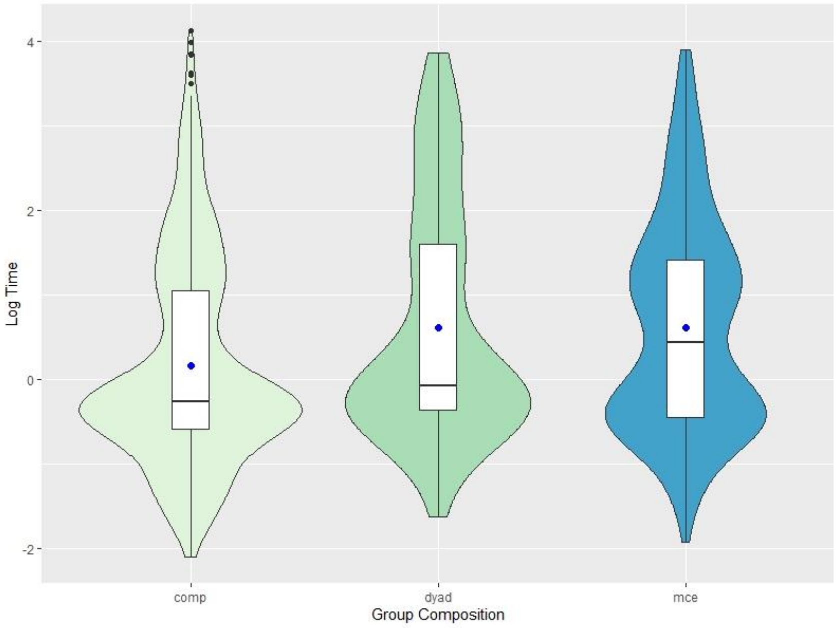

Figure 5. Violin plot depicting the logarithmic period (in minutes) between one call and the next, of all three group compositions: competitive groups (comp), dyads, and escorted mother-calf pairs (mce). The blue dot represents the mean values of each measurement. The internal box plot represents the median (centerline), interquartile range (box borders), and outliers (black dots). The surrounding kernel density plot shows the probability of distribution throughout the data set.

*Quantitative Analysis*

All mean measured frequency values were highest in escorted mother-calf pairs, except the fifth centile frequency. Mean peak frequency was 704 Hz in escorted mother-calf pairs, 684 Hz in competitive groups, and 453 Hz in dyads (Figure 6), with significant differences between all groups (Kruskal-Wallis, p = 3.74e-06; Wilcox pairwise, p < 0.0018). The mean center frequency was 810 Hz in escorted mother-calf pairs, 709 Hz in competitive groups, and 512 Hz in dyads, with significant differences between all group compositions (Kruskal-Wallis, p = 4.68e-09; Wilcox-pairwise, p < 0.0045). The mean first quartile frequency was 634 Hz in escorted mother-calf pairs, 601 Hz in competitive groups, and 410 Hz in dyads, with significant differences between all groups (Kruskal-Wallis, p = 4.88e-08; Wilcox-pairwise, p < 0.0016). The mean third quartile frequency measurement was 1026 Hz in escorted mother-calf pairs, 845 Hz in competitive groups, and 641 Hz in dyads with significant differences across all groups (Kruskal-Wallis, p = 4.13e-10; Wilcox-pairwise, p < 0.031). Fifth centile frequency measurements were the lowest frequencies with a mean of just 316 Hz in dyads, 437 Hz in escorted mother-calf pairs, and 475 Hz in competitive groups. Fifth centile frequencies varied significantly between all groups (Kruskal-Wallis, p = 1.36e-05 Wilcox-pairwise, p > 0.00709).

The ninety-fifth centile frequency measurements were the highest, with a mean of 1500 Hz in escorted mother-calf pairs, 1279 Hz in competitive groups, and 1066 Hz in dyads. The ninety-fifth centile frequency varied across groups as a whole (Kruskal-Wallis, p = 2.47e-06), but the differences measured between competition groups and dyads were not significant (Wilcox-pairwise, p = 0.0555).

