The cultural evolution of humpback whale song in the North Atlantic and South Pacific Oceans: a study of cumulative culture, fine-scale evolution, and public engagement

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General Abstract

This PhD thesis explores humpback whale song research, cumulative cultural evolution (CCE), aesthetics, and public engagement. It comprises five chapters, each offering a comprehensive analysis of these topics. Chapter 1 outlines humpback whale song research and its relevance to CCE and vocal learning debates. It emphasises the effective use of whale song in public engagement for science and conservation. Chapter 2 presents a conceptual analysis of the compatibility between CCE and aesthetics. Interdisciplinary discussions explore challenges in reconciling aesthetic culture with prevailing philosophical views. The chapter also highlights tensions between cultural evolution in aesthetic and technological domains, contributing to debates on reconstructive and preservative theories. Chapter 3 tracks the evolution of a specific humpback whale song unit type across different themes within a song type over a breeding season. Methodological efficiencies enable a larger dataset analysis, providing insights into vocal production learning hypotheses. Chapter 4 expands on Chapter 3 by examining the evolution of a song unit type over two seasons and in a different ocean basin. Matching song types across locations reveals the extraordinary scale of humpback song cultural evolution. Evidence supports the vocal production learning hypothesis and challenges the notion of an innate template. Chapter 5 diverges thematically and methodologically, focusing on two case studies in public engagement. An interactive science exhibition and a community science event demonstrate successful engagement and impact on low science capital public groups. This thesis contributes to understanding humpback whale song research, CCE, aesthetics, and public engagement. It offers interdisciplinary perspectives, empirical investigations, and valuable insights into cultural evolution complexities. The thesis emphasises the importance of engaging the public in science while showcasing the impact on both the public and the researcher.

1 Chapter 1: General Introduction

Human life is rich with culture, permeating every aspect of our lives, including science, technology, customs, beliefs, art, literature, and music. Culture can be defined as "group typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (Laland & Hoppitt, 2003: p.151). The transmission of cultures between groups of individuals can be achieved in three main ways: vertically, horizontally, and obliquely (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). Vertical transmission refers to the transmission of cultural information from one generation to the next i.e. when individuals learn from their parents. Oblique transmission refers to the transmission of cultural information between individuals who are not directly related such as from teachers to younger unrelated individuals. Horizontal transmission, on the other hand, involves the transmission of cultural information between individuals who are in the same generation. This type of transmission occurs when individuals learn from and imitate each other, sharing cultural knowledge and practices within a community or population. A great example of horizontal transmission in human culture is the case of Beatlemania in 1964, when the Beatles' music crossed the Atlantic Ocean, causing a revolution in American music. The Beatles were one of the world's first global bands, and their music serves as an excellent example of the transmission of human cultures horizontally. Passion for music is evident across the world, with many of us attending live music events or receiving music recommendations from friends and family. Through these interactions, we continually learn about music from others, showcasing the horizontal transmission of cultural information.

While the transmission of culture was once thought to be a distinguishing factor between humans and other animals, increasing evidence over the last few decades has shown that culture exists across the animal kingdom with evidence in nonhuman primates, cetaceans and birds (Aplin, 2019; Rendell & Whitehead, 2001; Whiten, 2021). One of the strongest pieces of evidence for nonhuman culture lies in the complex songs of humpback whales, which, much like the Beatles, can be transmitted at the ocean basin scale (Garland *et al.*, 2011; Rendell & Whitehead, 2001).

1.1 Vocal learning

Understanding the intricacies of acoustic communication and vocal production learning in animals is a fascinating area of research with broad implications. By investigating the mechanisms behind these abilities, we can gain insights into the evolution of communication systems, social interactions, and the underlying cognitive processes involved. This research contributes to our knowledge of how animals adapt and respond to their environment through acoustic signals, enhancing our understanding of the complex interplay between behaviour, ecology, and communication in the animal kingdom. Vocal learning can interact with social structures, leading to the convergence of calls within groups or populations. The study of vocal learning and convergence plays a crucial role in understanding the role of culture in animal populations.

