UNIVERSIDADE FEDERAL DE JUIZ DE FORA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE E CONSERVAÇÃO DA NATUREZA

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Alterations in the acoustic production of odontocetes across co-occurrence contexts

JUIZ DE FORA
2023

Juiz de Fora
2023

Yasmin Viana Pinto

Possible alterations in the acoustic production of odontocetes in co-occurrence contexts

Tese apresentada ao Programa de Pós-graduação em Biodiversidade e Conservação da Natureza da Universidade Federal de Juiz de Fora, como parte dos requisitos necessários à obtenção do grau de Doutorado em Biodiversidade e Conservação da Natureza na área de Concentração: Comportamento, Ecologia e Sistemática.

Orientador: Dr. Artur Andriolo
Coorientador: Dr Thiago Amorim

Ficha catalográfica elaborada através do programa de geração
automática da Biblioteca Universitária da UFJF,
com os dados fornecidos pelo(a) autor(a)

Viana Pinto, Yasmin.

Alterations in the acoustic production of odontocetes across co-occurrence contexts / Yasmin Viana Pinto. -- 2023.

111 f. : il.

Orientador: Artur Andriolo

Coorientador: Thiago Orion Simões Amorim

Tese (doutorado) - Universidade Federal de Juiz de Fora, Instituto de Ciências Biológicas. Programa de Pós-Graduação em Biodiversidade e Conservação da Natureza, 2023.

1. cetáceos. 2. vocalizações. 3. interação interespécies. I. Andriolo, Artur, orient. II. Orion Simões Amorim, Thiago.

YASMIN VIANA PINTO

Alterations in the acoustic production of odontocetes across co-occurrence contexts

Tese apresentada ao Programa de Pós-Graduação em Biodiversidade e Conservação da Natureza da Universidade Federal de Juiz de Fora como requisito parcial à obtenção do título de Doutora em Biodiversidade e Conservação da Natureza. Área de concentração: Comportamento, Ecologia e Sistemática.

Aprovada em 25 de agosto de 2023.

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DEDICATÓRIA

Dedico esta tese aos meus pais, Darci e Agnaldo e ao meu irmão, Yago (John), que vibram a cada uma de minhas conquistas e me apoiam desde criança em minha jornada de "baleióloga" ou "bichóloga", como diz o Vô Tião.

...Um conto iniciado outrora,
Sob o sol tépido do verão –
Mera cantiga, que apenas marcava
O ritmo de nossa embarcação–
Cujos ecos na memória persistem
E ao desafio dos anos resistem.
Somos só crianças crescidas, querida,
Inquietas, até que o sono nos dê guarida
– Lewis Carrol, em Através do Espelho

...Vozes grossas de tios avós
Conversas em meio ao silêncio
Móveis de madeira antiga
Infância entre besouros
Que entravam pela janela

Quero do passado
O que não deixamos pra trás
Um presente
De não se esquecer jamais
E meu futuro amarradinho
Esperando-me no cais.
- Ana Paula Rodrigues

AGRADECIMENTOS

"Lá de volta e outra vez…"
Gostaria de agradecer a todos que fizeram parte de minha jornada, obrigada pela partilha! De experiências, conhecimentos, risadas e silêncios e cafés.

Agradeço aos meus orientadores, Artur e Thiago, por me inspirarem com suas histórias e caminhadas (no mundo acadêmico e na vida), com vocês muito aprendi e me sinto tão sortuda por terem acreditado em mim e no trabalho desde o início. Obrigada pelas conversas, atenção e paciência.

Aos meus amigos LABEC/IA pela amizade, parceria e por me ajudarem tanto, inclusive a ingressar no doutorado! Sim, fizeram um verdadeiro mutirão para providenciar os documentos da inscrição. Vocês são demais! Um salve também pela torcida que fizeram em minhas apresentações orais nas RT-SOLAMAC! Alô também pro mutirão das análises dos cliques e assobios, helps nas plotagens dos gráficos e mapas e tratamento das fotos. Muito obrigada, queridos amigos: Fran, Nat, Rapha, Larissa, Gabi, Anne, Erika, Giovanne, Joice, Zé, Gustavo, Lucas, Mário. Às estagiárias Luana e Paloma pela extração dos cliques e assobios e em especial à Bárbara por toda ajuda na reta final com a formatação e João pela ajuda com cálculo dos índices.

Agradeço à minha família, meus pais, Darci e Agnaldo e meu irmão, John por apoiarem meus sonhos. Meus primos Ana P. e Tote pelas conversas que engrandeceram as discussões sobre o trabalho e por toda ajuda quando na minha primeira vez na 'zoropa' para a World Marine Mammal Conference. Falando na WMMC19, eu não poderia deixar de agradecer de todo coração à equipe VIVA, em especial à Mia Morette e à Marina Leite e Juliana Molás (*in memorian*) que através do auxílio recebido, pude realizar o sonho de apresentar os primeiros resultados do meu doutorado em um congresso da Society for Marine Mammalogy e European Cetacean Society. Obrigada por acreditarem no meu trabalho, meninas!

Agradeço aos meus grandes amigos Milton e Julia (Jujubinha) pelos conselhos, amizade (que por sinal completou 10 anos que nos conhecemos esse ano!), parceria e momentos vividos. Obrigada por serem minha família! Falando em família, um agradecimento especial à Marina, minha eterna "sister-in-law", pela amizade, apoio e inspiração.

Ao Rafael por ter sido tão companheiro e amigo. Por tantos momentos divididos, pelo apoio e importantes discussões que me ajudaram a enxergar situações diversas sob diferentes ângulos.

Ao Gilson e Luz, grandes amigos e super vizinhos, obrigada pelas conversas, rolês e ajuda com o Huguinho, juntamente com nossos amigos do Catan, Gabriela, André e João. Por falar no Hugo, obrigada Luana e Guilherme, por terem me ajudado tanto com o com ele, meus eternos vizinhos e amigos super legais.

Agradeço também à Mariana Santos pela contribuição com as informações dos grupos mistos. Ao Dr. Robin Baird, Dr. Alexandre Zerbini e Dra Liliane Lodi pelo auxílio na confirmação das espécies fotografadas.

Ao Hugo, Arpi e cetáceos por me acalmarem e inspirarem.

Ao Programa de Biodiversidade e Conservação da Natureza, às
meninas da secretaria, Rosi, Priscila, Dayane e Marlú, que sempre me ajudaram com prontidão.

À Universidade Federal de Juiz de Fora, e à CAPES pelo fornecimento da bolsa.

Ao Instituto Aqualie e Auset pelas oportunidades e suporte logístico.

Aos membros da banca por sua disponibilidade e tempo fornecido na leitura e comentários para enriquecimento da presente tese.

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RESUMO

Contextos de co-ocorrência entre odontocetos – Parvordem Odontoceti, Infraordem Cetacea - têm sido recorrentemente relatados; no entanto, as implicações da coexistência de espécies no espaço acústico ainda não estão claras. Uma vez que os odontocetos dependem fortemente dos sinais acústicos para forragear, navegar e se comunicar, compreender se as espécies alteram o uso e a estrutura dos sinais acústicos entre os diversos contextos de co-ocorrência de cetáceos pode aprimorar a compreensão do papel acústico na identificação de espécies, comportamento e interações ecológicas. A fim de avaliar o papel acústico e verificar se a estrutura acústica das vocalizações das espécies é afetada nessas interações, a presente tese foi organizada em três capítulos: O primeiro capítulo consiste em uma revisão bibliográfica sobre diferentes contextos de co-ocorrência sob a ótica acústica entre espécies de cetáceos, com foco em odontocetos, e discute as estratégias, especialmente as estratégias acústicas, empregadas por essas espécies em diferentes interações. Os capítulos dois e três utilizaram dados coletados no Oceano Atlântico Sul Ocidental por meio de uma matriz de arrasto acoplada com hidrofones em sua extremidade para avaliar a estrutura acústica entre grupos mistos (MSGs) em comparação com grupos de espécies sozinhas (SSGs). A revisão bibliográfica mostrou a dependência de fatores comportamentais, sociais e filogenéticos na resposta acústica dos animais envolvidos em uma interação interespécie. O capítulo dois utilizou a análise dos assobios para investigar as relações acústicas de *Tursiops truncatus* quando envolvido em diferentes contextos de grupo: em MSGs com outras duas espécies de delfinídeos e em SSGs. Para verificar as diferenças entre os assobios produzidos nesses contextos, foram implementadas análises de máquina de vetores de suporte e random forest. Ambas as análises mostraram uma nítida separação dos assobios dos MSGs em relação aos SSGs, bem como entre os próprios MSGs. Os resultados indicam que as associações interespecíficas podem influenciar a estrutura dos assobios e sugerem que os assobios de *T. truncatus* podem ser modificados durante interações interespecíficas. O capítulo três teve como objetivo avaliar o papel acústico e possíveis mudanças acústicas entre SSGs de *Peponocephala electra* e e MSGs formados por essas espécies através de modelos de classificação random forest construídos a partir dos cliques e assobios produzidos nesses contextos. De maneira geral, os resultados apresentaram diferenças na classificação dos diferentes sinais acústicos (cliques e assobios) ao classificar contextos de SSGs e MSGs: os cliques dos MSGs apresentaram uma baixa taxa de erro de classificação com os SSGs, enquanto os resultados da classificação dos assobios mostraram uma taxa maior de erro de classificação entre MSGs x SSGs em comparação com a classificação entre SSGs. Os resultados apresentam indicativos de que espécies simpátricas podem utilizar estratégias acústicas diferentes para coexistir, influenciadas pela natureza da co-ocorrência, comportamento e espécies envolvidas, uma vez que os odontocetos dependem da acústica para sobrevivência. Os resultados apresentados são úteis para a compreensão das implicações acústicas na formação e interação de grupos interespecíficos e são importantes para elucidar os possíveis fatores subjacentes à plasticidade comportamental e associações interespecíficas, além de aumentar a compreensão acerca da comunicação acústica dos golfinhos.

Palavras-chave: produção acústica, simpatria, cetáceos, grupos mistos.

ABSTRACT

Co-occurrence contexts among odontocetes – Parvorder Odontoceti, Infraorder Cetacea - have been reported by many scientists, yet, the implications of these coexistences in the acoustic space remain unclear. Once odontocetes rely on acoustic signals to forage, navigate and for social communication, understanding if species alter the use and structure of acoustic signals among the diverse cetacean co-occurrence contexts may enhance a better comprehension of the acoustic role on species identification, behavior, and ecological interactions. In order to evaluate the acoustic role and assess whether acoustic structures are affected within these interactions, this thesis was organized in three chapters: The first chapter consists on a literature review on different co-occurrence contexts under the acoustics perspective across cetacean species, focusing on odontocetes, and discussing the strategies, specially the acoustic strategies, employed by these species among different interactions. Chapter two and three used data collected in the Western South Atlantic Ocean through a towed array of hydrophones to evaluate acoustic structure among mixed-species groups (MSGs) compared to single-species groups (SSGs). Chapter one used whistles to investigate the acoustic relationships of *Tursiops truncatus* when involved in different group contexts: in MSGs with two other delphinid species and in SSG. Acoustic recordings of *T. truncatus* single species groups and in associations with *Globicephala melas* and *Grampus griseus* were collected. In order to verify the differences among whistles produced in such contexts a support vector machine and random forest analysis were implemented. Both analyses revealed a clear separation of whistles from the SSGs *versus* the MSGs as well as between both MSGs. The results indicate that interspecific associations may influence the whistle structure and suggest that *T. truncatus* whistles can be modified during interspecific interactions. Chapter three aimed to evaluate the acoustic role and possible acoustic changes between SSGs of *Peponocephala electra* and *Stenella attenuata* and MSGs formed by these species through random forest classification models of clicks and whistles produced among these contexts. Overall results showed differences on the classification under distinct acoustic signals when classifying single and mixed species contexts: the MSGs clicks presented a low percentage of misclassification with the SSGs whereas whistle classification results showed a higher misclassification rate among MSGs x SSGs compared to the classification between SSGs. The results from this study point that sympatric species may use different acoustic strategies to co-exist, influenced by the nature of the co-occurrence, behavior and species involved since odontocetes depend strongly on acoustics for survival. The presented results can be helpful on the understanding of the acoustic implications on interspecies group formation and interaction and are also important to elucidate the possible factors underlying behavioral plasticity and interspecific associations and to understand dolphins’ acoustic communication.

Keywords: odontocetes, sympatry, co-occurence, mixed-species groups.

1. GENERAL INTRODUCTION

Co-occurrence can be defined as the simultaneous presence of multiple species in a habitat or ecological community, whose study serves as an important component in order to understand biodiversity and the complexity of its relations. This phenomenon provides an opportunity to investigate species interactions, resource partitioning, and the mechanisms that promote species coexistence (CODY; DIAMOND, 1975; GILPIN; DIAMOND, 1982; GOTELLI, 2000; WEBB et al., 2002; VEECH, 2013; POLLOCK et al., 2014; SYME; KISZKA; PARRA, 2023).

While both theoretical models and empirical studies support the influence of ecological interactions on co-occurrence, it is important to note that co-occurrence itself does not provide direct evidence of ecological interactions between species (BLANCHET; CAZELLES; GRAVEL, 2020). Co-occurrence patterns can manifest in different ways, including associations in which there are benefits gained by coexisting species; competitive or predator-prey relationships, which indicate potential conflicts or predator avoidance strategies and random occurrences, which may arise from stochastic processes or environmental factors that influence species distributions (HUTCHINSON, 1957; CHESSON, 1978; CONNOR; SIMBERLOFF, 1979; WEIHER; KEDDY, 1999; ABRAMS, 2000; WEBB et al., 2002; MEMMOTT et al., 2006; THOMPSON, 2009; JORDANO, 2016).

Sympatry refers to the co-occurrence of two or more ecologically similar species in the same immediate habitat (JORGENSEN; FATH, 2008). There are various strategies employed by different species to coexist sympatrically, and thus, minimizing the likelihood of direct competition for resources. These strategies include the selection of a distinct microhabitat of choice, and the employment of behavioral, dietary, and physiological adaptations to establish habitat specializations, thereby avoiding direct competition (ROUGHGARDEN, 1976; BEARZI, 2005).

When species with similar resource requirements coexist in the same habitat, they often exhibit resource partitioning to reduce competition (ROUGHGARDEN, 1976; PIANKA, 1974). The differentiation of ecological niches may reduce the occurrence of competition for resources when species are in direct sympatry (BEARZI et al., 2003). Therefore, niche partitioning allows species to coexist sympatrically (GRINNELL, 1924; CHESSON, 2000; TOKESHI, 2009; SYME; KISZKA; PARRA, 2023a; SYME; KISZKA; PARRA, 2023b). Species can also hybridize, which is part of the evolution of lineages. To minimize acoustic overlap, species adopt a strategy of vocalization distribution by establishing an acoustic niche, encompassing spatial, temporal, and acoustical characteristics of their vocalizations (KRAUSE, 1993; DUARTE et al., 2019; VAN DER MESCHT et al., 2022). The acoustic niche hypothesis suggests that a species can adjust the frequency and/or temporal aspects of its sound emissions to prevent acoustic masking caused by signal overlap (KRAUSE, 1993; MOSSBRIDGE; THOMAS, 1999; SINSCH et al., 2012). This adaptive behavior allows for effective communication and reduces interference in acoustic signaling within a given ecological context. Other contexts that do not necessarily have a relationship with the acoustic niche hypothesis can also elicit acoustic responses and the adjustment of acoustic features such as agonistic encounters and predator-prey relationships (MAY-COLLADO, 2010; PARKS et al., 2019; NIELSEN et al., 2019).

Odontocetes possess acoustic repertoires encompassing various vocalizations used for communication, navigation, prey foraging, group cohesion, and predator avoidance. They are known to produce tonal frequency-modulated whistles, as well as broadband pulsed clicks and burst sounds (AU et al., 2008). The patterns of production for these acoustic signals exhibit variations influenced by factors such as geographic location, behavioral state, and the spatial arrangement of conspecifics (JONES; SAYIGH, 2002; LAMMERS; AU; HERZING, 2003; NOWACEK, 2005). Whistles are narrow-band frequency-modulated tonal sounds employed in intraspecific communication during social interactions (HERMAN, 1980; AU; HASTINGS, 2009). Whistles play important roles in parental care, individual recognition, group cohesion, and mating (JANIK; SAYIGH; WELLS, 2006; LAMMERS; SCHOTTEN; AU, 2006; ANDRIOLO et al., 2015; KING et al., 2016; KING et al., 2019). Pulsed signals, such as clicks and burst sounds are used primarily for echolocation but may also play a role in social communication (KLINCK; MELLINGER, 2011; YOSHIDA et al., 2014; ARRANZ et al., 2016; PÉREZ et al., 2017). Different instances of species co-occurrence among various odontocete members have been documented on a global scale (e.g., HERZINGL; JOHNSONZ, 1997; BENTI et al., 2021 COSENTINO et al., 2022). Therefore, given the significant number of interspecies co-occurrence contexts and the odontocetes' acoustic dependency, this thesis aims to evaluate the acoustic role within these interactions by examining whether acoustic structures are affected by species coexistence. The goal of chapter one of this doctoral dissertation is to review the present literature on the acoustics of different co-occurrence contexts across cetacean species, focusing on odontocetes, and discussing the strategies employed by these species among different interactions. Chapters two and three aimed to evaluate the acoustic role and possible acoustic changes between mixed and single species groups.

The study of the diverse odontocete co-occurrence contexts has important implications for our understanding of these animals' behavior, ecology, and conservation (DEECKE; FORD; SLATER, 2005; GOODALE; BEAUCHAMP; RUXTON, 2017; SYME; KISZKA; PARRA, 2021; MILLER et al., 2022). The identification of acoustic trends among species interactions provides valuable information into the intricate relationships between species (MAY-COLLADO, 2010). Investigating the factors influencing and influenced by species co-occurrence can aid in identifying key ecological interactions and consequently, prioritize conservation efforts, protect critical habitats, and mitigate potential negative impacts under changing environments as these interactions may influence the distribution, abundance, and genetic diversity of different species.

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CHAPTER I

2. ODONTOCETE CO-OCCURRENCE THROUGH THE ACOUSTICS PERSPECTIVE: A REVIEW

2. 1 INTRODUCTION

The species occurrence at the same time and space may imply the adoption of strategies to co-exist (KYHN et al., 2013). Many species rely on acoustics signals for communication, orientation in the environment, prey foraging, and predator avoidance. The use of acoustic tools can be of great usefulness in evaluating the influence of species co-occurrence on the general behavior and ecology dynamics of a great variety of interspecies interactions, from predation to mixed-species groups. It allows investigating if specie's co-signal, interact, and/or compete for the acoustic space.

Cetaceans are considered important components of ocean biodiversity since they play key roles in ecosystems' function and structure by reflecting ecological changes, influencing the material fluxes and species diversity (MOORE, 2008; BELLANTE et al., 2012; MANNOCCI et al., 2014; ROMAN et al., 2014; BRAULIK et al., 2018). These animals have an extraordinary ability to communicate using sound. Their acoustic signals are crucial in various aspects of their lives, such as social interaction, mating, foraging, and navigation (AU, 1993; AU; GREEN, 2000; AU; HASTINGS, 2009). Because this group depends strongly on acoustics for survival, understanding the acoustic dynamics among the diverse cetacean co-occurrence contexts may enhance a better comprehension of the acoustic role on species identification, behavior, and ecological interactions.

In the present chapter we review the co-occurrence studies among cetacean species, focusing on odontocetes, and discuss the spatiotemporal superposition through the acoustics perspective. Finally, we address the possible implications of these superpositions on cetacean behavior and ecology.