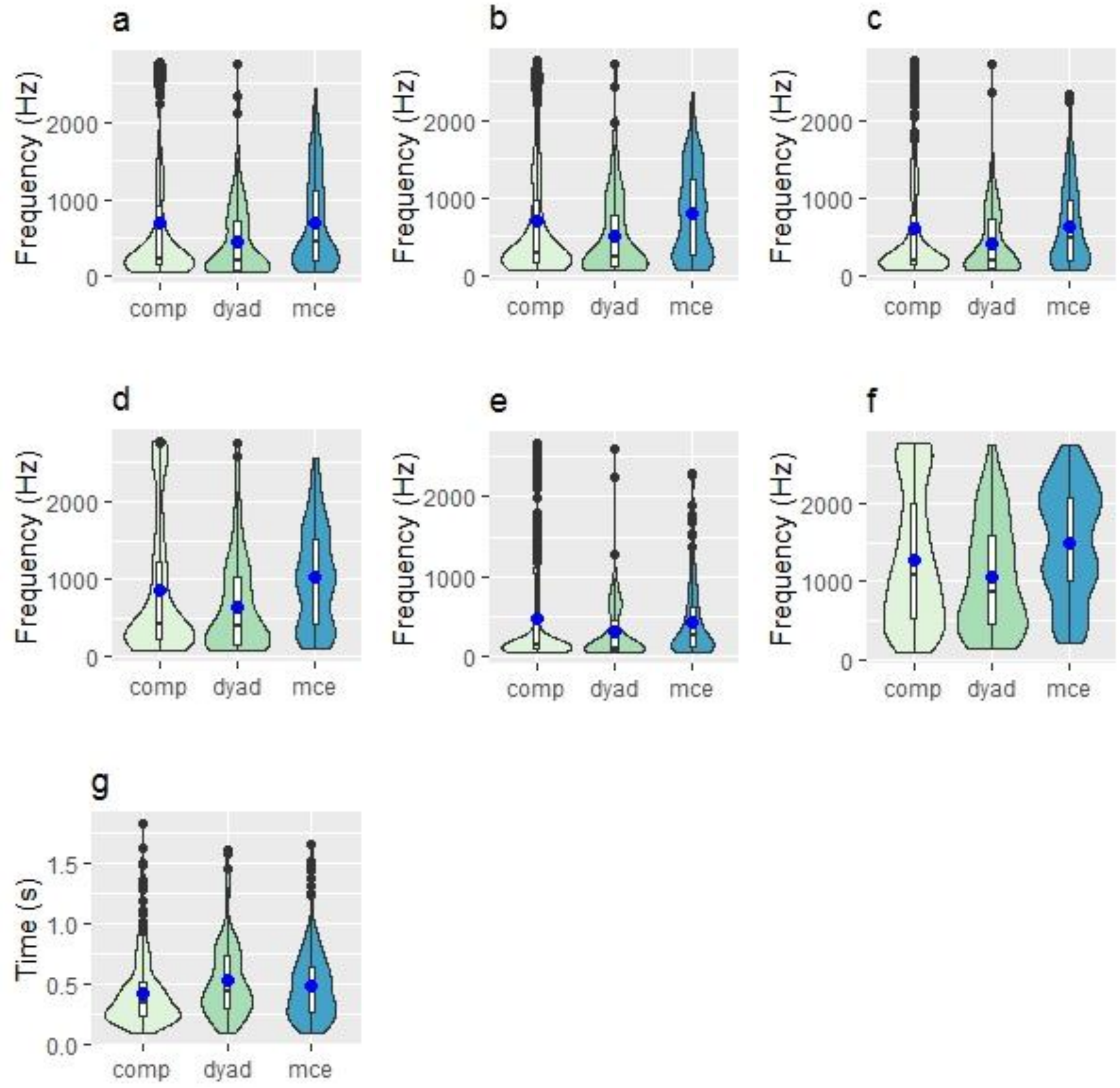

Figure 6. Violin plots showing the differences in (a) peak frequency, (b) center frequency, (c) first quartile frequency, (d) third quartile frequency, (e) fifth centile frequency, (f) ninety-fifth centile frequency, and (g) duration between three group compositions of humpback whales: competition groups (comp), dyads, and escorted mother-calf pairs (mce). The blue dot represents the mean values of each measurement. The internal box plot represents the median (centerline), interquartile range (box borders), and outliers (black dots). The surrounding kernel density plot shows the probability of distribution throughout the data set.

In addition to frequency measurements, the duration of calls was compared across all groups. The duration of calls was the longest in dyads, with calls averaging 0.523 seconds in length, followed by escorted mother-calf pairs (0.481 s) and competitive groups (0.418 s). While duration was significantly different across the three groups as a whole (Kruskal-Wallis, p = 7.73e-05), the difference in duration between dyads and escorted mother-calf pairs was not statistically significant (Wilcox pairwise, p = 0.31844).

## Discussion

While interest in the study of humpback whale social calls has grown in recent years (Dunlop et al. 2007, Stimpert et al. 2011, Rekdahl et al. 2013, Fournet et al. 2015, Rekdahl et al. 2015, Dunlop 2016, 2017, Rekdahl et al. 2017, Cusano et al. 2020, Indeck et al. 2020, Recalde-Salas et al. 2020), comparatively little work has been conducted to compare the social calling behavior across groups of varying composition. This study is among the first to examine variations of humpback whale social calling behavior between competitive groups, dyads, and escorted mother-calf pairs. We found that social call types were often shared across groups, but also that the frequency and temporal pattern in which these calls are produced varied significantly across all groups.

### *Call Types*

Of all the common calls recorded in our study, four call types were shared across all group compositions: 'bellows,' 'knocks,' 'squeaks,' and 'moos' (Figure 5). The 'knocks' and 'squeaks' observed in our study were named after knock and squeak calls previously recorded in Australia (Cusano et al. 2020) as they resembled these calls strongly both spectrally and in their acoustic properties, such as duration and frequency. It has been previously found that the use of these calls increased with the addition of single or multiple escorts to mother-calf