The acoustic communication abilities of animals play a crucial role in their survival and reproductive success. Throughout evolutionary history, species have developed intricate acoustic signalling mechanisms for various purposes, including species recognition, sexual selection, and group interactions such as alarm calls and contact calls (Chen & Wiens, 2020; Wilkins *et al*., 2013). While some animals produce sounds that are genetically encoded or innate, meaning they can generate these sounds without external input, others possess the capacity to learn and associate existing signals in novel contexts, a phenomenon known as contextual or usage learning (Janik, 2000; Janik & Slater, 1997). In addition to innate and contextual learning, certain animals demonstrate even more sophisticated abilities by acquiring and producing new acoustic signals through active listening to acoustic models. These animals create new auditory templates, against which they then match and modify their own acoustic signals (Janik & Knörnschild, 2021; Tyack, 2020). This form of vocal production learning involves the modification of a vocalisation's acoustic parameters as a result of experience with individuals of the same species or even different species, whether through live encounters or exposure to recorded vocalisations (Janik & Knörnschild, 2021). Vocal learning, the ability to acquire and modify vocalizations through auditory experience, is a rare and fascinating phenomenon observed in various animal species. While vocal production learning is most prevalent in birds, certain mammals such as humans, bats, elephants, pinnipeds, and cetaceans also possess this ability.

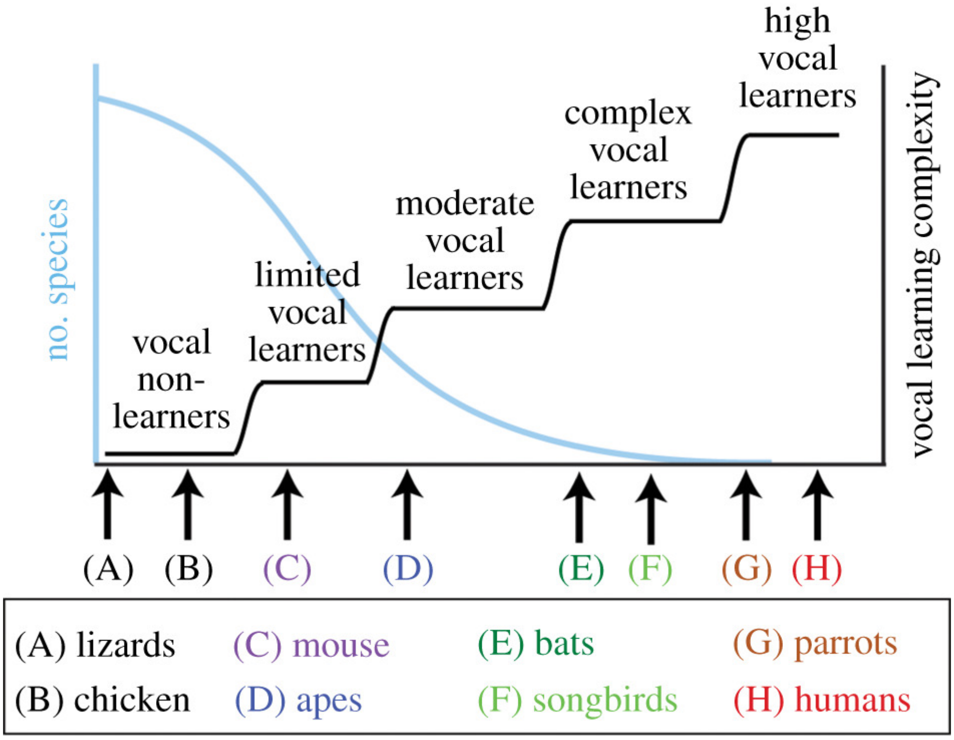

Figure 1.1: Figure reproduced after Patel (2021) The vocal learning continuum hypothesis, from Jarvis (2019). The diagram illustrates a hypothesised stepwise continuous ability of vocal learning among vertebrates, with increasing complexity represented along the x-axis. As vocal learning complexity rises, the number of species possessing this ability decreases, as indicated by the left y-axis. Each step on the continuum (A-H) represents proposed example species. The continuum spans from lizards, which lack vocalization and vocal learning, to nonhuman primates exhibiting limited vocal learning, to songbirds displaying complex vocal learning, and finally to parrots and humans demonstrating high levels of vocal learning. Figure reproduced after Patel (2021) and caption modified from Patel (2021).