2.2 SECTION I - Different cross-species co-occurrences

Some animal species tend to assemble fluidly, coming together and moving collectively in the same direction, and then in some cases separating again (GOODALE; BEAUCHAMP; RUXTON, 2017). The main drivers of these assemblages can be of different natures, such as antipredator and feeding advantages, social factors, and attraction to a common resource (CLUA; GROSVALET, 2001). Characterizing these different contexts of interspecies occurrence is challenging, especially in free-range moving species such as cetaceans. Syme et al. (2021) characterize different interspecies assemblages among different species (Table 1). There are aggregations, mixed-species groups and chance encounters and it is important to differentiate them based on functional benefits: This distinction involves assessing whether there is attraction among individuals, indicating the formation of a cohesive group, or if their spatiotemporal proximity is merely a result of overlapping habitat preferences or shared attraction to resources, indicating chance encounters or aggregations (WASER, 1984; WHITESIDES, 1989; GOODALE; BEAUCHAMP; RUXTON, 2017).

Co-occurrence patterns can take various forms, including competitive or predator-prey relationships, signifying the possibility of conflicts or predator avoidance strategies. Predator-prey interactions involve the pursuit, capture, and consumption of prey by predators, affecting prey populations through mortality and selective pressures (MINELLI, 2008). Various mechanisms, such as predator-foraging strategies, prey defenses, and environmental factors, influence the dynamics of these interactions. Predation can regulate prey populations, influence community structure, and drive evolutionary adaptations in predator and prey species. Understanding of species co-occurrences complexities may enhance a better comprehension of species coexistence, ecosystem functioning and, consequently, the conservation and management of natural systems (STEELE; THORPE; TUREKIAN, 2009; JESCHKE et al., 2022).

Table 1 Glossary of terms

Term	Definition	References
Mixed-species group	A set of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group.	STENSLAND; ANGERBJÖRN; BERGGREN, 2003
Chance encouter	A set of individuals of two or more species that are found in spatial proximity due to chance alone.	WASER, 1982 WHITESIDES, 1989
Aggregation	A set of individuals of two or more species that are dound in spatial proximity because they are attracted toward a common resource or respond to the same environmental stimuli.	WASER, 1982 POWELL; STOKER, 1985 GOODALE; BEAUCHAMP; RUXTON, 2017

Adapted from SYME, J.; KISZKA, J. J.; PARRA, G. J. Dynamics of Cetacean Mixed-Species Groups: A Review and Conceptual Framework for Assessing Their Functional Significance. **Frontiers in Marine Science**, v. 8, n. 678173, jun. 2021.

2.3 SECTION II - Species co-occurrences and the acoustic role

Few studies have addressed acoustic interspecies interactions in cetaceans (DING; WÜRSIG; LEATHERWOOD, 2001; MAY-COLLADO, 2010; HERZING, 2015; COSENTINO et al., 2022; VIANA et al., 2022). The acoustic niche theory suggests that species tend to distribute their vocalizations through the acoustic space to avoid acoustic overlap by developing an acoustic niche, which involves the spatial, temporal, and acoustical characteristics of their sounds (KRAUSE, 1993; DUARTE et al., 2019; VAN DER MESCHT et al., 2022). Sympatric species commonly present different acoustic features to optimize intraspecies communication and segregate conspecifics from heterospecifics (STEINER, 1981; MATYJASIAK, 2005; ESKESEN et al., 2011; KYHN et al., 2013; ANDRIOLO et al., 2015; KAPLAN; REISS, 2017). Ding et al. (2001) found apparent frequency segregation between the Amazon River Dolphin (*Inia geoffrensis)* and the Tucuxi (*Sotalia fluviatilis)* mixed-species groups, in which the lower frequencies would be occupied by the former and the higher frequencies by the latter. This hypothesis was reinforced by analyzing recordings from both species' single species groups, yet the authors emphasize the need for more data since conclusions were based on few recordings.

Aggressive non-predatory encounters among cetacean species have been documented (PALACIOS; MATE, 1996; CIANO; JOORGENSEN, 2000; WEDEKIN; DAURA-JORGE; SIMÕES-LOPES, 2004; COTTER; MALDINI; JEFFERSON, 2012; BACON; MACKAY, 2019; CRESPO-PICAZO et al., 2021) and yet, the acoustic role beyond these interactions remains unclear. Different synchronized signals were found among intra and interspecific aggressions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*): individuals using acoustic rhythmic signals, leading to the coordination of movements The timing between sounds in various dolphin vocalizations indicates the significance of temporal aspects in individual and group coordination. This highlights the importance of behavioral synchronization through rhythmic signals for coordinated movements in dolphins (HERZING, 2015). Palacios & Mate (1996) reported distinctive, high-pitched whistles produced by false killer whales (*Pseudorca crassidens*) on an aggressive encounter with sperm whales (*Physeter macrocephalus*). Whistles are known as communicative sounds involved in individual recognition and group cohesion used during social contexts (JANIK; SLATER, 1998; HERZING, 2000; LAMMERS; AU; HERZING, 2003; JANIK; SAYIGH; WELLS, 2006; LAMMERS; SCHOTTEN; AU, 2006; ANDRIOLO et al., 2015; KING et al., 2016, 2019). Clicks and codas produced by the attacked species were also heard at more irregular intervals. Codas are sounds known to be involved in social communication in clans among sperm whales (WEILGART; WHITEHEAD, 1997; GERO; WHITEHEAD; RENDELL, 2016; AMORIM et al., 2020). It was hypothesized that the harassment could be a way to force the pursued animal regurgitate a recent meal (kleptoparasitism), consequently reducing energy expenditure required while foraging (SMULTEA; BACON, 2012; CORDS; WÜRSIG, 2014; BACON et al., 2017). In one agonistic encounter between short-finned pilot whales (*Globicephala macrorhynchus)* and sperm whales, the last species maintained a stereotypical steady vocal pulsing, while the pilot whale produced mostly infrequent whistles, with occasional burst pulse signals (WELLER et al., 1996). The authors also report the production of several four-, six-, and seven-pulse codas by the sperm whales at the start and end of the interaction, and once the pilot whales departed the area, and after a series of codas, the sperm whales slowly became silent. Cephalopod pieces regurgitated from the sperm whales were also present. Diáz-Gamboa et al. (2022) reported a change in acoustic emissions by sperm whales minutes before the approximation of a pod of short-finned pilot whales; specifically, they changed the vocalizations from usual clicks to codas and creaks and also began making shallow dives. In both reports, Weller et al. (1996) and Diáz-Gamboa et al. (2022) hypothesize that food competition is a possible driver of this harassment, either by competitive exclusion or by food robbery. Other hypotheses raised were play or training predation practices as described in Arnbom (1987) for killer whales (*Orcinus orca*) attacking a group of sperm whales. Food competition was also one of the possible drivers hypothesized by Selbmann et al. 2022 to agonistic interactions between killer whales and long-finned pilot whales (*Globicephala melas*), where the latter was found pursuing the killer whales in a chase. Furthermore, playback experiments with killer whale vocalizations showed strong attraction towards the sound by both short- and long-finned pilot whales (CURÉ et al., 2012, 2019; BOWERS et al., 2018). Courts et al. (2020) found a possible mimicking of killer whale vocalizations by sympatric long-finned pilot whales. The authors discussed this acoustic approximation as an anti-predator mechanism to mask the caller while allowing the food scavenge of remnants from killer whales.

Behavioral plasticity by altering the aggressive behavior based on the opponent when facing an agonistic encounter has been documented (RELYEA, 2001; VOLKER; HERZING, 2021). Whistles recorded in interspecific associations of social aggressive nature between bottlenose dolphins towards Guiana dolphins (*Sotalia guianensis)* presented a change in acoustic structure through intermediate values in frequency, and temporal parameters compared with single species groups. Signal convergence and signal stress by mimicking signals in the “aggressor language” were hypothesized to be the main drivers of this signal modification (MAY-COLLADO, 2010). Bottlenose dolphins' playback sounds were documented to elicit increased coordinated movements by Guiana dolphins by performing a collective escape when facing the sounds of this potential aggressor (PIERRY et al., 2023). As bottlenose dolphins were recognized as a different species, the behavioral plasticity enabled the species to change its behavior accordingly (RELYEA, 2001; VOLKER; HERZING, 2021).

There is evidence of odontocetes’ vocal production learning, acoustic plasticity, and mimicking ability on human-made, conspecific, and heterospecific sounds. Dolphins have been recorded producing sounds similar to sonars (DERUITER et al., 2013; ALVES et al., 2014) and imitating conspecific sounds, both in captive and free-ranging conditions (e.g. TYACK, 1986; JANIK, 2000; WATWOOD; TYACK; WELLS, 2004). Different studies have shown the cetaceans' capability of acoustical approximation with other species' vocalization when sharing the same habitat (FOOTE et al., 2006; MUSSER et al., 2014; FAVARO et al., 2016; PANOVA; AGAFONOV, 2017; COURTS et al., 2020; COSENTINO et al., 2022). The acoustic approximation by bottlenose dolphins when interacting on mixed-species groups was suggested by acoustical differences between intra and interspecific contexts (VIANA et al., 2022). Cosentino et al. (2022) found the production of harbor porpoise-like clicks (polycyclic narrow band high-frequency clicks) by a solitary common dolphin which was sighted several times with harbor porpoises (*Phocoena phocoena*) on interactions of affiliative nature (RYAN et al., 2017). The authors also related, among the interactions, the emission of burst pulses by a porpoise in a v-shaped pattern production rate and suggested the possibility of them being social calls based on CLAUSEN et al. (2011) and SØRENSEN et al. (2018). In an area where California sea lions (*Zalophus californianus*) were present, a socially isolated killer whale produced barks similar to those of the sea lions (Foote et al. 2006). Motivation for social contact was speculated as the main driver of the imitation attempt. Captive killer whales and belugas (*Delphinapterus leucas*) cross-socialized with bottlenose dolphins and started to produce sounds similar to the ones produced by the bottlenose dolphin (MUSSER et al., 2014; PANOVA; AGAFONOV, 2017). Musser et al. (2014) also hypothesized that the killer whales shaped the incidence of clicking and whistling behaviors to be more similar to their dolphin social partners since the killer whales cross-socialized with bottlenose dolphins produced 17 times as many click trains and up to four times as many whistles in comparison with other killer whales that had been housed only with other killer whales. The production of some whistles by one of the killer whales was similar to the stereotyped whistle used frequently by its most common dolphin companion and was noticed four times. The authors highlight the evidence on the difficulty or lack of precision in these whistles imitations since they contained abrupt steps in frequency that were not typical of the dolphin's stereotyped whistle. Additionally, the chirp series produced by the killer whales had frequency ranges half that of the dolphins' chirps, providing other evidence of the difficulty in producing accurate imitations. Pavanova and Agafonov

(2017) also present evidence of vocal accommodation due to new social companions: imitations of dolphins' whistles, including signature whistles belonging to the three adult dolphins, were produced by a beluga whale socialized with bottlenose dolphins. The imitation of signature whistles is known to occur in groups of bottlenose dolphins (TYACK, 1986; KING et al., 2013; KING; HARLEY; JANIK, 2014), and it is possibly affiliative and useful in addressing the specific individual associated with that whistle (KING; HARLEY; JANIK, 2014). Although the imitations of the whistles were regularly detected among the beluga's vocalizations, the authors found only one case in which the dolphins produced short calls resembling those of the beluga. However, they were not identical in physical parameters. Similarity among whistles was also found in a Risso's dolphin (*Grampus griseus)* raised by a group of bottlenose dolphins; the individual's overall whistle parameters were closer to the bottlenoses' than wild Risso's dolphins (FAVARO et al., 2016).

The phenomenon of vocal convergence, the approximation of acoustic features of a given vocalization, is documented in diverse vocal species, from birds to mammals (see TYACK, 2008) and, despite some exceptions, is suggested to strengthen social bonds and improve cohesion among group members (JANIK; SLATER, 1997, 1998; TYACK, 2008; KING et al., 2013; JANIK, 2014). The signal matching across cetacean heterospecifics is poorly understood. However, at least among social interactions, the emission of similar vocal repertoires between species suggests motivation for behavioral conformity with social associates. More similarities than differences were found in the use of specific behaviors in potentially communicative situations across single species groups of Atlantic spotted dolphins and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (PAULOS; DUDZINSKI; KUCZAJ, 2008b). The sharing of behavioral repertoire in interspecific associations was described in the Bahamas bank across the long-term interspecific interactions between Atlantic spotted dolphins and bottlenose dolphins (HERZING; JOHNSON, 1997; VOLKER; HERZING, 2021). Additionally in a study of interspecific alloparental care under the form of long-term adoption of a melon-headed whale (*Peponocephala electra*) calf by a bottlenose dolphin adult female at Rangiroa atoll, French Polynesia, the adopted calf exhibit typical bottlenose dolphin leaping behavior (CARZON et al., 2019) suggesting the capability of reproduction of a heterospecific behavior for behavioral conformity with social associates.

2.4 SECTION III - Acoustic recognition among species

The interspecific signaling recognition can be advantageous by providing cues that may optimize energy expenditure, among other benefits. By analyzing Risso's dolphins eavesdropping in different conspecific playback sounds, Barluet de Beauchesne et al. (2022) related the dolphins' attraction to foraging and social female-calf sounds and avoidance from social male sounds. It is suggested that dolphins rely on information obtained from the returning echoes generated by the echolocation signals of conspecifics (BARRETT-LENNARD; FORD; HEISE, 1996; GÖTZ; VERFUSS; SCHNITZLER, 2006; GREGG; DUDZINSKI; SMITH, 2007; JONES; ALLEN; MOSS, 2021). The sharing of information between group members was suggested due to the decreasing echolocation rates per individual and increasing group size among killer whales (BARRETT-LENNARD; FORD; HEISE, 1996). Delphinid mixed species groups are generally larger than single species groups due to the fusion of the species groups; therefore, in individual numbers, these groups are among the largest mixed species groups systems known (GOODALE; BEAUCHAMP; RUXTON, 2017). Therefore, sharing information among interspecific groups may enhance foraging by optimizing feeding efforts, or at least for one of the species involved by eavesdropping on heterospecific signals; however, as pointed by Janik (2000), the extent to which individuals engage in eavesdropping on acoustic interactions and utilize acquired information remains unclear. Several mixed species groups where species were sighted foraging together are reported (QUÉROUIL et al., 2008; ZAESCHMAR; DWYER; STOCKIN, 2013); nonetheless, no information about interspecific sharing of information has been found. Zaeschmar et al. 2013 related an organization in turns between false killer whales and bottlenose dolphins in cooperative hunting. Therefore, the occurrence of communication among heterospecifics in order to coordinate group movements is plalusible.

The costs and benefits of associating with a heterospecific can be asymmetrical, where the benefits that generate selective forces may apply only to some individuals of some species (GOODALE; BEAUCHAMP; RUXTON, 2017). When individuals from different species interact in a non-predatory context, there is a trade-off involving the costs associated with competition for resources, such as food, and the benefits derived from group formation, including reduced predation risk, energy efficiency, and advantages of cooperative care for offspring (alloparental behavior) (GYGAX, 2002). Therefore, the motivations to join a mixed-species group can vary among species and individuals.

Dominance relations also may result in differences on association costs (WINDFELDER, 2001); delphinid agonistic encounters commonly represent individuals of the larger species chasing, attacking, or sexually harassing those of smaller species (HERZING; JOHNSON, 1997; PSARAKOS; HERZING; MARTEN, 2003; HERZING; ELLISER, 2013; WEDEKIN; DAURA-JORGE; SIMÕES-LOPES, 2004; MAY-COLLADO, 2010; ROSS; WILSON, 1996, PATTERSON et al., 1998). The use of pursuit behavior (a more overt and energy-intensive behavior) by Atlantic spotted dolphins towards bottlenose dolphins was hypothesized as a manner to effectively communicate with a different species since the comprehension of the intent of this behavior may be more widespread across the delphinid world, thus, more intelligible (VOLKER; HERZING, 2021). Accordingly, the edge of interspecific signaling recognition may alter species' behavior during aggressive encounters. Eierman et al. 2019, by analyzing pectoral fin contact among interspecies interactions between Atlantic spotted and bottlenose dolphins, suggested similar individual cost-benefits trade-off in choosing a social partner in both conspecific and heterospecific interactions even though the nature of the contact diverged per species where contacts by Atlantic spotted dolphins were affiliative while contacts by bottlenose dolphins were sociosexual. Socio-sexual interactions, including sexually aggressive encounters, were hypothesized as one of the causes of hybridization among delphinid species commonly found in mixed species groups (HERZING; ELLISER, 2013; VAN GEEL et al., 2022). The possibility of hybrid-specific vocalizations was suggested (VAN GEEL et al., 2022), since atypical signals were attributed to hybrids of blue (*Balaenoptera musculus*) and fin whale (*Balaenoptera physalus*) (STAFFORD et al., 2007). Moreover, diverse hybrids or putative hybrids were found interacting in mixed species groups (ACEVEDO-GUTIÉRREZ et al., 2005; HODGINS; DOLMAN; WEIR, 2014; ESPADA et al., 2019; VAN GEEL et al., 2022).

Many marine mammals rely primarily on sound to localize prey or to detect the approach of predators; therefore, interspecific signaling recognition also plays an important role in ecological interactions involving predator-prey. Acoustic signal recognition and assessment may enhance the differentiation of a potential predator from a non-menace, since studies have shown that killer whales ecotypes have specific vocalizations and acoustic behavior which allow their differentiation (FORD; FISHER, 1982; BARRETT-LENNARD; FORD; HEISE, 1996; RIESCH; DEECKE, 2011). Playback experiments with mammal and fish-eating killer whale sounds have demonstrated different strategies adopted by some cetacean species when exposed to the sound, which suggests the capability to discriminate between vocalizations of different killer whale ecotypes and perceive mammal-eating killer whale sounds as a potential predation risk. For example, Curé et al. (2019) presented evidence of long-finned pilot whales' capability to acoustically discriminate between familiar fish and unfamiliar mammal-eating killer whale ecotypes. Reduction and cessation of foraging behavior were observed in the presence of mammal-eating killer whale sounds. Additionally, there was an increase in the production of fast click trains near the surface. This led to a tightening of individual spacing within groups and a decrease in the amount of time spent at the surface. On the other hand, in response to fish-eating killer whale sounds, there was an increase in the production rate of social calls. This was accompanied by the joining of different subgroups and an attraction towards the source of the sound. The fast click trains produced near the surface were hypothesized by the authors as an attempt to inspect an unfamiliar sound through echolocation or a way of communicating near the surface and/or in a more effective and/or more discrete way (i.e., more directional or short-range distance) in comparison of social calls which can reach longer distances (NORRIS; DOHL, 1979; WURSIG; PERRIN, 2009). Playbacks with mammal- and fish-eating killer whale sounds also elicited different responses in humpback whales (*Megaptera novaeangliae*) (BENTI et al., 2021): a clear approximation towards the source of familiar fish-eating killer whale sounds was observed, whereas the unfamiliar mammal-eating killer whale sounds were likely perceived as a threat.