pairs (Cusano et al. 2020). It has been suggested that the use of these calls may be related to the state of arousal of the signaler (Cusano et al. 2020). We observed the use of these calls in comparatively "low arousal" dyads, "moderate arousal" escorted mother-calf pairs, and “high arousal” competitive groups, suggesting perhaps a more nuanced relationship. However, because the common call types in our study were established from a random sampling of the data rather than a review of all individual calls recorded, further investigation is needed to confirm whether the rate at which 'knocks' were used significantly varied across groups.

Squeaks, which were commonly recorded in this study, were short, high-frequency, broadband calls (Figure 4). It has been suggested that broadband calls are easier to detect at close range and therefore best suited for close-range signaling (Waser 1982, Bradbury and Vehrencamp 2011). Therefore, the broadband nature and common use of squeaks across all group compositions suggest that this call may be important in communicating or maintaining contact with nearby group members.

### *Temporal Patterns*

The temporal patterns in which social calls are produced may indicate the motivational context and arousal of the signaler (Morton 1977, August and Anderson 1987, Cusano et al. 2020). Call rates may increase in situations that increase the arousal levels of the signaler, such as those associated with mating behavior (e.g. red deer, Clutton-Brock and Albon 1979). The temporal pattern of calling observed in competitive groups reflected the nature of these social interactions. These competitions can last for many hours (Tyack and Whitehead 1983, Clapham et al. 1992) and can be energetically costly for the whales involved. It is often observed that there are intense periods of aggressive behaviors (bubble streaming, head lunging, etc.) (Baker and Herman 1984, Herman et al. 2007) where attempts are made to overtake the dominant primary escort position, followed by periods of calm. Periods between calls in competitive groups were the shortest out of all groups, with just a few periods of extended silence between calls. It is possible that short inter-call periods occurred during periods of aggression in the competition and periods of silence coincided with breaks in the competition. This could indicate that social calls are used in competition to convey a heightened state of arousal from the signaler; however, longer periods of behavioral observation would be required to confirm this.