The field of vocal production learning in animals has witnessed recent and ongoing debates regarding the definition and classification of different types of vocal learning (Martins & Boeckx, 2020). These discussions aim to enhance our understanding and advance the research in this field. The hypothesis known as the "vocal learning continuum" (VLC) or simply, continuum hypothesis, organises species on a spectrum of growing complexity (Petrov *et al*., 2012; Janik and Knornschild, 2021). As an example, minor alterations to an existing call type are categorised as being on the "lower" end, whereas the imitation of vocalisations from other species or the production of novel sounds are classified as being on the "higher" end. It is widely assumed that the "higher" forms of vocal production learning entail greater cognitive demands (Janik & Knörnschild, 2021) (see Figure 1.1).

While the continuum hypothesis has garnered support for its ability to differentiate between various forms of vocal production learning, some researchers have expressed concerns that this approach implies a predetermined evolutionary trajectory towards a specific type of learning (Martins & Boeckx, 2020; Wirthlin *et al.*, 2019). Instead, an alternative perspective has been advocated, suggesting a modular approach that acknowledges the presence of multiple interconnected components contributing to the behavioural phenotype of vocal learning. This modular framework allows for separate analysis of these components, highlighting their distinct nature and potential independent evolutionary trajectories (Wirthlin *et al.*, 2019).

In their study, Wirthlin *et al*. (2019) propose three fundamental sub-traits or modules that underlie vocal learning: vocal coordination, vocal production variability, and vocal versatility. These sub-traits represent key aspects of the vocal learning process and provide a comprehensive framework for understanding the complexity of vocal production learning. Vocal coordination refers to the ability to precisely coordinate vocalisations, while vocal production variability encompasses the capacity to generate a wide range of vocal sounds. Vocal versatility, on the other hand, involves the flexibility to modify and adapt vocalizations in response to various social and environmental contexts. By dissecting vocal learning into these distinct sub-traits, researchers can gain a deeper understanding of the underlying mechanisms and evolutionary dynamics driving vocal learning behaviours.

Furthermore, Tyack (2020) makes a distinction between two types of vocal production learning referred to as 'limited vocal learning' and 'complex vocal learning.' The former entails the refinement of an inherited motor pattern, while the latter involves the ability to match a learned template. According to Tyack (2020), limited vocal learning is characterised by the ability to fine-tune the acoustic features of species-specific vocalisations, which can develop even in the absence of auditory input, as innate motor programs can generate the species-specific pattern. In contrast, complex vocal learning is less prevalent and relies on matching a learned template. It is defined by the requirement to hear a sound in order to form a learned auditory template before the animal can produce a vocalisation that matches the template. Tyack emphasises the importance of distinguishing between limited and complex vocal production learning due to the broad taxonomic distribution of limited vocal learning, whereas complex vocal learning has only been observed in songbirds and humans thus far.