Regardless the apparent capability of signal recognition, some studies demonstrate cetacean avoidance of fish-eating killer whale sounds (CUMMINGS; THOMPSON, 1971; FISH; VANIA, 1971; DEECKE, 2006). One possibility that could be eliciting cetacean avoidance from some killer whale sounds would be due to the unfamiliarity with the sounds; therefore, the sound discrimination would be the result of selective habituation where familiar killer whale fish eating sounds would not represent a risk, whereas unfamiliar fish or mammal-eating killer whale sounds would elicit an antipredatory response (DEECKE, 2006). However, there is more evidence supporting the cetacean capability to discern between fish and mammal-eating killer whale sounds: Mobbing and/or altruistic behavior by humpback whales was strongly more common towards mammal-eating killer whales attacks than fish-eating. The majority happened when the mammal-eating killer whales' groups were already attacking or feeding on various prey species. In some cases, the killer whales were out of humpback whale visual range and were possibly acoustically detected including two episodes recorded with hydrophones where killer whale's vocalizations at an attack site were detected before the humpback's arrival (PITMAN et al., 2017). Unfamiliarity with sounds also was not the only driver to explain the reaction of pilot whales to unfamiliar killer whale mammal eating sounds explored by Curé et al. (2019) since there was a different combination of behavioral changes exhibited by long-finned pilot whales in response to two unfamiliar sound stimuli (mammal-eating Killer Whale sounds and control artificial sounds). Additionally, the anti-predator reaction to familiar fish-eating killer whale sounds and also novel mammal or fish-eating killer whale sounds can be explained by a remnant past historical antipredator strategies (SIH et al., 2013; DE STEPHANIS et al., 2015; HETTENA; MUNOZ; BLUMSTEIN, 2014; CURÉ et al., 2019).

The call structure, such as the presence and rate of non-linear phenomena, may convey information that may help the recognition of potential predation risk. The two-component call has been identified in various mammal-eating populations. Its suggested role as a group identifier within mammal-eating killer whale pods is currently under consideration (TYSON; NOWACEK; MILLER, 2007; FILATOVA et al., 2009, 2012). Bowers et al. (2018) found a strong response by long-finned pilot whales and Risso's dolphins when specific familiar mammal-eating killer whale call types containing multiple non-linear properties were present in the playback stimuli. The authors suggested that the calls might convey information about the behavior or intent of the predators.

Other features, such as the general behavior of the callers, may also give cues that help in accessing the potential danger, such as non-vocal sounds emitted - simultaneously to the vocalizations or not - by the predator. Some fish-eating killer whales are known to use multiple echolocation clicks and tail slaps as a foraging strategy (SIMON; MCGREGOR; UGARTE, 2007; CURÉ et al., 2012), whereas mammal-eating killer whales produce fewer echolocation clicks and no tail slaps (DEECKE; FORD; SLATER, 2005). Studies suggest that these mammal-eaters tend to be more silent when hunting to avoid being detected by their acoustically sensitive prey, relying more on passive listening before the launch of the attack (BARRETT-LENNARD; FORD; HEISE, 1996; DEECKE; FORD; SLATER, 2005; DEECKE; SHAPIRO; MILLER, 2013; RIESCH; DEECKE, 2011). After prey detection and during its kill and consumption, they commonly become vocally active (MORTON, 1990; GOLEY; STRALEY, 1994; BARRETT-LENNARD; FORD; HEISE, 1996; DEECKE; FORD; SLATER, 2005; FORD et al., 2005; DEECKE et al., 2011; RIESCH; DEECKE, 2011), possibly as a coordination of the attack or a manner to call other individuals for assisting or sharing the hunt or even socialize (DEECKE; FORD; SLATER, 2005; REEVES; BERGER; CLAPHAM, 2006). Humpback whales exhibited anti predatory response in the post-exposure of killer whale mammal-eating sounds period in comparison of fish-eating killer whale sounds (BENTI et al., 2021) and sperm whales exhibited anti predatory response in the post-exposure of killer whale mammal-eating sounds period in comparison of low-frequency sonar (ISOJUNNO et al., 2016). A possible explanation would be that the cessation of the predator vocalizations could signal that the perceived predation risk had increased or even that a hunt is about to start (ISOJUNNO et al., 2016; BENTI et al., 2021).

Several cetacean species possibly rely on acoustic cues such as the rate and features of the vocalizations and tail slaps to detect the presence of a potential mammal-eating killer whale. A wide variety of strategies adopted by cetaceans due to the predator acoustic presence has been documented, such as total or partial reduction or increasing of acoustic behavior, reduction or interruption of foraging behavior, mobbing behavior, rapid escape, reduced exposure, synchronic behavior and visual search by spy hops (CUMMINGS; THOMPSON, 1971; FISH; VANIA, 1971; RANKIN; ARCHER; BARLOW, 2013; CURÉ et al., 2012, Curé 2013; NIELSEN et al., 2019; AGUILAR DE SOTO et al., 2020; BENTI et al., 2021). Changes in acoustic behavior were related to sperm whales exposed to playback calls of mammal-eating killer whales; the individuals produced fewer echolocation clicks and buzzes and emitted social/alerting sounds as codas (CURÉ et al., 2013, 2016). Humpback whales, when close to attacking killer whales, responded with various underwater sounds and bellowing behavior (WHITEHEAD; GLASS, 1985; DOLPHIN, 1987; BENTI et al., 2021). Although bellowing behavior is commonly present among aggressive interaction between males (TYACK; WHITEHEAD, 1982), Benti et al. (2021) suggest that of bellowing and underwater vocalizations serve as alerts or summon signals to other humpback whales in the vicinity.

Acoustic crypsis, a phenomenon described in diverse cetacean species, consists in the reduction of the animal signals detectability through adaptations in sound production behavior (VIDESEN et al., 2017; CLAUSEN et al., 2011; KYHN et al., 2013; FENTON et al., 2014). Blainville's beaked whales (*Mesoplodon densirostris*) are known only to produce sounds at depth and remain mostly silent whenever shallower than 170 m depth, and this has been proposed to represent a strategy to limit the detection by shallow diving predators such as killer whales (AGUILAR DE SOTO et al., 2020). The narrow band high-frequency clicks, produced by porpoises, dolphins of the genus *Cephalorhynchus, Lagenorhyinchus* and Kogiids are characterized by the absence of relevant energy below 100 kHz and thus, along with the loss or low rate of lower-frequency whistle production, linked by many authors to an acoustic crypsis from killer whales, which effective hearing range is below 100 kHz (ANDERSEN; AMUNDIN, 1976; SZYMANSKI et al., 1999; MADSEN et al., 2005; MORISAKA; CONNOR, 2007; CLAUSEN et al., 2011; KYHN et al., 2013; FENTON et al., 2014). Lower call rates of higher-amplitude vocalizations and the production of reduced-amplitude sounds by mother-calf pairs of humpback and North (*Eubalaena glacialis*) and Southern right whales (*Eubalaena australis*) are also linked to the acoustic crypsis phenomenon (VIDESEN et al., 2017; PARKS et al., 2019; NIELSEN et al., 2019). The habitat characteristics also seem to play an important role in acoustic crypsis strategies, Southern right whales, when in breeding grounds, are commonly sighted in depths that have the most limited acoustic detection range for their calls (ZEH; DOMBROSKI; PARKS, 2022).

The potential of interspecific relationship to imply momentaneous or permanent acoustic shifts, including the "acoustics arms race" between predator and prey and the acoustics role among mixed species groups, is an interesting avenue of investigation in odontocetes (TYACK; CLARK, 2000; MAY-COLLADO, 2010; RIESCH; DEECKE, 2011; GOODALE; BEAUCHAMP; RUXTON, 2017; VOLKER; HERZING, 2021). Possibly there is a pressure among conspecifics to keep their communication private from potential prey, predators or competitors. On the other hand, it is unclear whether individuals want to be detected by heterospecifics to gain benefits by interacting in the same group since studies have shown that some mixed groups do not occur by chance (SYME; KISZKA; PARRA, 2023). Cetaceans may rely on eavesdropping as a primary way to obtain information and make decisions when facing interspecific encounters, therefore interspecific acoustic discrimination may be widespread among marine mammals (BENTI et al., 2021). Acoustical eavesdropping on conspecifics, for example, allows dolphins to anticipate potential threatening or beneficial situations and also to discriminate between social and behavioral contexts and (BARLUET DE BEAUCHESNE et al., 2022). However, the full odontocete's ability to learn and understand cross-species signals, the fidelity of their vocal imitations, context for matching, and the edge of interspecific communication are still unclear (MUSSER et al., 2014; VOLKER; HERZING, 2021a). Assessing whether a specific signal structure is altered or remains across interspecific interactions can be a hard task given the complexity of odontocete social structure, bond formation, acoustic plasticity, and remarkable cognitive abilities (CONNOR; HEITHAUS; BARRE, 2001; MARINO et al., 2007; FURUICHI; CONNOR; HASHIMOTO, 2014; CANTOR et al., 2015; FAVARO et al., 2016).

2.5 INSIGHTS AND GUIDANCE FOR FURTHER ACTION

Assessing the nature of the co-occurrence as well as group composition may be one of the driving steps for understanding its influence on acoustic since changes in acoustic features or use of different acoustic signals in odontocetes are documented to depend not only on species, but also on the group composition, as in sperm whales where different acoustic signals are present across different group compositions, social; behavioral; or environmental contexts (WEILGART; WHITEHEAD, 1997; OLIVEIRA et al., 2013; DERUITER et al., 2013; GRIDLEY et al., 2016; LA MANNA et al., 2019; DÍAZ LÓPEZ, 2022; SAYIGH et al., 2023).

The description of the characteristics of acoustic signals of a given population may provide insights into how the repertoire varies in different social and physical environments, including the influence of the sympatry (KAPLAN; REISS, 2017). Studies that account for the group composition can elucidate the species response to the heterospecific presence; for example, humpback whales' response to mammal-eating killer whale playbacks can be influenced by the presence of vulnerable calves in humpback whale groups (CURÉ et al., 2015).

The nature of interactions, whether they involve nursery activities, socio-sexual behavior, or feeding, can influence the use of specific acoustic signals and their modulation. This modulation is evident in various interactions, such as social and aggressive encounters. Understanding group dynamics is crucial for comprehending spatial organization and acoustic utilization in delphinids. Many delphinids form "fission-fusion societies," where group membership rapidly changes among individuals. Consequently, mixed species groups may undergo swift compositional changes (CORDS; WÜRSIG, 2014; GOODALE; BEAUCHAMP; RUXTON, 2017). These changes likely result in distinct interactions of different natures among both heterospecific and conspecific individuals. Significant interspecies variations have been observed across spotted and bottlenose dolphins mixed species groups. Spotted dolphins exhibit higher resighting rates, larger group sizes during aggressive encounters, a prevalence of male alliances spanning multiple orders (including associations beyond these alliances), and intraspecies associations within mixed-species groups that mirror their intraspecific interactions. In contrast, bottlenose dolphins demonstrate more individualized participation, smaller group sizes, limited male alliances, and dissimilar intraspecific interactions within mixed-species groups, including random associations (ELLISER; HERZING, 2016). Therefore, the nature, group composition, and also different motivations across species and individuals may influence the acoustic repertoire used in interspecific interactions. For example, the clustering of conspecifics found in cooperative hunting between false killer whales and bottlenose dolphins (ZAESCHMAR; DWYER; STOCKIN, 2013) appears to be a social norm for this mixed species group's composition and organization. Eierman et al. (2019) found similar rates and the number of contacts among conspecific and heterospecific dolphins, despite that, for one species, the heterospecific contact was from an affiliative nature, and for the other it was sociosexual. Costa et al. (2022) found apparent different drivers for mixed group formation among delphinids in the Azores, the striped dolphin (*Stenella coeruleoalba*) appears to associate by foraging reasons, and the common dolphin (*Delphinus delphis*) for group size increasing. Accordingly, behavioral differences between species indicate that interspecific interactions are dynamic and context-dependent associations that cannot be simplified to a static dominance hierarchy (TANNER; ADLER, 2009). Concerning predator-prey relationships, for example, anti-predator strategies in animals are likely to exhibit variation based on internal states, habitat characteristics, and the nature of the threat (FORD; REEVES, 2008). Through an examination of the different drivers of co-occurrence contexts and their associated consequences, it is possible to acquire more comprehension of the social dynamics and ecological interactions that influence delphinid acoustics.

Species co-occurring and sharing the same habitat, but without directly interacting with each other, may imply the acoustic organization of the acoustic space, fitting on the acoustic niche theory, since sympatry may lead to niche partitioning in order to avoid heterospecific competition (MOSSBRIDGE; THOMAS, 1999; VAN DER MESCHT et al., 2022; DUARTE et al., 2019). Otherwise, if different drivers can influence interspecies interactions and different factors can influence on acoustics, the presence of a heterospecific partner may evoke changes in acoustic niche organization as long as species evolved are able to change their signals. Maybe, under certain contexts, species share the acoustic space, by overlapping acoustic parameters and/or approximating acoustically, instead of competing for it. Additionally, as odontocetes are extremely fluid, mobile and plastic mammals with complex social structures, high encephalization levels, and cultural transmission would be plausible an acoustic alteration due to an interaction according to the trade-off between benefits and costs of the interaction and interest in being detected and interacted with. As pointed out by Bearzi (2005), in dolphins, given the potential relationship between fission/fusion grouping, their intelligence, social complexity, and a complex foraging environment, it raises questions about its impact on sympatric associations. The acoustic niche may not be totally static and is possibly influenced by odontocete social dynamics. Interspecies interactions among odontocetes possibly go beyond simply ecological interactions. The study of the multiple cultural layers across non-human species may help the understanding of the acoustic role on social bond formation between species and even the possibility of consciousness to decide across different co-occurrence situations such as the adhesion to non-conspecific groups.

Systematic studies done on acoustic differentiation in co-occurrent contexts among odontocetes may help assess these groups' acoustics across different interactions. For example, the whistle presence seems to be more common in mixed species groups in comparison to single species groups, at least in tropical waters. Oswald et. al 2008, showed that whistles were heard from 66% of single species schools and from 98% of mixed species schools during a survey of tropical waters in the eastern tropical Pacific Ocean. Long-term studies allied with passive acoustic technology are important in the monitoring of species that recurrently are sighted interacting together due to finding patterns, such as individuals that are most sighted among interactions as well as the acoustic behavior of the involved species when interacting *versus* when not. The use of acoustic indices can also be an interesting tool in order to assess if there are major changes in biophony across different cross-species contexts. Furthermore, acoustics tags may also help in understanding the possible heterospecific interference patterns, specifically concerning individual acoustic responses.

The anthropogenic effects on cetaceans are also important when studying odontocete co-occurrence. As a result of environmental changes, the possibility of population reduction or displacement and species overlap increases as communities are forced into new habitats. Therefore, the possibility of mixed groups increasement can expand the appearance of hybrids, which represents potential evolutionary consequences (BÉRUBÉ; PALSBØLL, 2018). Also, due to environmental changes, behavioral plasticity studies on the animal’s capability to learn and alter their vocal behavior as well as their ability to socialize with new groups - of con- and heterospecifics - are of great importance (MUSSER et al., 2014; VOLKER; HERZING, 2021). Spatial and temporal overlap can lead to an increase of the frequency of interspecific interactions turning the possible impacts of those interactions likely higher (SELBMANN et al., 2022), such as the impact of increased direct predation by killer whales due to melting sea ice that arctic cetaceans may face (MILLER et al., 2022). Additionally, both low-frequency anthropogenic sonars and mammal-eating killer whale playbacks elicited similar responses on odontocete species, which denotes that these similar responses to predators and generalized threatening stimuli seem to be related (SIH et al., 2013; CURÉ et al., 2016; ISOJUNNO et al., 2016; MILLER et al., 2022).

In conclusion, different species co-occurrence contexts seem to influence odontocetes’ acoustic response. In general, harassment, predator-prey and other agonistic/competitive encounters elicit synchronized acoustic behaviors, reduction of foraging sounds, reduction or increasement of social and communicative sounds and heterospecific mimicking, the latter also found during affiliative encounters and possibly motivated by social contact (e.g.: MUSSER et al. 2014; HERZING, 2015; CURÉ et al., 2016; ISOJUNNO et al., 2016; COSENTINO et al., 2022; MILLER et al., 2022). Whether species co-signal, interact, compete and/or search for “acoustic private channels” in the acoustic space may be related to the extent to which species understand each other and also to risk assessment of a given interaction. Attention should be given to the cornucopia of cetacean co-occurrences along with changing habitats to understand the acoustic role across this mash of interactions in which the acoustic organization may follow different pathways. The understanding of cetacean co-occurrences is important for the knowledge of its functions as well as its formations and acoustic characteristics since most part of published data about those interactions are mostly descriptive and there is a necessity of the gathering of these concepts.

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CHAPTER II

3. ARE DOLPHINS MODULATING WHISTLES IN MIXED-GROUP CONTEXTS?

Published in Bioacoustics (04 Jan 2022)

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3.1. INTRODUCTION

Mixed-species associations (MSAs) in cetaceans are encounters between different species that can be temporary or long-term interactions (Quérouil et al. 2008; May- Collado 2010; Elliser and Herzing 2016a; Volker and Herzing 2021). These encounters can be advantageous in foraging and predator detection and avoidance (Norris and Schilt 1988; Clua and Grosvalet 2001; Kiszka et al. 2011). Social factors, such as dominance, reproduction, and practice of sexual behaviours (Baraff and Asmutis- Silvia 1998; Stensland et al. 2003; Bearzi 2005; Rossi-Santos et al. 2009; Bacon et al. 2017), may also induce the association of different species. However, few studies have attempted to investigate the driving factors and functions of these interactions (Zaeschmar et al. 2013).

Given the possible advantages of MSAs, these associations may play an essential role in the acoustic dynamics of the species involved (Ding et al. 2001; May-Collado 2010). Studies investigating interspecific interaction from the acoustic perspective are sparse (e.g. Ding et al. 2001; May-Collado 2010; Herzing 2015). To avoid acoustic overlap, species tend to distribute their vocalisations by establishing an acoustic niche, which encompasses the spatial, temporal, and acoustical characteristics of their vocalisations (Krause 1993; Duarte et al. 2019; van der Mescht et al. 2021).

Social sounds, such as whistles, are consistent vocalisations used for species differentiation and to investigate acoustic dynamics in interspecific contexts (Amorim et al. 2019). Whistles are narrow-band frequency-modulated tonal sounds used in intraspecific communication (Herman and Tavolga 1980; Au and Hastings 2008) during social contexts (Janik and Slater 1998; Herzing 2000; Lammers et al. 2003). These signals are believed important for parental care, individual recognition, group cohesion, and mating (Janik et al. 2006; Lammers et al. 2006; Andriolo et al. 2015; King et al. 2016, 2019) and might be related to ecological factors such as geographical variation (Oswald et al. 2008; Gridley et al. 2015; Moron et al. 2015).

The bottlenose dolphin (*Tursiops truncatus)* is known for its acoustical plasticity (McCowan and Reiss 1995; La Manna et al. 2013; Fouda et al. 2018). Furthermore, the interspecific associations between this species and other delphinids have been demonstrated both in captivity (Terry 1984; Favaro et al. 2016) and in the wild (Herzing 1996; Wedekin et al. 2004; Acevedo-Gutiérrez et al. 2005; Cotter et al. 2012; Zaeschmar et al. 2014; Lima et al. 2021). Such interactions include foraging, travelling, playing, alloparental care, aggressive behaviour, and sexual activity.

Considering the limited information about the whistle dynamics in MSAs (May-Collado 2010) and the aforementioned *T. truncatus* acoustic plasticity, we investigated the acoustic dynamics of this species in different group contexts: among MSAs with Risso's dolphin (*Grampus griseus*), with the long-finned pilot whale (*Globicephala melas*) and between *T. truncatus* single-species groups *versus* the MSAs.