In contrast to competitive groups, escorted mother-calf pairs are not typically characterized by long displays of aggressive behavior amongst group members, although females will insert themselves between the escort and their calf as a physical barrier (Sardi et al. 2005). The increased periods of time between calls in escorted mother-calf pairs could be explained by the role an escort plays in these groups. Escorts are believed to remain close to mother-calf pairs in hopes that females will come into post-partum estrus (Chittleborough 1958, Pallin et al. 2018), and they might have the chance to mate. Alternatively, a singular escort may serve as protection from outside male harassment (Cartwright and Sullivan 2009). It is unlikely that either of these roles would require extensive communication within the group, which could explain the extended time periods between calls. Furthermore, the temporal patterns observed in this study may also be an attempt by mother-calf pairs to avoid detection by other whales. Mother-calf pairs have been shown to vocalize at a lower rate than other groups (Dunlop et al. 2008, Videsen et al. 2017) and it has been documented that whales adapt their signaling behavior in the presence of "bystanders" to avoid detection (Dunlop 2016). While the additional companionship of a single escort may be beneficial, (Cartwright and Sullivan 2009, von Ziegesar et al. 2020), on many occasions, the addition of escorts to a mother-calf pair increases energy expenditure (Craig et al. 2014) and could result in injuries to the calf or separation from its mother (Smultea 1994). This may explain why escorted mother-calf pairs produced social calls more infrequently than competitive groups. While these groups typically remained quiet, there was an exciting time in one tag deployment, which occurred after midnight, when the group began producing calls frequently. As there was, of course, no visual observations at this hour, it is difficult to determine what may have caused such a drastic change in calling behavior. However, studies have shown that at the time when an additional whale joins a group, there is often an increase in signaling (Silber 1986, Rekdahl et al. 2015). Furthermore, a recent study has suggested that mother-calf pairs increase their vocalization rate and use of call bouts, rather than single calls, when the number of escorts increases (Cusano et al. 2020). Therefore, it is possible that the joining of an additional escort could explain the increased calling rate, but this cannot be known for certain.

Of all the groups, dyads are associated with the lowest level of arousal and were expected to produce the fewest social calls. While these groups did produce the most infrequent calls out of all groups, we did not find the call rate (calls/hour) to vary significantly between groups. The temporal pattern in which calls were produced was not significantly different from that of escorted mother-calf pairs, with a relatively long inter-call period being observed. These results may be partly due to lower arousal levels in these group compositions. It may also reflect a reduced need for these whales to communicate acoustically when in close proximity (Cusano et al. 2020).

### *Call Measurements*

Previous studies have indicated that social calls produced in high arousal agonistic situations are generally higher in frequency and longer in duration than those produced in lower arousal situations (Lemasson et al. 2012). Our study suggests that this pattern is also found in humpback whales. Competitive groups had the median frequency values of all the groups.

Aversive calls are typically associated with higher frequencies (Morton 1977, August and Anderson 1987, Dunlop 2017), and aggressive calls are often characterized by lower frequencies and broader bandwidths, which has been observed previously in humpback whales (Dunlop 2017) and other species (e.g. elk, Feighny et al. 2006, e.g., white-faced capuchins, Gros-Louis et al. 2008). The combined use of aversive and aggressive calls in competitive groups likely explains the median frequency values observed in these groups.