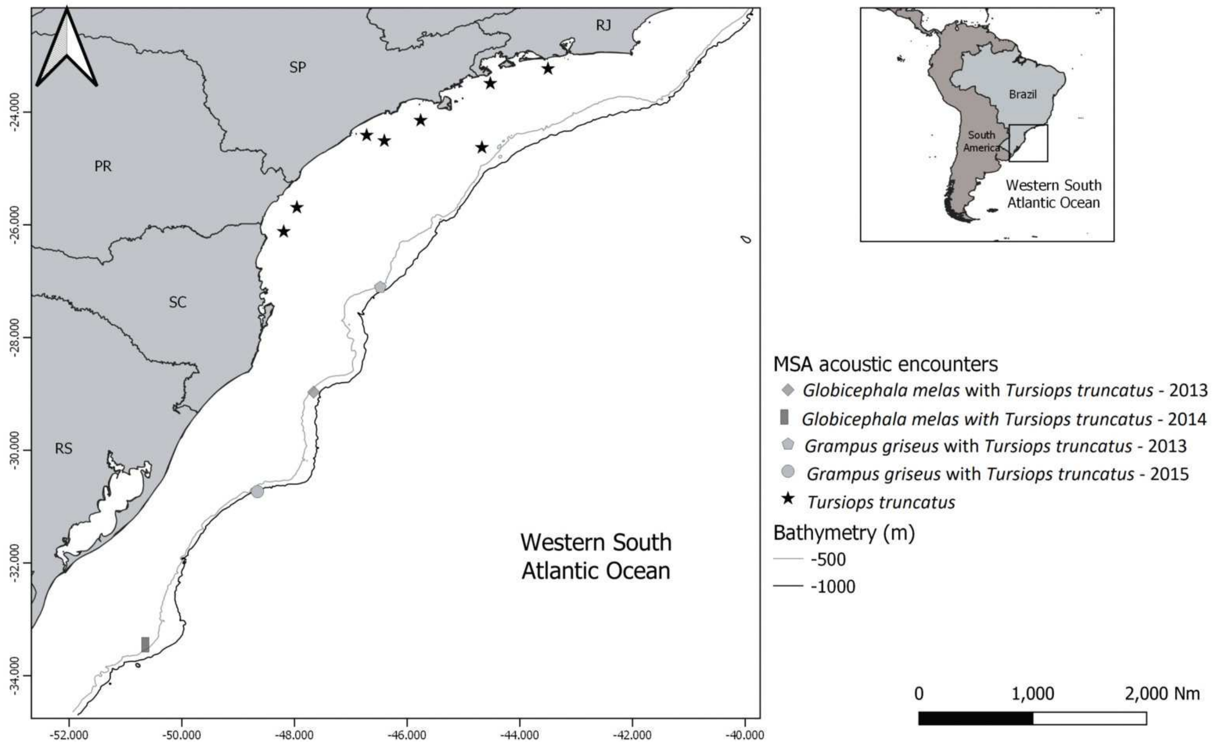
3.2. MATERIALS AND METHODS

3.2.1. Study area and data collection

Data recordings were collected during two comprehensive vessel-based cetacean survey efforts in coastal and oceanic waters of South and Southeast Brazil (Talude Project and Cetacean Monitoring Project in Santos Basin; PMC-BS). These surveys collected cetacean visual and acoustic data from 2013 to 2018 in the Western South Atlantic Ocean (23º to 33º S, Figure 1).

Acoustical data from seven cruises, totalling 12 encounters with the targeted species, were used (Table 1).

Figure 1.



Study site map indicating the places where the acoustic recordings were registered.

Table 1. Encounters data from the mixed and single-species groups. The number of analysed whistles are presented in parenthesis.

Encounter	**Coordinates**		**Recording year**	**Group Context**
	Long	**Lat**		
I (*n*=287)	-46.477	-27.107	2013	*Grampus griseus* + *Tursiops truncatus*
II (*n*=332)	-47.66	-28.967	2013	*Globicephala melas* + *Tursiops truncatus*
III (*n*=258)	-50.583	-33.45	2014	*Globicephala melas* + *Tursiops truncatus*
IV (*n*=149)	-48.657	-30.732	2015	*Grampus griseus* + *Tursiops truncatus*
V(*n*=7)	-44.673	-24.628	2015	*Tursiops truncatus*
VI(*n*=90)	-43.500	-23.230	2016	*Tursiops truncatus*

VII(*n*=15)	-47.957	-25.691	2016	*Tursiops truncatus*
VIII(*n*=12)	-44.524	-23.490	2017	*Tursiops truncatus*
IX(*n*=9)	-46.719	-24.410	2017	*Tursiops truncatus*
X(*n*=3)	-45.761	-24.146	2018	*Tursiops truncatus*
XI(*n*=4)	-46.405	-24.508	2018	*Tursiops truncatus*
XII(*n*=1)	-48.191	-26.119	2018	*Tursiops truncatus*

Acoustical recordings were performed using a towed array of hydrophones. Different hydrophone array configurations and data acquisition electronics were used for the two cetacean survey projects. The data were high-pass filtered with a cut-off frequency of 0.499 Hz for the Talude Project and 1000 Hz for PMC-BS. Digital recorders had a sampling frequency of at least 96 kHz/24 bits (see supplementary material for acoustical recording details). Experienced marine mammal observers visually confirmed the species identifications from acoustic records during sightings or by analysing pictures taken during sightings that could confirm species diagnostic characteristics. Two subspecies of *T. truncatus* are recognised in the study area, and all acoustic recordings corresponded to the offshore form (*T. truncatus truncatus*).

3.2.2. Acoustical analysis

The recordings were analysed using Raven Pro 1.5 (Cornell Laboratory of Ornithology, NY). The spectrograms were inspected to manually detect whistles and extract the following parameters (Hann window of 1843 points, DFT of 2048 points, and 50% overlap): low frequency, high frequency, delta frequency (i.e. the difference between high and low frequencies), centre frequency, beginning and ending frequencies, first and third quartiles of frequency, interquartile range of frequency bandwidth, frequency 95% and 5% (the frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection, respectively), and whistle duration. The selection was based on the signal- to-noise ratio (≥ 10 dB) for whistles with a clear contour shape. Measurements were made only on the fundamental frequency of whistle contours, and therefore, harmonics were not considered.

3.2.3. Statistical analysis

A support vector machine (SVM), a machine learning tool to detect patterns between groups of different classes, was implemented using a radial basis function kernel. For the parameter choice, permutation tests with 100,000 bootstraps were employed since the data had evidence of non-normality (*p*-values less than 0.05). These permutation tests compare different groups of data. The comparison was made first between both MSA groups and then each MSA *versus* the single-species group. Based on the significant parameters in the permutation tests, the SVM was built from 60% of the data (training sample), and its misclassification rate was calculated with respect to the 40% remaining observations. To obtain a more detailed analysis, the SVM procedure was replicated 500 times, and its average misclassification rate was computed for each paired context.

Additionally, a random forest analysis, a machine learning classification method, was performed with the significant parameters using 75% of the data as a training sample and 25% for validation of the model. Multivariate dispersions using Euclidian distance were plotted to visualise separation among groups. Then, to validate the classification models, the receiver operating characteristic (ROC) curves were plotted and the area under these curves was computed.

The analyses were performed with the software R 3.5 (R Development Core Team 2015) using packages ‘lmPerm’ for permutation (Wheeler and Torchiano 2016), ‘e1071' for SVM (Meyer et al. 2019), ‘randomForest’ for random forest analysis (Liaw and Wiener 2002), ‘pROC’ for ROC curves (Robin et al. 2011), and ‘vegan’ for multivariate dispersion (Oksanen et al. 2013).

3.3. RESULTS

In total, 1,267 whistles were analysed from the spectrograms. Among these whistles, 590 were from *G. melas* + *T. truncatus* encounters, 536 were from *G. griseus* + *T. truncatus* encounters, and 141 were from *T. truncatus* single-species contexts.

Table 2. Average misclassification rate of the 500 classification matrixes from each comparison obtained through SVM.

pair contexts	**average misclassification rate**
G. melas + *T. truncatus versus G. griseus* + *T. truncatus*	27%
G. melas + *T. truncatus versus T. truncatus*	10%
G. griseus + *T. truncatus versus* T. *truncatus*	8%

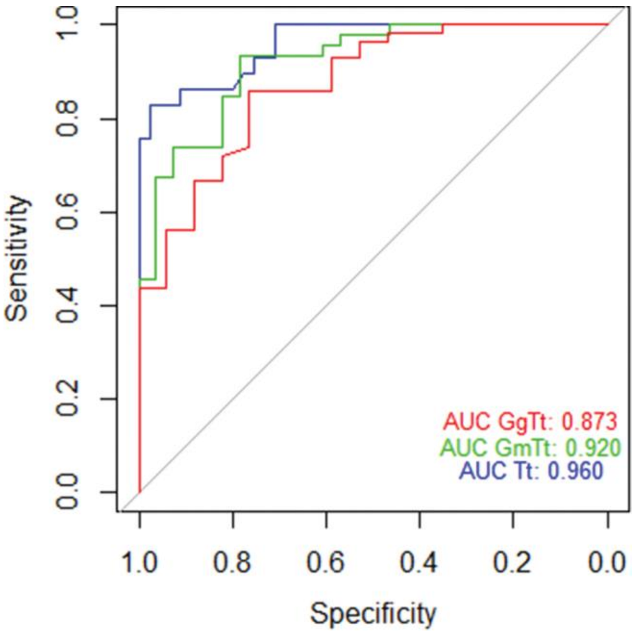


Figure 2. ROC curves indicating the goodness of fit of the random forest model. The area under the curve (AUC) values ranged from 0.87 to 0.96. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

The parameters that presented significant differences in all permutation tests (between the MSAs and with each MSA *versus* the single-species context) were high frequency, delta frequency, frequency 95%, beginning and ending frequencies and duration (box plots are presented in the supplementary material, Figures S1- S6).

The SVM misclassification rates for context pairs are presented in Table 2. Overall, 500 trees were generated through the random forest analysis, resulting in an accuracy of 78.3%. The area under the curve values from ROC curves ranged from 0.87 to 0.96 (Figure 2), indicating the strong classification power of the model. Frequency 95%, duration and beginning frequency had the lowest mean decrease accuracies (see supplementary material, Figure S8). The out-of-bag error, a value related to the data validation error (Liaw and Wiener 2002), was 25.94%, and the 500-tree generated plot is provided in supplementary material, Figure S9. The multivariate dispersion plot showed the separation of the *T. truncatus* single-species context from the MSAs (see supplementary material, Figure S7).

4.4. DISCUSSION

The results reveal a low percentage of classification errors from all group contexts (Table 2). The average misclassification rate of 27% between the interspecific group contexts (*T. truncatus* in MSA with G. *melas* or *G. griseus*) denotes a clear separation of the whistles produced in both contexts; this distinct separation between groups is reinforced by the presence of different species (*G. melas and G. griseus*) in the comparison. However, the separation is also evidence that *T. truncatus* change their whistle parameters depending on the MSA they have joined. If this species maintained the same whistle characteristics in both interspecific group contexts, a higher misclassification was expected representing the *T. truncatus* whistles (common species in both contexts). This finding is an indication that *T. truncatus* whistles can be modified in different interspecific associations due to its considerable acoustical plasticity (La Manna et al. 2013; van Ginkel et al. 2018), vocal learning capacity (Janik 2014), and mimicry ability (Kuczaj and Yeater 2006; King et al. 2013), driving an acoustical approximation with the involved species. Moreover, *T. truncatus* was the most frequently sighted species in MSAs in the oceanic waters of the Western South Atlantic (Lima et al. 2021), demonstrating that this species commonly interacts in MSAs in our study area.

When classifying the MSA of the *T. truncatus* + *G. melas versus T. truncatus* single-species context, the low average misclassification rate (10%) indicates that *T. truncatus* single-species whistles are different from those of the MSA. When comparing *G. griseus* + *T. truncatus* MSA *versus* the single *T. truncatus* context, the average misclassification rate is smaller (8%). The clear separation between the MSAs and the single-species context presented in the random forest analysis (Figure 2) reinforces the SVM results. Interactions between *T. truncatus* and other species are known to involve foraging; travelling; and social behaviours, such as sexual and aggressive activities, play, alloparental care and cooperative interactions (Ross and Wilson 1996; Herzing and Johnson 1997; Zaeschmar et al. 2013; Elliser and Herzing 2016b; Estrade and Dulau 2017). Whistles are used primarily in a social context for group communication and cohesion (Herman and Tavolga 1980; Janik and Slater 1998; Azevedo et al. 2007; King et al. 2016); thus, an acoustical convergence by the present species is expected since such behavioural activities are shared in MSAs.

Sharing vocal repertoire and gestural signals was suggested in interspecific associations of spotted dolphins (*Stenella frontalis*) and bottlenose dolphins in the Bahamas (Herzing and Johnson 1997; Volker and Herzing 2021). Moreover, the signal recognition ability has been described between these two species in captivity (Caldwell et al. 1971). A change in whistle structure occurring in social events between bottlenose dolphins and Guiana dolphins (*Sotalia guianensis)* was indicated (May-Collado 2010); specifically, intermediate whistle structure compared to that present in intraspecific groups was found in harassment and aggressive interactions where species were directly interacting with each other. The possibilities discussed were an attempt of the Guiana dolphins to emit threats intelligible to the aggressors or to express stress and signal convergence between interacting species. Therefore, at least in social interactions, an attempt to whistle match is plausible in MSAs.

Our results indicate that *T. truncatus* may adjust its acoustical parameters based on the interspecific context, emitting similar whistles to those emitted by the other species present. A possible explanation for this strategy is an attempt of *T. truncatus* to acoustically interact with the other species in the group. The low misclassification rate in groups with different species removes the bias of only a species interfering with the whistle structure in interaction with *T. truncatus*. Nevertheless, we cannot discard that the other species modulation capabilities and whistle rate during the MSA have the potential to influence the misclassification results and extol the differences.

In a study in which a *G. griseus* individual was raised by a group of *T. truncatus*, the authors noted that the individual used overall whistle parameters closer to *T. truncatus* than wild *G. griseus* (Favaro et al. 2016). Likewise, *G. melas* may change their calls to vocally match naval sonar signals (Alves et al. 2014) and could possibly be mimicking sympatric killer whales' (*Orcinus orca*) vocalisations (Courts et al. 2020).

The acoustic niche hypothesis presupposes that one species may organise its sound emissions' in the frequency and/or time domains to avoid acoustic masking due to signal overlapping (Krause 1993; Mossbridge and Thomas 1999; Sinsch et al. 2012). Through the results of this work, we suggest that individuals, with a similar repertoire or frequency range, do not compete for the acoustic space when interacting in interspecific associations but converge their acoustic signals, perhaps even communicating with each other in a shared environment.

The reciprocal signalling convergence, rather than divergence, among coexisting species has been suggested in birds and other taxa because similarities increase the efficacy of aggressive signals used in interspecific contests (Orians and Wilson 1964; Cody 1969). Laiolo (2012) noted that co-existing species of larks respond aggressively to congener territorial calls, which converge in many acoustic properties. Morton (1977) discusses the existence of signal similarities across birds and mammal by elucidating a structural convergence of many sounds used in 'hostile' and 'friendly' contexts. Although commonly described as temporary, some research may suggest that long-term MSAs are more common than previously documented (Elliser and Herzing 2016a; Ryan et al. 2017; Volker and Herzing 2021) and it is probable that interspecific signals that have evolved for a similar function within species would be utilised and potentially decoded by these animals; thus, species may have shared communication and social signals (Psarakos et al. 2003). In a study with *S. frontalis* and *T. truncatus*, the species organisation in MSAs was suggested as an essential component of the ability to coexist as sympatric species (Elliser and Herzing 2016b). However, as Volker and Herzing (2021) explain, at least two questions still remain: the edge of the interspecific communication breakdown and the extent to which the cross-species signals are understood.

In conclusion, our findings highlight that, although MSAs can be a type of sympatry, we believe they are potentially different from a classical sympatric situation in which acoustic differences among species optimise intraspecies communication, reducing heterospecific mating, optimising communication during feedings activities, and differentiating conspecifics from non-conspecifics (Steiner 1981; Matyjasiak 2005; Andriolo et al. 2015; Kaplan and Reiss 2017). Social benefits were suggested for heterospecific partners between *T. truncatus* and *S. frontalis*, providing support for reproductive benefits for both and outweighing the potential costs in mixed groups near Bimini, Bahamas (Eierman et al. 2019). The advantage of signal adjustment optimising the utilisation of mating resources can not be discarded since MSAs provide opportunities for cross-species sexual interaction and the possibility for hybridisation (Frantzis and Herzing 2002; Bérubé 2009; Herzing and Elliser 2013). In addition, the presence of potential hybrids has been registered among mixed species interactions (e.g. Herzing et al. 2003; Hodgins et al. 2014; Koper and Plön 2016; Espada et al. 2019). The benefits of joining an MSA may overcome the costs of interacting with a non-conspecific, at least for one species involved. Therefore, we reasonably suppose the plasticity of the acoustic repertoire of *T. truncatus* related to the ability to modulate and convert its signals may enable this species to acoustically interact with other delphinids, as long as they are in the same group. Accordingly, such plasticity may help the communication between the species and the formation of mixed species associations.

3.5. REFERENCES

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CHAPTER III

4. ACOUSTICAL ALTERATION BETWEEN SINGLE AND MIXED SPECIES GROUPS OF *PEPONOCEPHALA ELECTRA* AND *STENELLA ATTENUATA*

4.1. INTRODUCTION

Living in sympatry may be challenging once a shared habitat may impose strategies for the coexistence of species (MOSSBRIDGE; THOMAS, 1999; SINSCH et al., 2012; DUARTE et al., 2019). In areas of niche overlap, species may coexist in close spatiotemporal proximity and potentially establish mixed-species groups (SYME; KISZKA; PARRA, 2023b). These grouping behaviors occur when interspecifics, by mutual or unilateral attraction, are found in temporary or long-term interactions (QUÉROUIL et al., 2008; MAY-COLLADO, 2010; ELLISER; HERZING, 2016; VOLKER; HERZING, 2021; SYME; KISZKA; PARRA, 2023a).

The co-occurrence of species on the same group can provide evolutionary advantages in foraging; predator detection and avoidance and also social interaction benefits (NORRIS; SCHILT, 1988; BARAFF; ASMUTIS-SILVIA, 1998; STENSLAND; ANGERBJÖRN; BERGGREN, 2003; BEARZI, 2005; ROSSI-SANTOS; SANTOS-NETO; BARACHO, 2009; KISZKA et al., 2011; BACON et al., 2017). Although Mixed-species groups (MSGs) are common among cetaceans (BEARZI, 2005; HERZING; ELLISER, 2013; ZAESCHMAR et al., 2014) accessing the acoustic dynamics of these interactions remains challenging given the difficulty of addressing which vocalization belongs to which species and whether it is altered or not due to the interaction (VIANA et al., 2012).

Acoustic classifiers have been developed to provide identification from passive acoustic monitoring data to species level (OSWALD; BARLOW; NORRIS, 2003; OSWALD; RANKIN; BARLOW, 2008; SIMÕES AMORIM et al., 2019; AMORIM et al., 2022). However, until the moment they were generated using recordings of single species schools, therefore classifiers may have difficulties to identify mixed species schools. The MSGs data impose challenges such as the need to ascertain if the classification of the sound as multiple species is because of a classification error or the presence of multiple species on the recording (OSWALD; BARLOW; NORRIS, 2003). To solve this problem, the whistle classifier ROCCA developers, for example, intend to develop decision criteria for identifying schools as mixed versus single species by including the analysis of recordings of mixed species schools (OSWALD; BARLOW; NORRIS, 2003).

The Melon-headed whale (*Peponocephala electra*) is a delphinid species found in warm tropical and temperate oceans globally (JEFFERSON; BARROS, 1997; SHALLENBERGER, 1981; LODI; SICILIANO; CAPISTRANO, 1990; BAIRD et al., 2003; PERRYMAN; DANIL, 2018). Melon-headed whales form social groups in great group sizes from dozens to hundreds of individuals (HUGGINS et al., 2005; BROWNELL JR et al., 2009). This species is commonly interacts with other cetacean species such as humpback whales (*Megaptera novaeangliae*), rough-toothed dolphins (*Steno bredanensis)*, pantropical-spotted dolphins (*Stenella attenuata*), short-finned pilot whales (*Globicephala macrorhynchus*), bottlenose dolphins (*Tursiops truncatus*), and Fraser's dolphins *(Lagenodelphis hosei*) (HUGGINS et al., 2005; JEFFERSON et al., 2006; MAZE-FOLEY; MULLIN, 2006; ROSSI-SANTOS; SANTOS-NETO; BARACHO, 2009; FRANKEL; YIN, 2010; ASCHETTINO et al., 2012; MIGURA; MEADOWS, 2002; SCOTT; CHIVERS, 1990). Melon-headed whales exhibit a diverse repertoire of acoustic signals, including echolocation click trains, burst-pulse sounds, and whistles (WATKINS et al., 1998; BAUMANN-PICKERING et al., 2010; FRANKEL; YIN, 2010; KAPLAN et al., 2014).

The pantropical spotted dolphin (*Stenella attenuata*) is a widely distributed oceanic delphinid that occur in latitudes from 40°N to 40°S (PERRIN et al., 1987; WURSIG; PERRIN, 2009; WANG, 2012; JEFFERSON; WEBBER; PITMAN, 2011). School sizes comprehend from few individuals to several hundreds (PRYOR; KANG-SHALLENBERGER, 1991). Pantropical spotted dolphins are often sighted on associations with spinner dolphins (*Stenella longirostris*) (PERRIN et al., 1973; POLACHECK, 1987; GANNIER, 2002; REEVES; FOLKENS, 2002; PSARAKOS; HERZING; MARTEN, 2003; KISZKA et al., 2011), but were also sighted with other species such as melon headed whales, short-finned pilot whales and bottlenose dolphins, Fraser dolphins and striped dolphins (*Stenella coeruleoalba*) (SCOTT; CHIVERS, 1990; GANNIER, 2002; DOLAR et al., 2006; MAZE-FOLEY; MULLIN, 2006; ROSSI-SANTOS; SANTOS-NETO; BARACHO, 2009; PERRYMAN; DANIL, 2018). The species is known to produce whistles, click trains and burs-pulsed sounds (MOORE, 1990; SILVA et al., 2016; GONG et al., 2019).

The present study aims to provide an exploration of *P. electra* and *S. attenuata* MSGs through the acoustical perspective when the recorded species are on single species groups (SSGs) and when they are involved on MSGs. We also discuss the drivers behind their formation, the nature, and the implications of these associations for our understanding of delphinid acoustics, ecology and behavior.

4.2. MATERIALS AND METHODS

4.2.1 Study area and data collection

Acoustic recordings were made during several vessel-based seismic survey efforts in oceanic waters of Northeastern and Southeastern Brazil aboard seismic supply boats (and one from the seismic vessel). These surveys collected cetacean visual and acoustic data from 2017 to 2022, in the Western South Atlantic Ocean (04º to 22º S, Figure 1). Acoustical data from four cruises, totalling nine encounters with the targeted species, were used (Table 1).

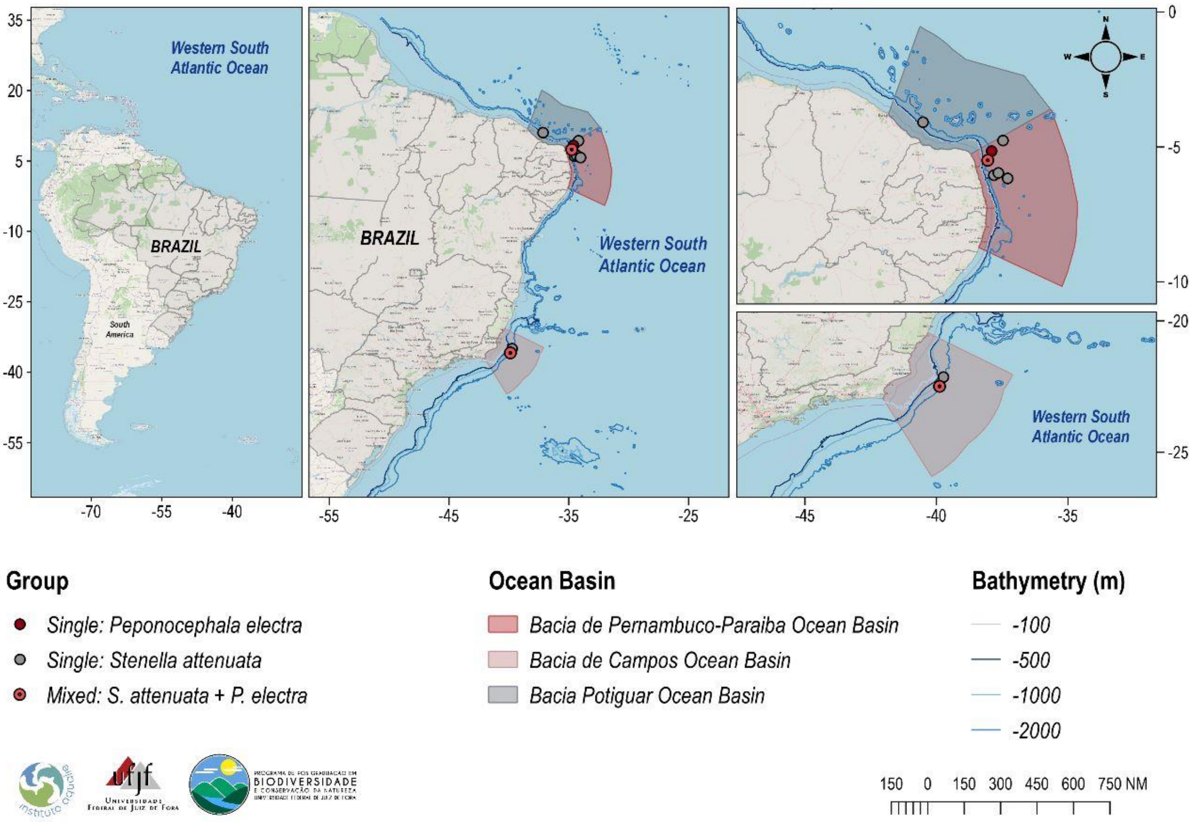

Figure 1: Study area where single and mixed species groups data were collected.

Recordings were collected continuously throughout day and night hours by a 300 m four-element, omnidirectional hydrophone array (Auset) (0,499 Hz High Pass filter, -205 hydrophone sensibility). Table I summarizes the data used for analysis and sampling rate information.

Table 1 Overview of data used in the analysis, including number of sightings, time of the recordings and coordinates

Context	**Long**	**Lat**	**Date**	**Recording time**	**Group size**	**Sample Rate (kHz)**
S. attenuata	-3.715.662	-4.086.625	12 Aug 2017	08:14am	NA	192
S. attenuata	-3.419.556	-4.763.056	19 Mar 2020	07:52am	15	500
S. attenuata	-3.453.472	-6.049.167	27 Mar 2020	04:04pm	200	500
S. attenuata	-3.436.833	-5.964.722	28 Mar 2020	06:58am	15	500
S. attenuata	-3.402.417	-6.166.944	30 Mar 2020	05:36am	12	500
S. attenuata	-397.384	-22.140	23 Feb 2022	09:02am	07	500
P. electra	-346.169	-51.547	02 Mar 2020	07:06am	100	500
S. attenuata + P.electra	-34.7606	-54.956	03 Mar 2020	05:00pm	50 Pe + 15 Sa	500
S. attenuata + P.electra	-39.88593	-22.49335	09 Dec 2021	11:31am	50*	500

Elaborated by the author *it was not possible to access the number of individuals of each species

During daylight, whenever a cetacean group was sighted by onboard observers, information such as geographical coordinates; weather parameters; depth; group size and behavior were collected. Marine mammal observers confirmed the recorded species by analyzing pictures taken during sightings that confirm species diagnostic characteristics. For *P. electra*, specifically, pictures were sent to four specialists to help on species' diagnosis in order to avoid misattribution to the very morphologically similar pygmy killer whale (*Feresa attenuata)*.

4.2.2 Acoustical analysis

The periods containing biological acoustic activity were identified through visual and aural inspection using Raven Pro 1.6 (Cornell Laboratory of Ornithology, NY). Only acoustic files with simultaneous sighting data of the identified species were inspected. Whistles and click trains were manually selected from spectrograms (Hann window of 1843 points, DFT of 2048 points, and 70% overlap) and the following whistle parameters were extracted: low frequency, high frequency, delta frequency (i.e. the difference between high and low frequencies), center frequency, beginning and ending frequencies, and whistle duration. The selection was based on the signal- to-noise ratio (≥ 10 dB) for whistles with a clear contour shape and whistles highly overlapped by other whistles were avoided. Measurements were made only on the fundamental frequency of whistle contours. The selected click trains were used to create subsets from the original file and the following parameters were extracted through a MATLAB (Mathworks, Natick, MA) custom routine: peak frequency, 3 dB bandwidth, 10 dB bandwidth and inter-click interval (ICI). A high pass filter with a cut-off at 2 kHz was applied to the subset files of click trains to minimize the influence of low frequency noise. Only trains that were not overlapped with each other were considered for ICI measurements.

4.2.3 Statistical analysis

To verify whether the three groups of data (*P. electra* SSGs; *P. electra* + *S. attenuata* MSGs; *S. attenuata* SSGs) could be classified based on their whistles and clicks, a random forest analysis (RFA) was performed. For clicks models, 70% of the data were randomly selected as training sample and 30% were selected for validation. For the whistles model, 60% of the data were selected as training sample and 40% as validation. The analysis was made using a randomly balanced dataset among the MSGs and single-species groups for clicks and whistles models. We trained 1000 trees and the number of variables randomly selected at each node (*mtry*) was used as a tuning parameter in the RFA which allows adjustment to achieve a high accuracy rate from the model training data. Multivariate plots using Euclidean distance were constructed to visualize the dispersions of data among groups. Then, to account for the goodness of fit of the models, the receiver operating characteristic (ROC) curves were plotted and the areas under the curves were computed. Finally, the importance measure mean decrease accuracy was calculated to rank the acoustical parameters most important to the classification.

Permutation tests an analysis which compares differences in pairs of data, with 100,000 bootstraps were used to test which parameters of whistle and clicks significantly differed between groups (SSGs *versus* MSGs).

All statistical analyses were performed with the software R 4.2.1 (R Development Core Team 2015) using packages ‘lmPerm’ for permutation (WHEELER; TORCHIANO, 2016), ‘randomForest’ for random forest analysis (LIAW; WIENER, 2002), ‘pROC’ for ROC curves (ROBIN et al., 2011), and ‘vegan’ for multivariate dispersion (OKSANEN et al. 2013). Outliers were removed prior to running all the analysis.

4.3. RESULTS

A total of 3h44m of recordings were analyzed from nine acoustic encounters (Figure 1, Table 1). The number of whistles and clicks per group (3 groups: *P. electra* SSG; *S. attenuata* SSGs; and MSGs) used to run the RFA was 150 and 1000 respectively (with exception of *P. electra* SSG, in which the number of clicks was 974). Confusion matrices generated with classification results are presented in Tables 2 and 3.

Table 2 Confusion matrix from clicks model presenting the misclassification rates

Clicks

Prediction	**Pe SSG**	**MSG**	**Sa SSG**	**Sensitivity**	**Specificity**
Pe SSG	62%	10%	28%	0.6245	0.8182
MSG	12%	66%	22%	0.6948	0.8068
Sa SSG	22%	22%	56%	0.5000	0.7829
Balanced Accuracy	0.7214	0.7508	0.6415	-	
OOB: 37,0%			**Accuracy:** 0.6058		

Elaborated by the author. OOB: Out of Bag Error

Table 3 Confusion matrix from whistles model presenting the misclassification rates

Whistles

Prediction	**Pe SSG**	**Msg**	**Sa SSG**	**Sensitivity**	**Specificity**
Pe SSG	70%	19%	11%	0.8276	0.7869
MSG	27%	39%	34%	0.4590	0.8403
As SSG	6%	40%	53%	0.6721	0.8487
Balanced Accuracy	0.8072	0.6497	0.7604	-	
OOB: 47,7%			**Accuracy:** 0.5667		

Elaborated by the author. OOB: Out of Bag Error

Overall, 1000 trees were generated through the random forest analysis, resulting in an accuracy of 60.5% for clicks and 56.6% for whistles. The learning curves of the models of whistles and clicks are presented in Figures 2, 3 and the ROC curves are presented in Figures 4 and 5. Final frequency was the parameter with the highest mean decrease accuracies for whistles and peak frequency for clicks (Figures 6 and 7).

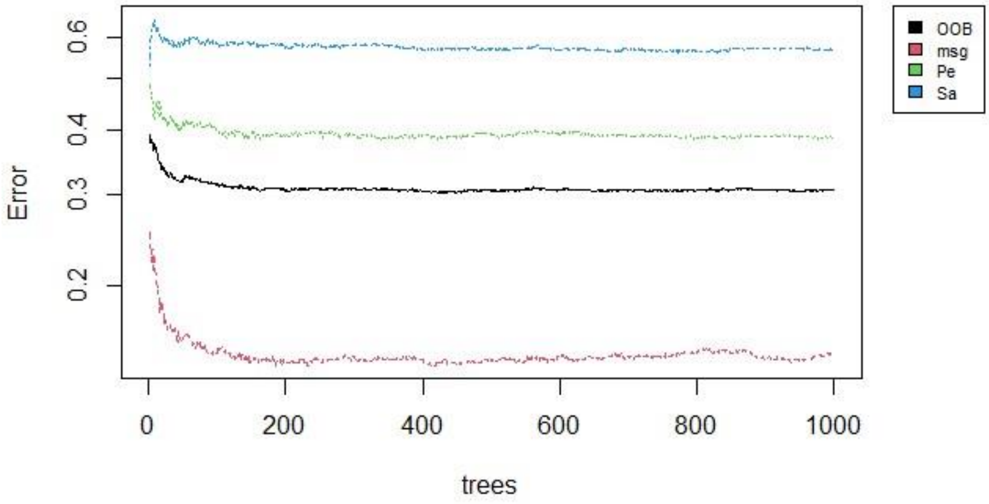

Figure 2 - Out-of-bag errors and the 1000-tree generated plot from clicks classification models. Pe: *P. electra*; msg: Mixed-species groups; Sa: *S. attenuata*

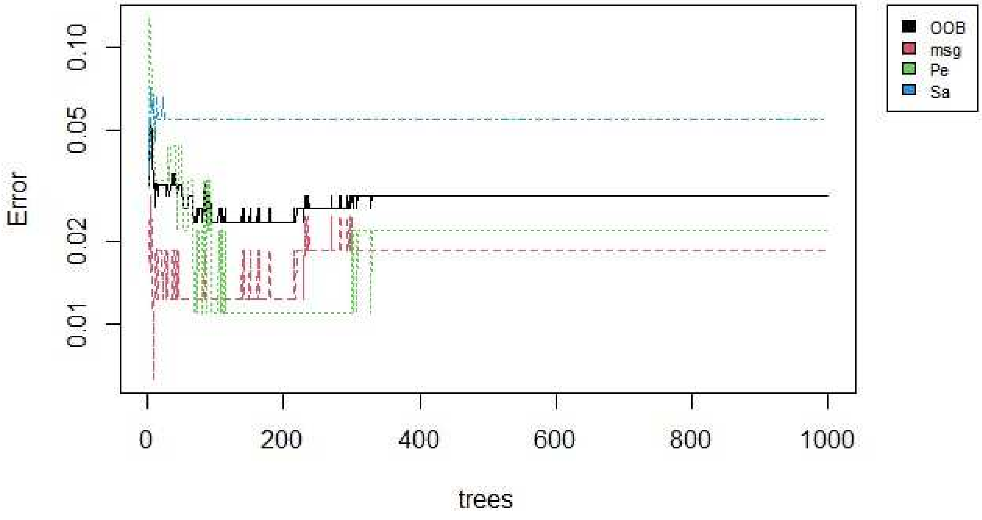

Figure 3 - Out-of-bag errors and the 1000-tree generated plot from whistles classification models. Pe: *P. electra*; msg: Mixed-species groups; Sa: *S. attenuata*

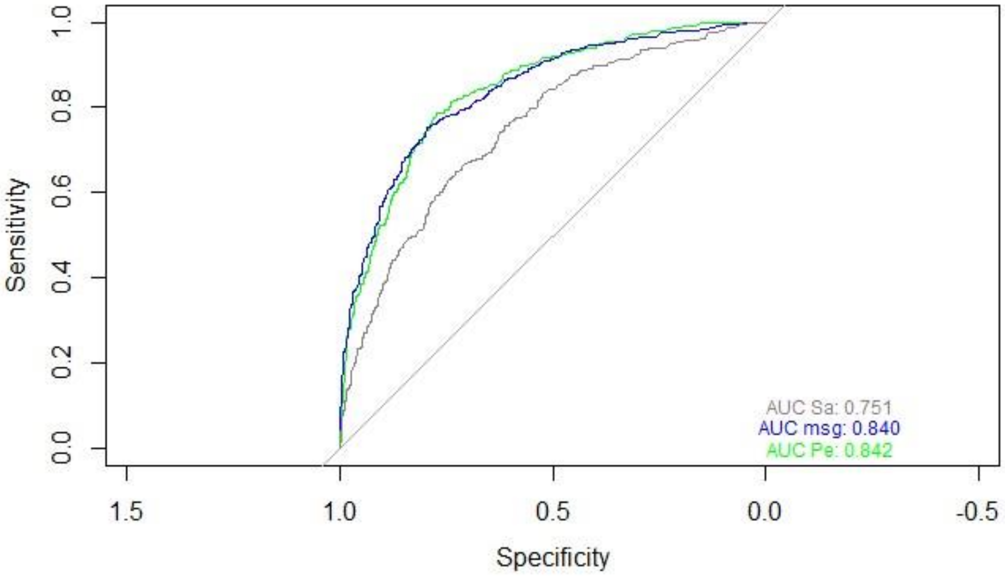

Figure 4 - ROC curves and areas under the curves generated plot from clicks classification models. Pe: *P. electra*; msg: Mixed-species groups; Sa: *S. attenuata*

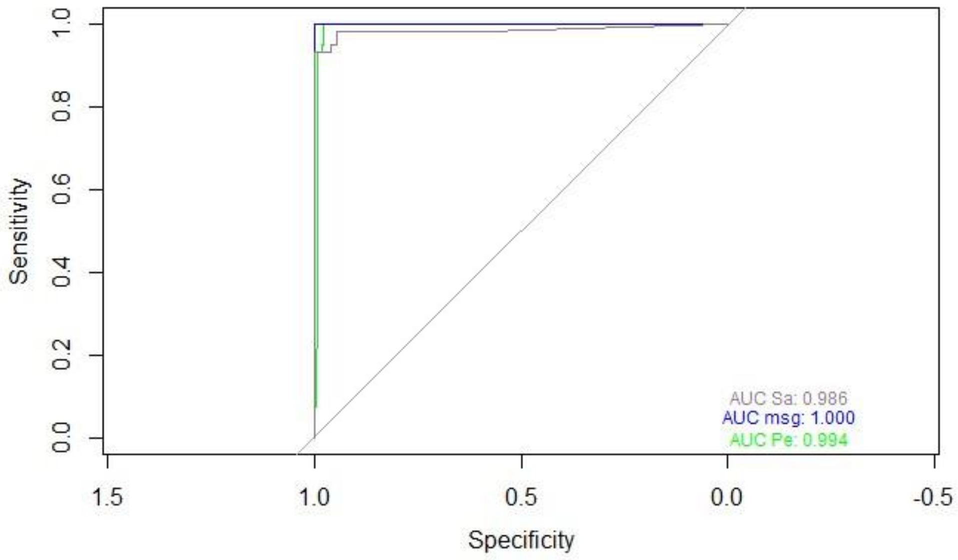

Figure 5 - ROC curves and areas under the curves generated plot from whistles classification models. Pe: *P. electra*; msg: Mixed-species groups; Sa: *S. attenuata*