Escorted mother-calf pairs produced the highest frequency calls of all the groups. The contribution of calf calls could potentially explain the high frequencies observed in these groups. To an extent, the minimum frequency of calls in mysticete whales is limited by animal size (May-Collado et al. 2007, Martin et al. 2017), with smaller animals being incapable of producing the lowest frequency calls. Therefore, if calf calls, which are recorded at higher frequencies (Zoidis et al. 2008, Indeck et al. 2020), contributed strongly to the social calls recorded, it could have skewed the mean toward a higher frequency. Additionally, escorted mother-calf pairs typically try to avoid the attention of male whales (Smultea 1994, Craig et al. 2014), which may make them more likely to produce aversive calls than the other groups. As previously mentioned, aversive calls are typically characterized by higher frequencies; therefore, the high frequency of calls observed in escorted mother-calf pairs could indicate that these calls are used to convey a heightened state of arousal or an aversion toward an unwanted escort.

While the results seen with the frequency measurements were consistent with expected patterns, the same could not be said for the duration of calls. High arousal contexts are typically associated with longer calls, and low arousal contexts are associated with shorter calls (Lemasson et al. 2012). The duration of calls in groups showed an inverse relationship to what was expected. Dyads, which are considered to have the lowest arousal levels, had the longest duration of their calls and competitive groups, which are deemed to have the highest arousal, had the shortest calls. The pattern that we observed in our study has also been seen in mother-calf pairs, where the duration of 'squeaks' was shown to decrease with the addition of escorts to mother-calf pairs (Cusano et al. 2020). Therefore, it is possible that the duration of humpback whale social calls is influenced by factors other than the level of arousal or that our assumptions about the arousal level of the groups sampled is incorrect.

### *Conclusion*

Our study makes progress toward a better understanding of social communication within humpback whale groups while also raising further questions that warrant investigation. For example, it would be useful to investigate how the position of a whale in a competitive group affects social signaling behavior. As the primary escort is the dominant position in a competitive group, it would be interesting to know if these whales signal more or less than their secondary counterparts. Furthermore, we still know little about how the gender of the signaler affects calling behavior. On more than one occasion in our study, when the tagged whale was presumed female, diverse calling behavior was observed, but it cannot be determined whether she was the signaler. While the analysis of acoustic signaling in humpback whales remains difficult, studies like this one continue to increase our understanding of the social signaling behavior of this species and provide guidance for the path ahead for future studies.