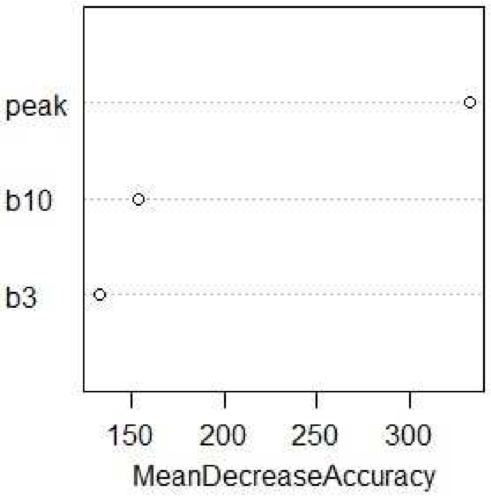

Figure 6 - Mean Decrease Accuracy from clicks classification models. Peak: peak frequency; b10: 10 dB bandwidth; b3: 3 dB bandwidth

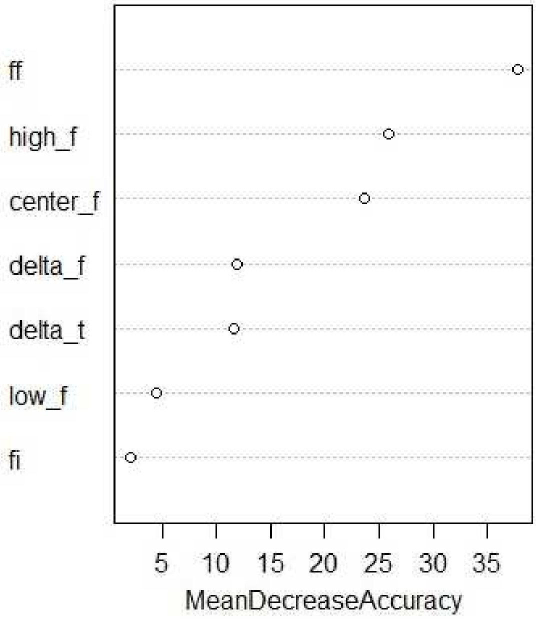

Figure 7 - Mean Decrease Accuracy from whistles classification models. ff: final frequency; high_f: high frequency; center_f: center frequency; delta_f: delta frequency; delta_t: delta time; low_f: low frequency; fi: final frequency

The multivariate dispersion plots presents different pattern in the data distribution of the single species context from the MSGs: Although there is a clear superposition of the SSGs with the MSGs on the whistle multivariate dispersion plot, the same pattern is not visible on the clicks multivariate plot where is possible to see a higher superposition between the SSGs but not with those with the MSGs (Figures 8 and 9).

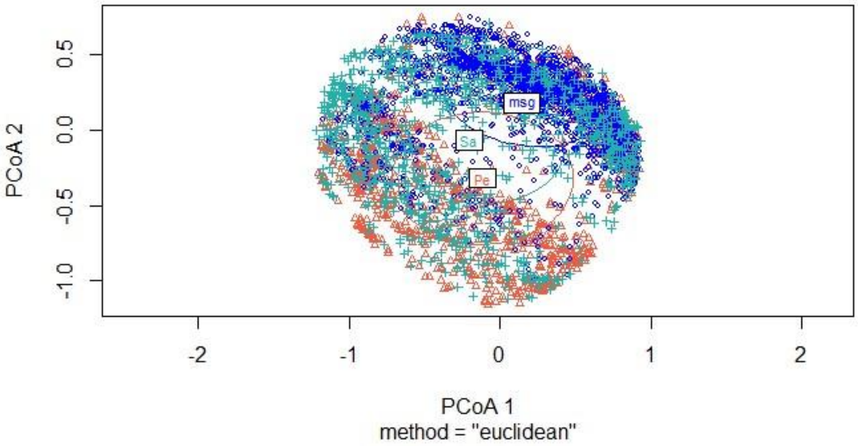

Figure 8 - Multivariate plot with Euclidian distances from clicks data. Pe: *P. electra*; msg: Mixed species groups; Sa: *S. attenuata*

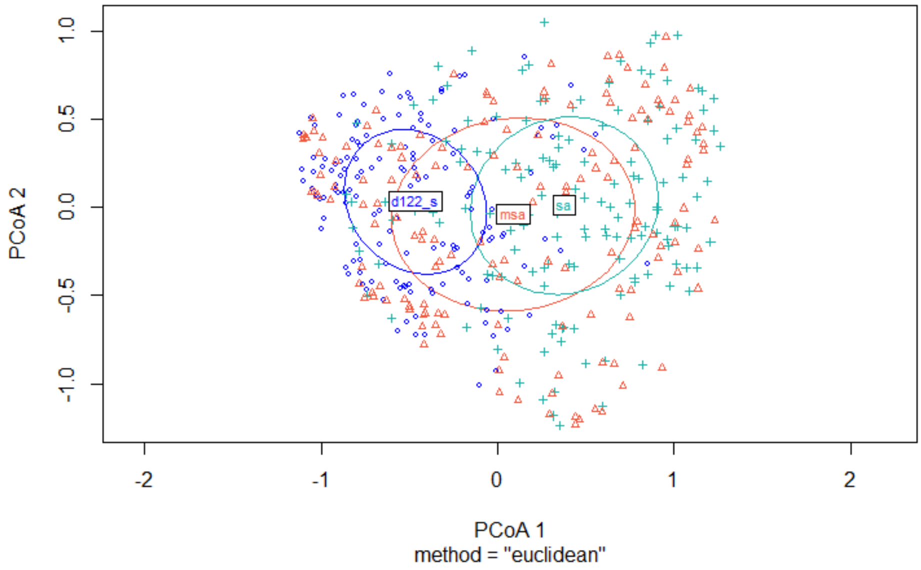

Figure 9 - Multivariate plot with Euclidian distances from whistles data. Pe: *P. electra*; msg: Mixed species groups; Sa: *S. attenuata*

We examined if acoustic parameters (8 for whistles and 4 for clicks) ranked as most important on the models were also the ones which show significant difference between the groups through permutation tests. For clicks, peak frequency (most important) and 3dB bandwidth were significantly different, and for whistles, high frequency (second most important), center frequency and delta frequency were significantly different (p<0.001) between all MSGs x SSG permutations, although final frequency was the most important parameter on the models. Boxplots and permutation results are provided in Supplementary Material (Figures S10 to S13).

4.4. DISCUSSION

In this study we aimed to assess the potential acoustic changes among different grouping categories (MSGs and SSG) by building classification models.

The MSGs clicks presented a low percentage of misclassification with the SSGs (12% with *P. electra* and 22% with *S. attenuata* SSG, respectively). This low rate of classification errors brings the possibility that the MSGs clicks possess a peculiarity, which belongs to the interaction, that is not present when species are in

SSG. On the other hand, a higher sample of *P. electra* SSG encounters could clarify this scenario, although in this study, for *S. attenuata,* even using six encounters in order to certify a considerable amount of data, the misclassification rate of this species with the MSGs was less than 25% (Table 2).

This low misclassification rate also raises the possibility of species changing particularities of their own click emissions in order to enable the interaction of mixed groups. Cosentino et al. (2022) studied a common dolphin (*Delphinus delphis*) which was seen interacting with harbor porpoises (*Phocoena phocoena*) producing clicks that were similar to porpoise clicks both in time and frequency characteristics. There is also a chance that species, when interacting, emit intermediary characteristics of their clicks due to the interaction. Thus, the 66% of correct classification on MSGs clicks could be addressed to this pool of clicks that possess intermediate characteristics between both species and could not be classified as single species separately. Although using more samples of *P. electra* single species encounters could reduce the misclassification of this species with *S. attenuata*, it is important to discuss that *P. electra* and *S. attenuata* have more similar clicks than between *P. electra* and MSGs, reinforcing the hypothesis that MSGs present their own intermediary acoustic characteristics, at least among click emissions.

Overall MSGs whistle classification results show a higher misclassification rate among MSGs x SSGs compared to the classification between SSGs (Table 2). Although there is a clear separation between the SSGs, possibly due to the species-specific whistle properties, whistles between MSGs and SSGs show a high misclassification rate, contrasting with previous findings by Viana et al. (2022) where low misclassification rates were found in comparison of whistles between single and mixed species groups. May-Collado (2010) found an intermediate whistle structure in aggressive interactions between the bottlenose dolphin *(T. truncatus)* and the Guiana dolphin (*S. guianensis)* and discussed this finding as an attempt of the Guiana dolphins to emit threats intelligible to the aggressors or to express stress and signal convergence between interacting species. The nature of the observed mixed groups in the present study did not seem to be aggressive since heterospecifics were seen sharing social behaviors such as breaching, bow riding, and, at least in one of the MGSs, also swimming side by side and making pectoral fin contact. Paulos et al. (2008) found more similarities than differences between Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and the Atlantic Spotted dolphin (*Stenella frontalis*) in their use of specific behaviors in potentially communicative situations across SSGs. In addition, the sharing behavioral repertoire has been documented across interspecies interactions (ELLISER; HERZING, 2016; SYME; KISZKA; PARRA, 2023) and the heterospecific pectoral fin contact was described as an important part of social bond formation (EIERMAN et al., 2019).

Despite the existence of MSGs reports in which the involved species are sighted foraging together (ZAESCHMAR et al., 2014; SYME; KISZKA; PARRA, 2023), no foraging behavior was observed on both MSGs analyzed. Baumann-Pickering et al (2015) had demonstrated a high whistle production by *P. electra* during daytime periods, periods in which the species is likely to be more involved in resting and socializing behaviors and the nighttime periods seems to be mostly used for foraging.

The clear separation between *P. electra* and *S. attenuata* SSGs suggests that the whistles from SSGs maintain some time-frequency characteristics, allowing them to be correctly classified more often than when species interact on MSGs. The whistle MSGs data, in comparison to clicks, presumably captured more acoustic variability since this signal has a communicative function and it is used on different behavioral states, group composition, and environment (GRIDLEY et al., 2016; DÍAZ LÓPEZ, 2022). This characteristic added to *S. attenuata* already described whistle plasticity (PAPALE et al., 2017) may be responsible for the lower classification rates with MSGs. Other model-building configurations could improve the percentage of correct classification on whistles among groups. Barkley et al. (2019) showed classification improvement in whistles of different false killer whale (*Pseudorca crassidens*) populations for most acoustic encounters through pairwise models.

The parameters that showed significant differences on all permutation tests and the most contributions for model accuracy were high frequency, center frequency and delta frequency for whistles, and peak frequency for clicks, being the 3dB bandwidth the least contribution for model accuracy. Other classification models in the Southwest Atlantic Ocean bring peak frequency and 3 dB bandwidth as the most important parameters for model improvement (AMORIM et al., 2019; AMORIM et al., 2022), whereas for whistles, other parameters were ranked as the most important ones.

The genetic and acoustic plasticity of delphinids species has been described (FAVARO et al. 2016; MUSSER et al. 2014; COSENTINO et al., 2022) and copulation attempts, and potential hybrids have been found among mixed-species associations (HEARZING; MOEWE; BRUNNICK, 2003; HODGINS; DOLMAN; WEIR, 2014; KOPER; PLÖN, 2016; ESPADA et al., 2019; VAN GEEL et al., 2022). Although no copulation attempt has been seen, hybridization between *P. electra* and *Steno bredanensis* has been documented (BAIRD et al., 2018). and hybridization of the genus *Stenella* with another delphinid species has been discussed (ELLISER; HERZING, 2016).Van Geel et al. (2022) suggest the study of existence of hybrid-specific vocalizations, such as altered or atypical signals, since, for now, the 52 Hz call found by Watkins et al (2004) is hypothesized to be transmitted by the hybrids of blue whale (*Balaenoptera musculus*) and fin whale (*Balaenoptera physalus*) (STAFFORD et al., 2007).

In one of the two MSGs analyzed it was not possible to access the number of individuals per species (Table 1). One may ask about the possibility of the outnumbered species being extolling the results, however, at least to our knowledge, it is not possible to affirm that the outnumbered species is the most vocalizing one at the moment. The presence of calves, from both species, was sighted in one of the MSGs. Despite the existence of MSGs with a nursery nature across delphinid species (SYME; KISZKA; PARRA, 2023) and cross adoption of a *P. electra* calf by a *T. truncatus* adult female (CARZON et al., 2019), no interspecific alloparental care was observed.

P. electra and *S. attenuata* clicks were documented to achieve high correct classification rates in a classifier of delphinids whistles from single species groups (LIN; CHOU, 2015) and *P.electra* clicks were passable of discrimination among other delphinids (BAUMANN-PICKERING et al., 2010), yet, there is the possibility of MSGs correctly classified signals present subtle characteristics that would make it difficult to discern from single species data. The use of more time-frequency parameters and a higher volume of repetitions/encounters may enhance the classification performance, although we do not know whether interaction enables acoustic changes making some part of mixed species signals unique. The comparison of confusion matrices generated from known mixed species schools with those generated from single species schools perhaps could shed a light on patterns that would aid in discerning actual mixed species schools from classification errors (OSWALD; BARLOW; NORRIS, 2003).

This study showed differences on the classification under distinct acoustic signals when classifying single and mixed species contexts: MSG clicks showed a higher percentage of correct classification in comparison to whistles. Although we cannot ascertain, through this analysis, if the MSGs clicks were produced mainly by one species or by both, the 66% of correctly classified clicks produced during MSG present distinct characteristics which allowed them to be separated by the SSG clicks, turning feasible hypothesize acoustic modulation produced by one or both species due to the MSG context indicating some specific property on clicks in MSG contexts. Different from Viana et al. (2022), in which remarkable differences between *T. truncatus* MSG and SSG whistles were found, the whistles similarity between mixed and single species groups found in this study may indicate that possibly other factors may influence the chance of signal and modulation types, such as, the nature of the mixed group, the behavior and species composition. Although the role of acoustic communication on MSGs remains unclear, the results from this study may shed some light on future acoustic classification among sympatric species that share similar traits in their ecology. Also, our findings help on the understanding of the acoustic implications on interspecies group formation and interaction.

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5. SUPPLEMENTARY MATERIAL

5.1 CHAPTER II

5.1.2. Acoustical recording details

From Talude project: 250 meters matrix array Auset® with three-elements (-40 dB, -161 dB re: 1V / µPa) distant five meters from each other, coupled to a digital recorder Fostex® FR-2 LE (sampling frequency of 96 kHz / 24 bits and configured with a high pass filter of 1.592 Hz) - for the 2013 and 2014 surveys. In 2015, it was used a 300 meters matrix array Auset® with three-elements (-40 dB, -161 dB re: 1V / µPa) distant five meters and three meters from each other, respectively. Both were coupled to a digital recorder Fostex® FR-2 LE (sampling frequency of 96 kHz / 24 bits and configured with a high pass filter of 0.499 Hz). Whenever possible, the acoustic signals were transmitted to a digitizer board (Iotech model - PersonalDaq / 3000 Series) sampling at 100 kHz / 24 bits.

From PMC project: 400 meters matrix array Biowaves consisting of an oil filled polyurethane tube with four elements and custom pre-amplifiers, containing a pair of low frequency (LF) hydrophones (APC 42-1021) and a pair of high frequency (HF) hydrophones (Reson TC4013). Only records from the LF hydrophone pair was used for the purpose of this study. The acoustic processing system consisted of amplifiers with adjustable gain and filters. For the LF system the gain was set between 10 to 20 dB and the audio was filtered using an eight-pole bandpass filter between 1 - 48 kHz. A soundcard (ASUS XONAR 7) digitized the audio at 192 kHz/ 16 bit sampling frequency.

5.1.3. Supporting Figures

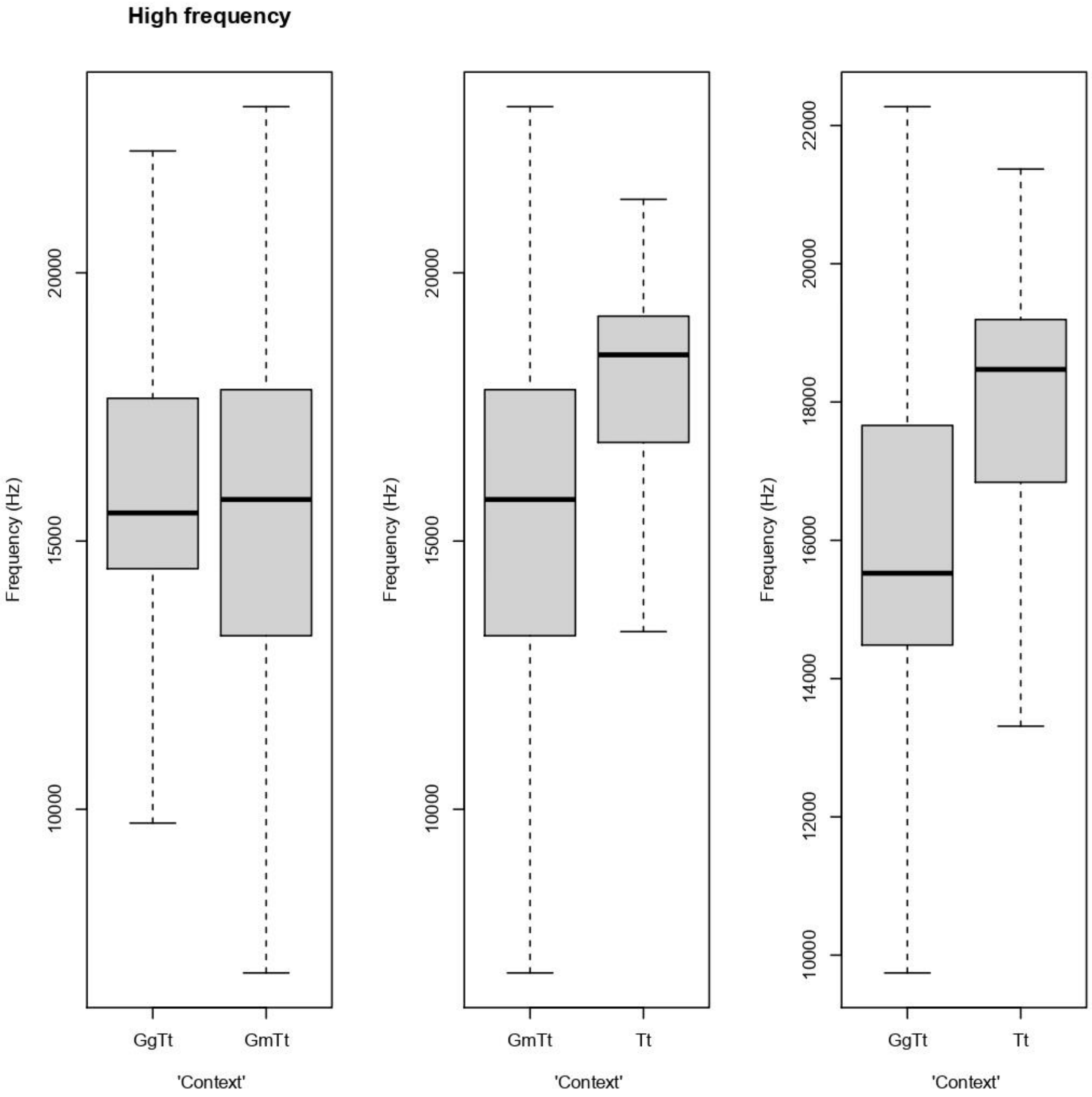

Figure S1. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of high frequency parameter among the contexts. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

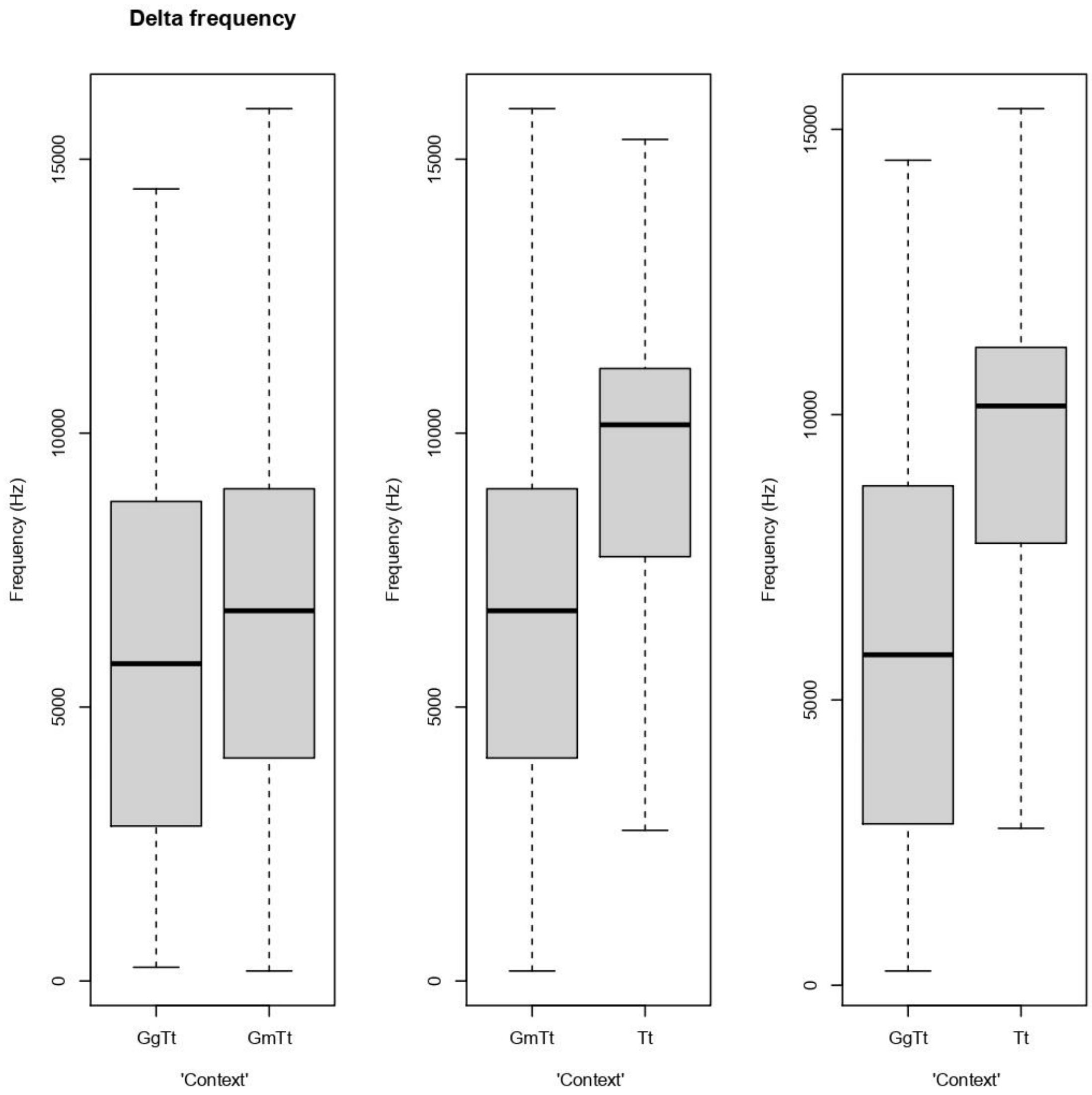

Figure S2. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of delta frequency parameter among the contexts. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

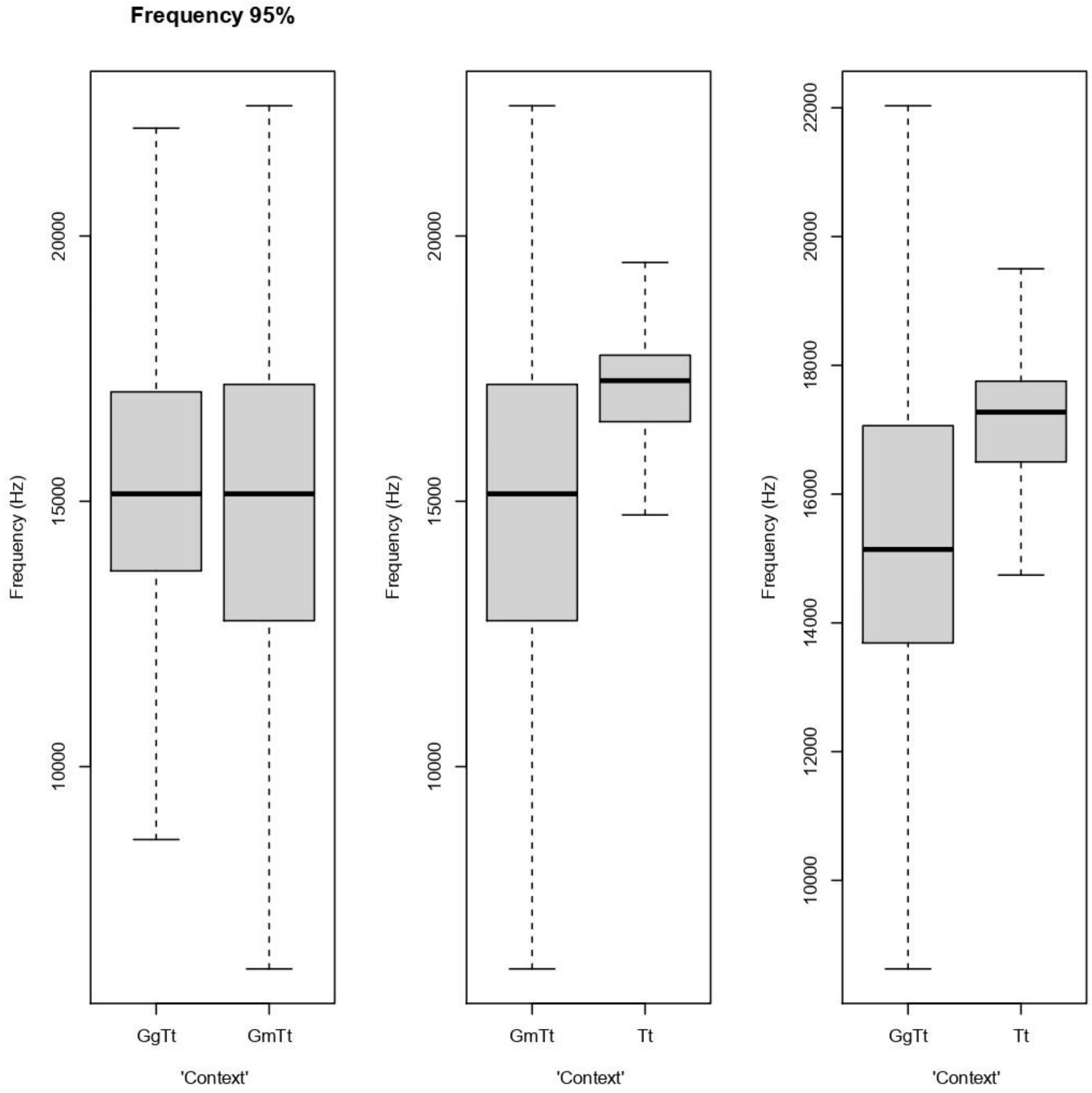

Figure S3. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of frequency 95% parameter among the contexts. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

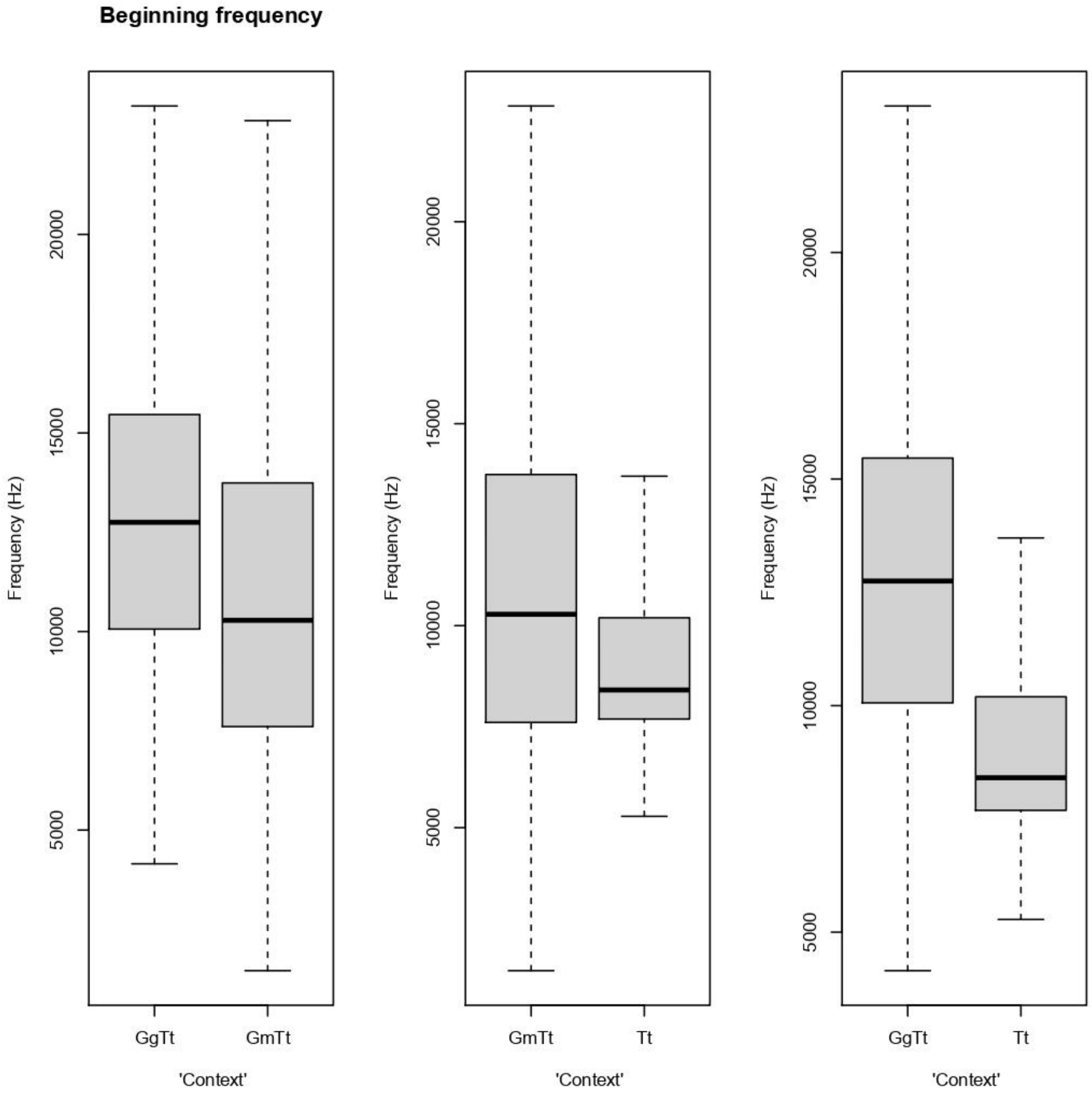

Figure S4. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of beginning frequency parameter among the contexts. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

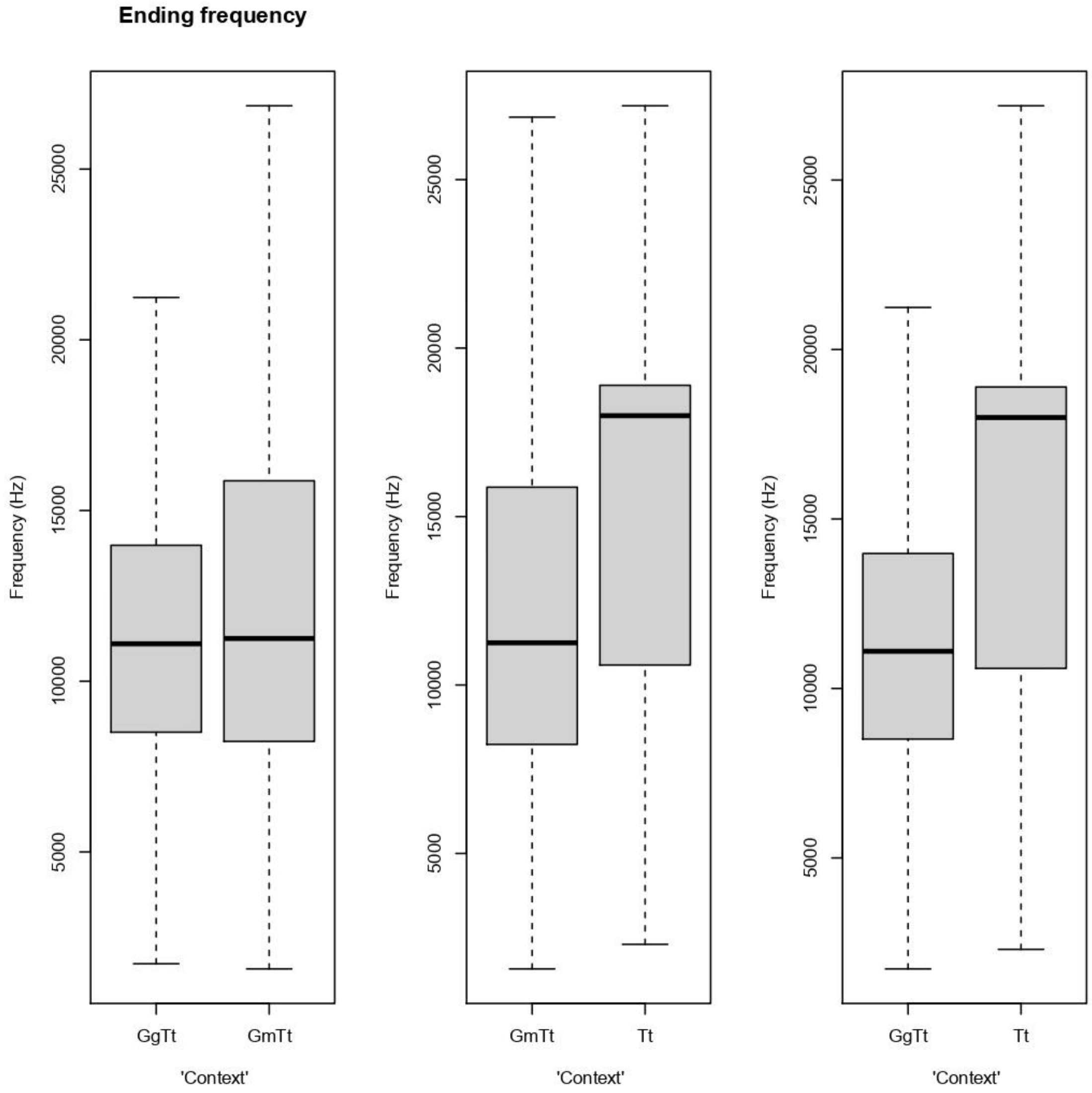

Figure S5. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of ending frequency parameter among the contexts. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

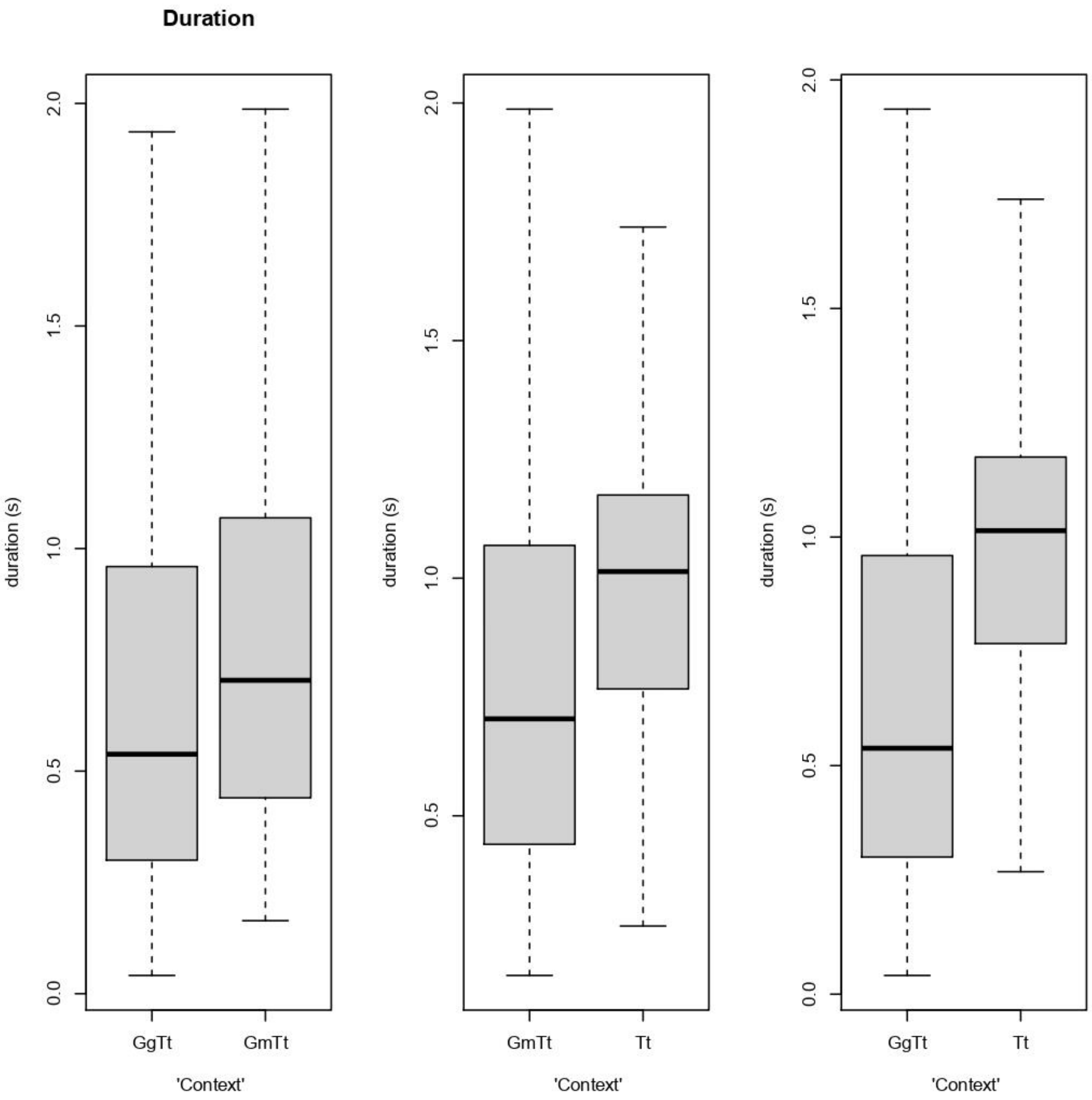

Figure S6. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of duration parameter among the contexts. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