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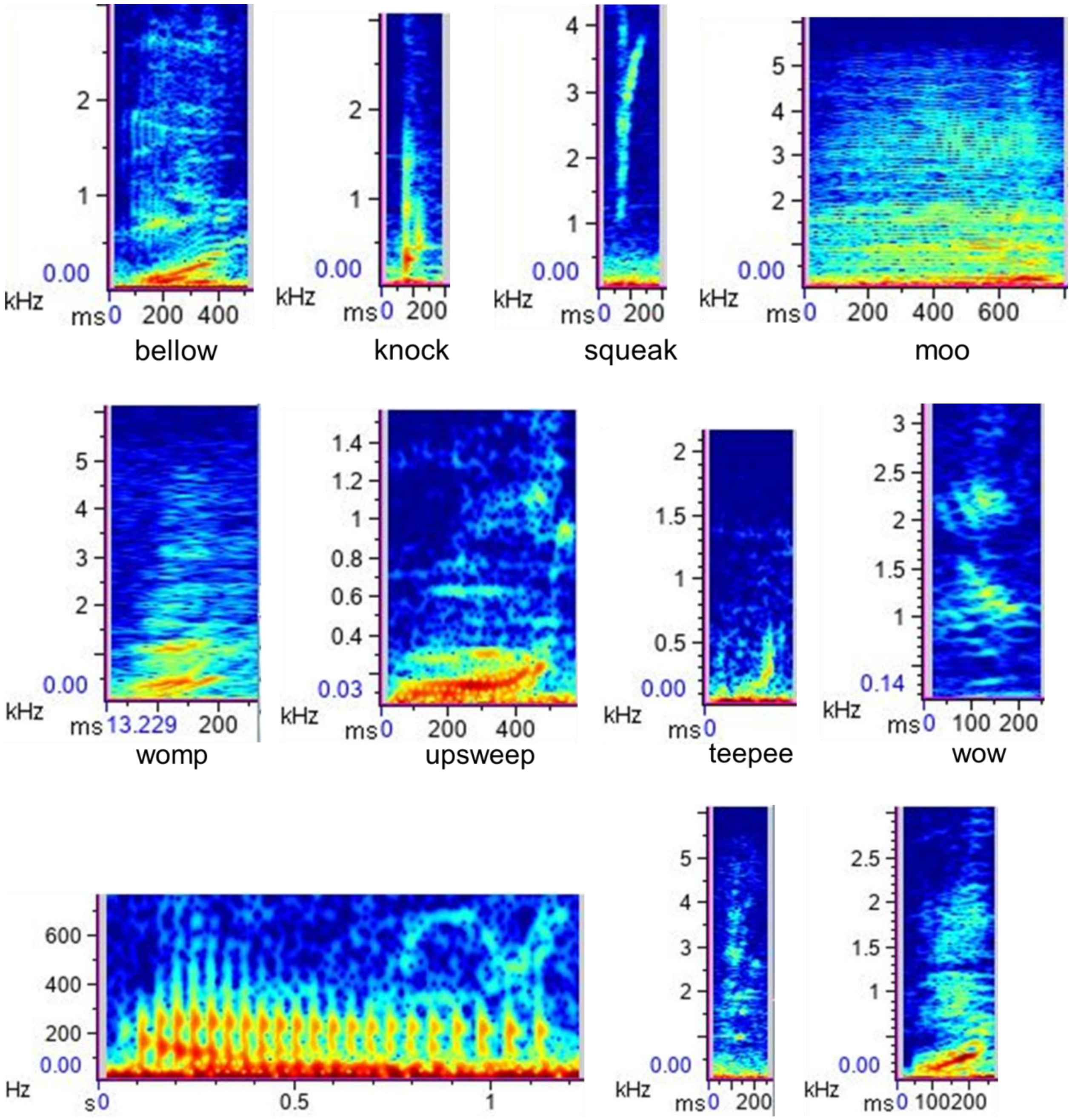
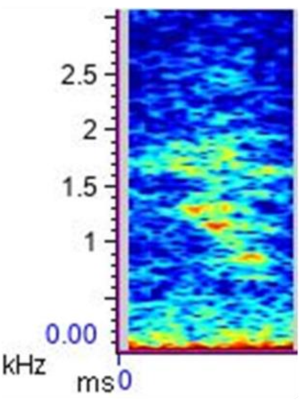
**Appendix -** Spectrograms of all twenty-two common social call types recorded.