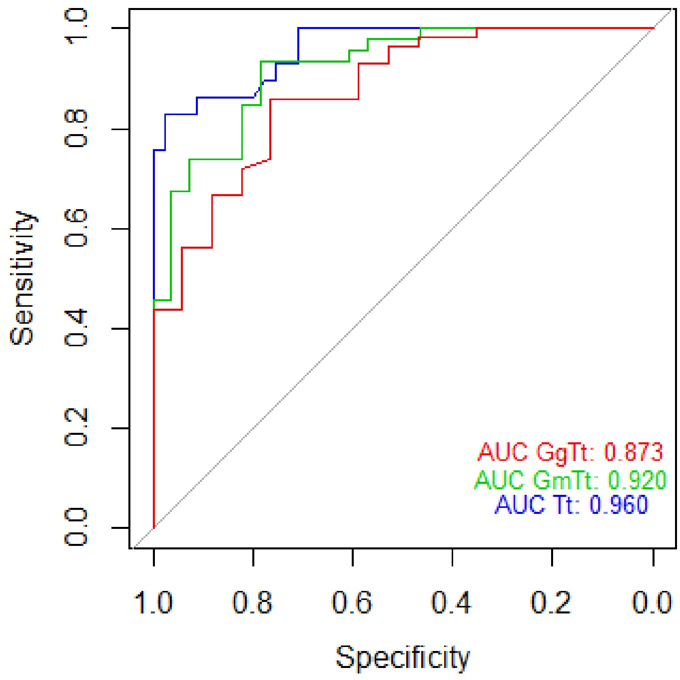

Figure S7. ROC curves indicating the goodness of fit of the Random Forest model. The Area Under the Curve (AUC) values ranged from 0.87 to 0.96. GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

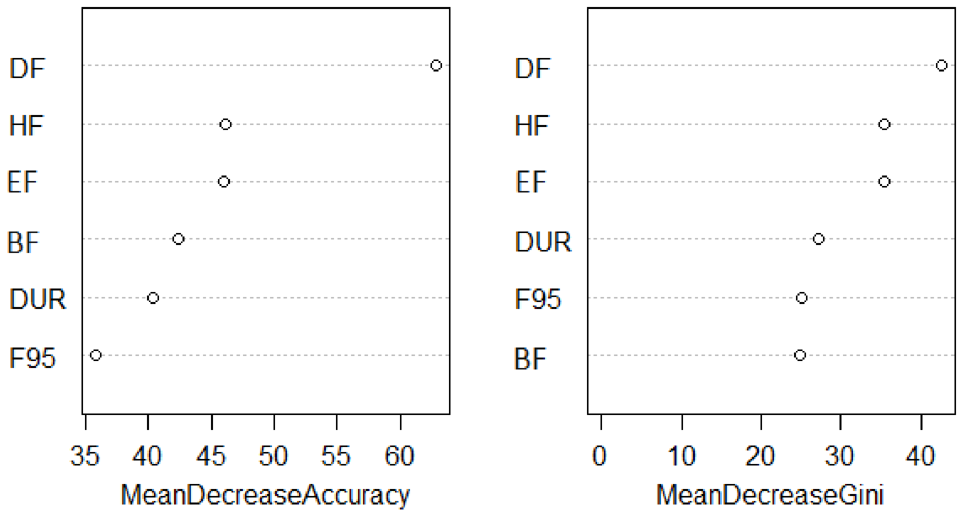

Figure S8. Decrease Accuracy and decrease Gini of each acoustical parameter used to develop the Random Forest model. Frequency 95%, duration and beginning frequency were the parameters that showed the lowest mean decrease accuracy

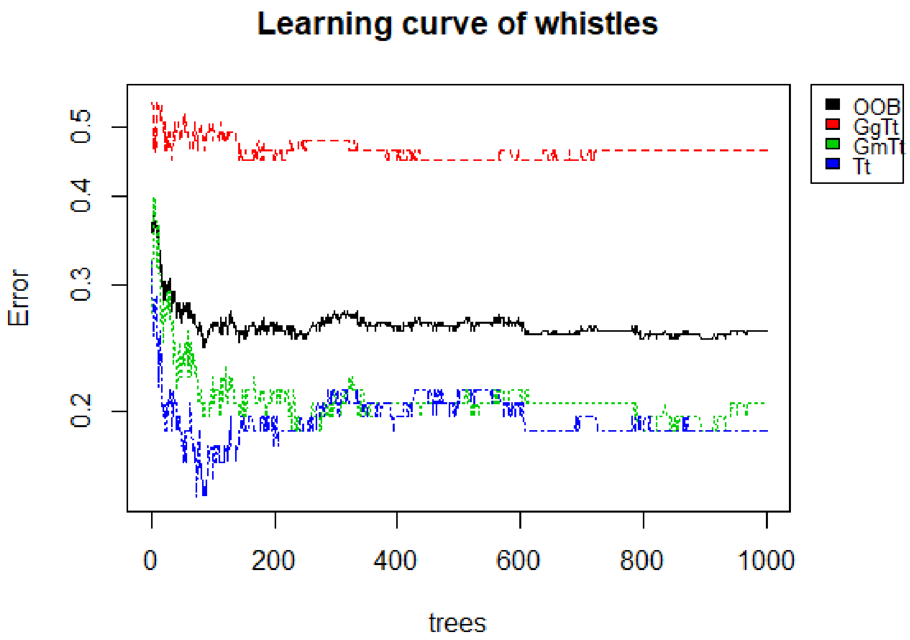

Figure S9. Error associated to each of the 500 trees generated in the Random Forest model. It is represented the Out of Bag (OOB) error and the errors for GgTt: *G. griseus* and *T. truncatus* whistles; GmTt: *G. melas* and *T. truncatus* whistles; Tt: *T. truncatus* single species whistles.

5.2 CHAPTER III

5.2.1. Supporting Figures

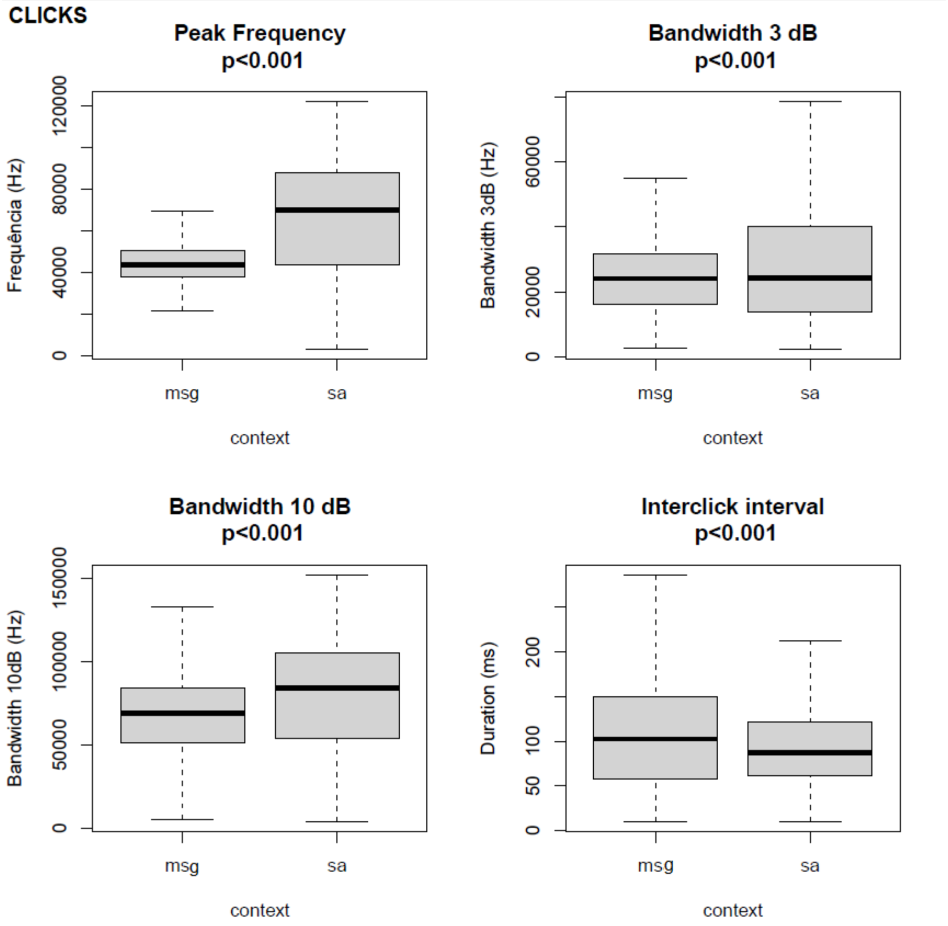

Figure S10. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of clicks parameters among the contexts. msg: mixed-species groups; Sa: *Stenella attenuata* single species groups.

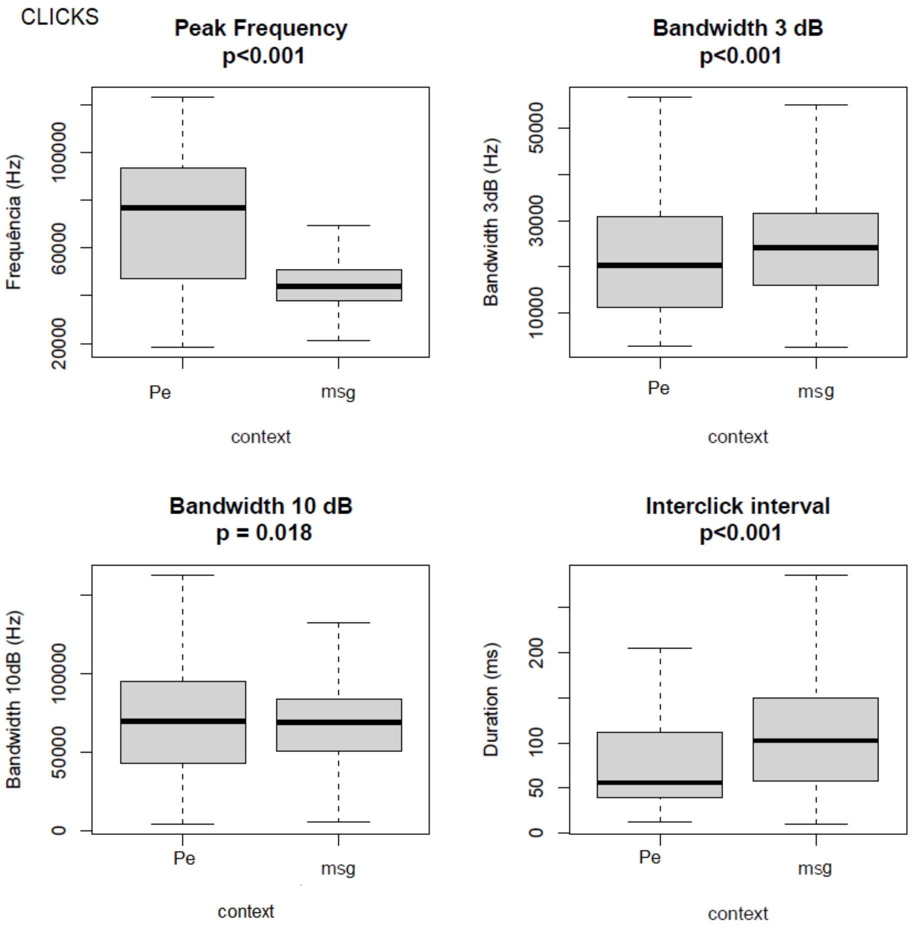

Figure S11. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of clicks parameters among the contexts. msg: mixed-species groups; Pe: *Peponocephala electra* single species group.

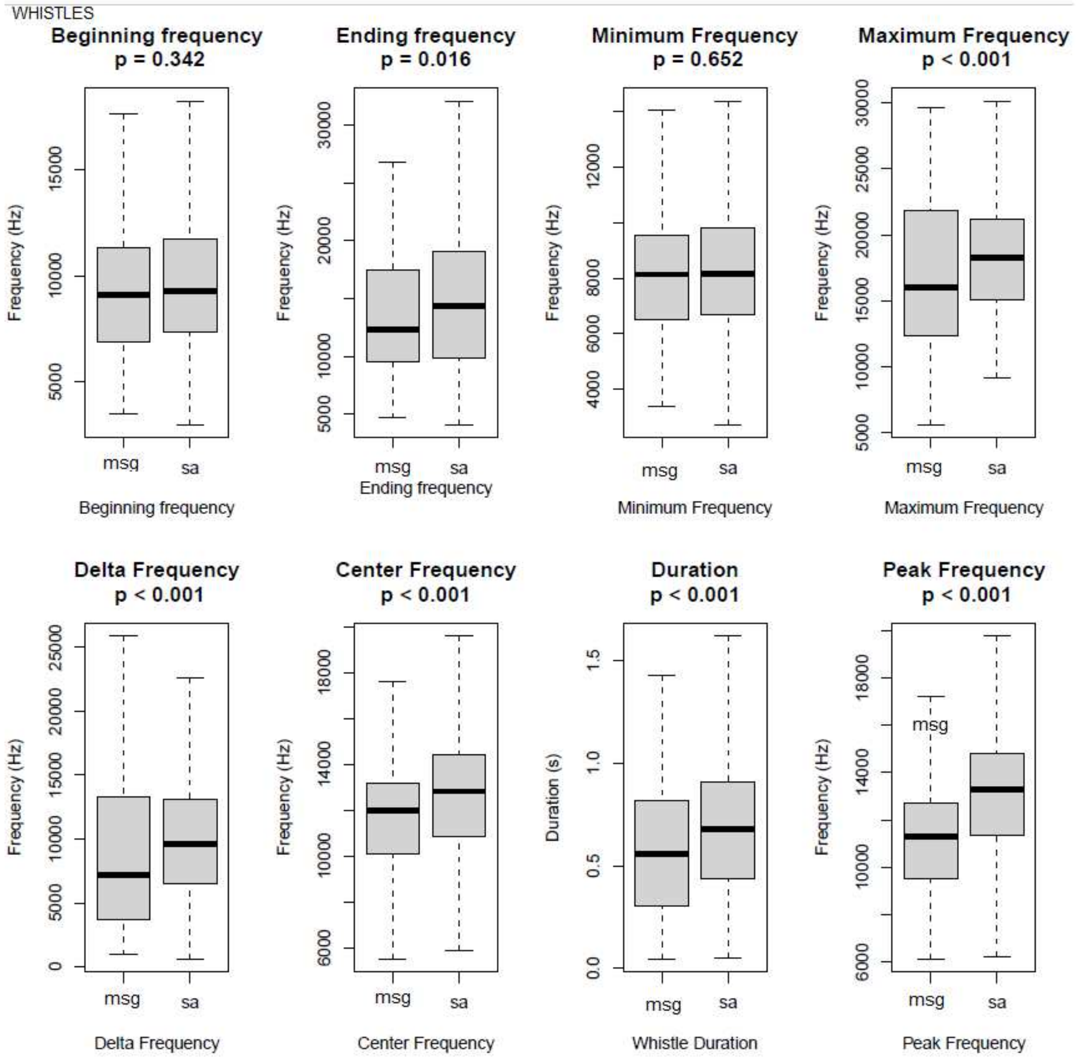

Figure S12. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of whistles parameters among the contexts. msg: mixed-species groups; Sa: *Stenella attenuata* single species groups.

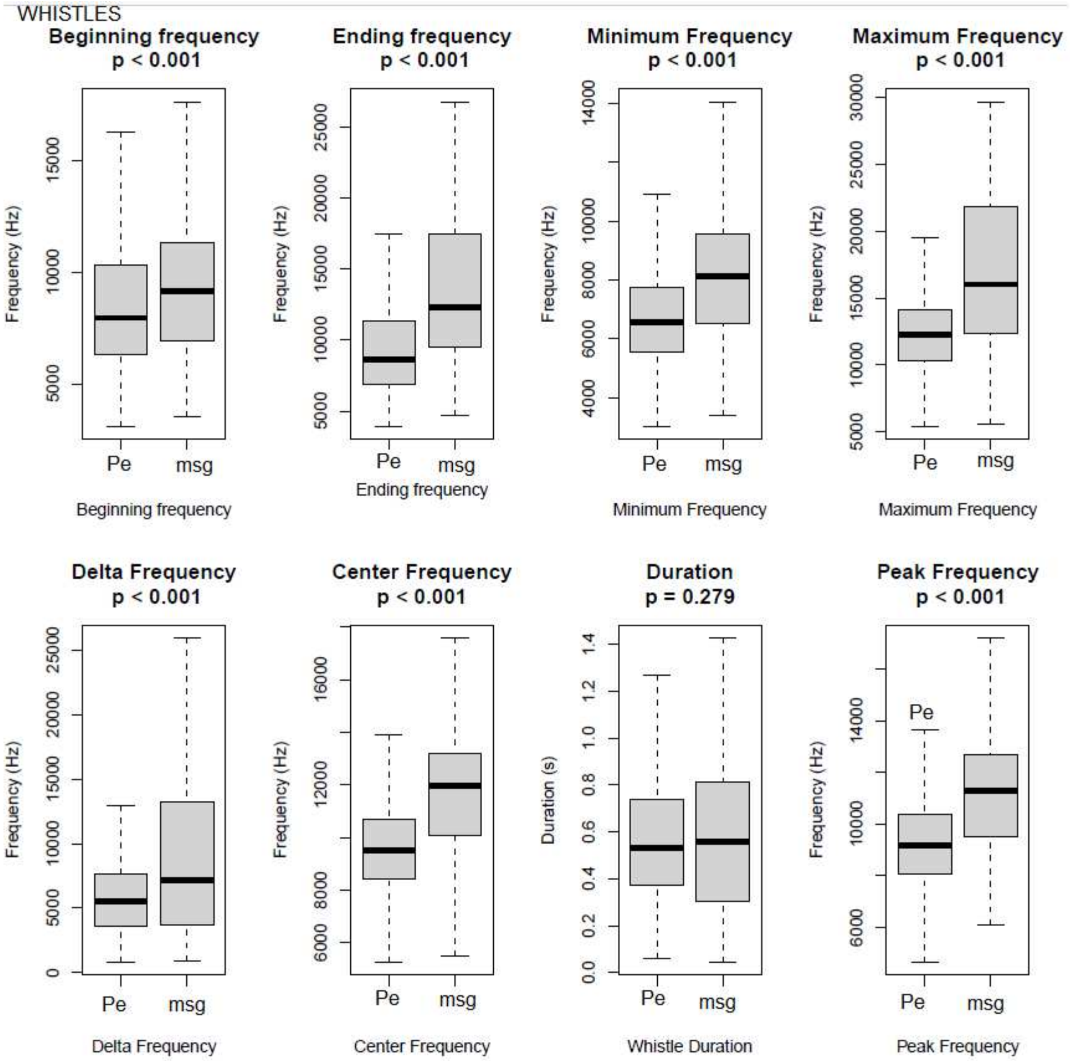

Figure S13. Box plots presenting the median (bar), interquartile range (box) and non-outlier range (whiskers) of clicks parameters among the contexts. msg: mixed-species groups; Pe: *Peponocephala electra* single species groups.