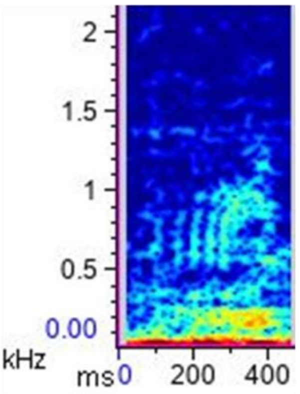
bellow knock squeak moo

womp upsweep teepee wow

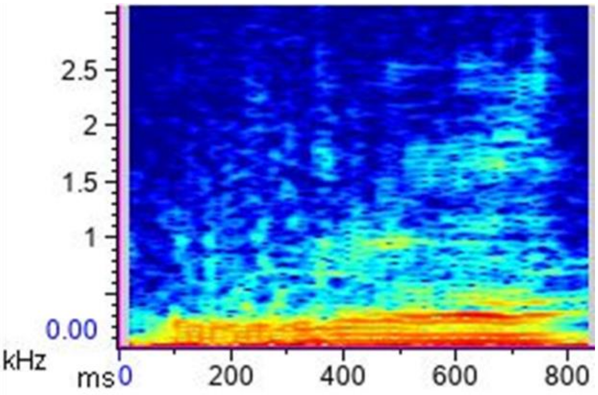
purr squeal short upsweep



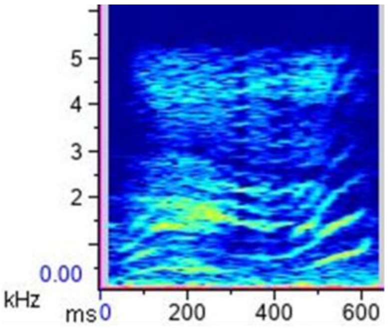
shoo



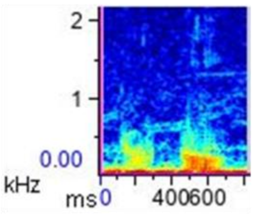
groan



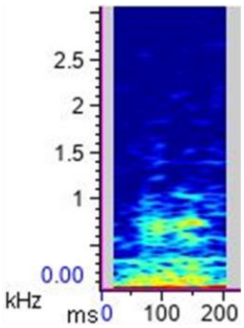
long groan



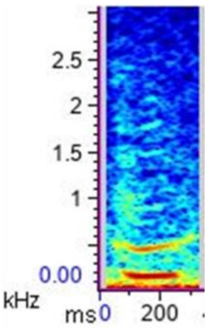
modulated cry



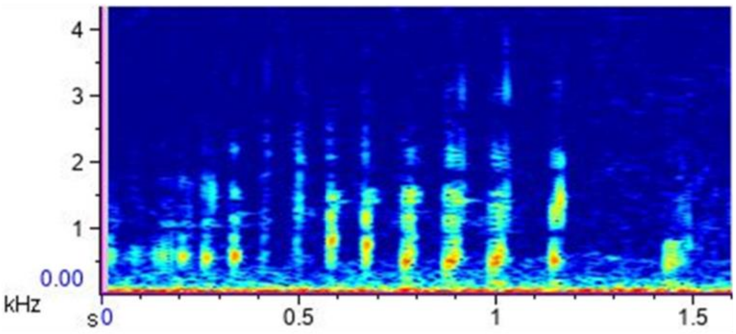
paired croak



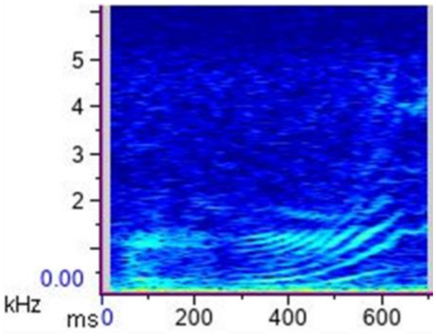
grunt



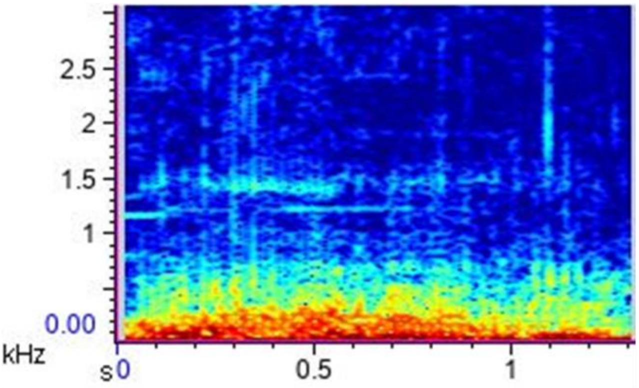
bark



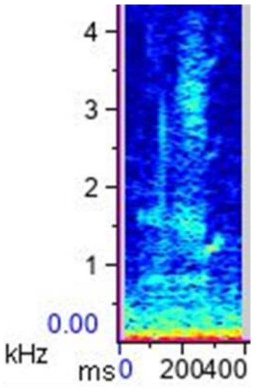
chuckle



ascending cry



growl



yap