1.2 Humpback whale song

In the 1950s, the US Navy made the initial recordings of humpback whale song, although the origin of these intriguing sounds remained uncertain at the time (Payne & McVay, 1971). It wasn't until the 1960s that researchers began focusing on humpback whale song in the field after hearing US Navy's recordings (Payne & McVay, 1971). In a ground-breaking study Payne and McVay (1971) described the complex hierarchical structure of humpback whale song (see Figure 1.2). Payne and McVay's research revealed that humpback whale songs were not just random vocalisations but rather highly organised and repetitive sequences of sounds. They found that humpback whale song is a long, stereotyped acoustic signal with a hierarchical structure, such that each song is composed of a set of themes, each theme is composed of phrases and each phrase is composed of a stereotyped sequence of units (Payne & McVay, 1971). It is useful to explain each level of the song hierarchy in ascending order. The fundamental level of the song hierarchy is the unit which Payne and McVay (1971) defined as the smallest sound that seems continuous to the human ear. Units exhibit a wide variation in both the temporal and frequency domains, spanning from less than half a second to several seconds long and from as low as approximately 100 Hz to 4 kHz, with harmonics exceeding 20 kHz (Au *et al.*, 2006; Tyack & Clark, 2000). Unit types are traditionally named as onomatopoeic words representing the characteristics of the sound, in a similar manner to social calls (Dunlop *et al.*, 2007; Saloma *et al.*, 2022) such as 'moans', 'groans', 'trumpets' or 'squeaks'. These unit types can be further subdivided into unit variations, for example a moan could be further divided into ascending or descending moans or modulated moans depending on how fine-scale an analysis is being conducted. Over the years, advancements in technology, such as hydrophones and digital recording equipment, have facilitated more detailed and comprehensive investigations into humpback whale songs. For example, Pace *et al.*, (2010) employed an energy detector and automatic classification to determine the possibility of sub-units as being the actual fundamental building blocks of songs, however this intriguing possibility is yet to be further investigated.

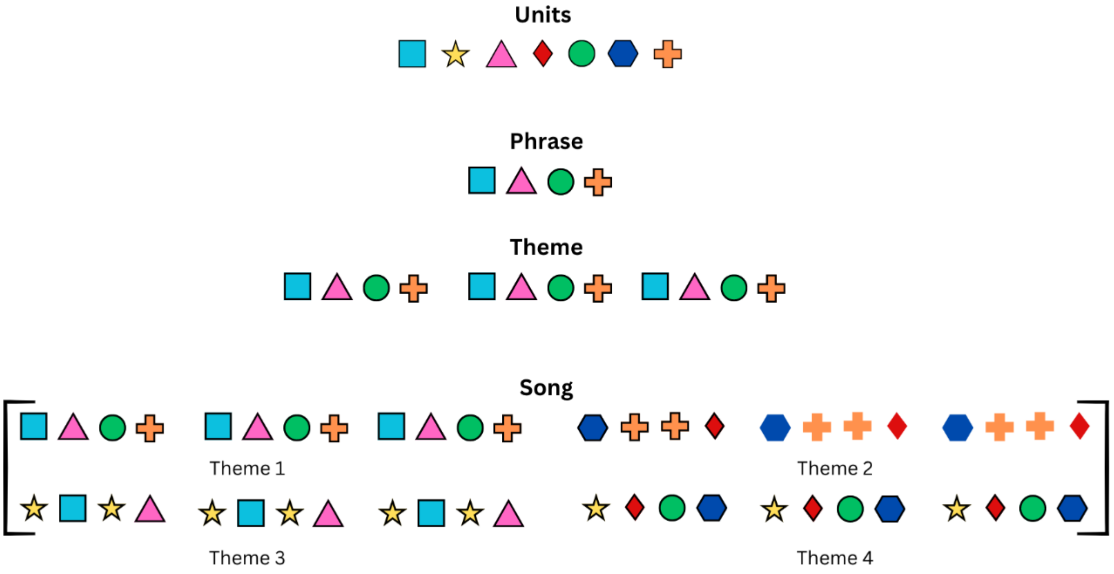

Figure 1.2: Humpback Whale Song Hierarchy illustrating the organisation of different song units. The distinct levels including units, phrases, themes, and songs are highlighted. Each unit is represented by coloured symbols, distinguishing various types of whale song units.

Different types of units are strung together to form a pattern called a phrase, the next level in the humpback whale song hierarchy. For example, a moan might be followed by a trumpet, a squeak and a bark. Phrases are not always exact replicas of each other and there be variation in the number of units present in each phrase rendition of a theme (Cholewiak *et al*., 2013; Payne & McVay, 1971) (e.g. two barks instead of one). Humpback whale songs exhibit remarkable stability in terms of phrase duration, with minimal variation observed both within and between individuals (Cholewiak *et al*., 2013). However, phrases can show consistent variation in forming connected sub-themes in which a particular unit of the phrase is swapped for another unit or removed altogether. This change is consistently repeated as an alternative version of the phrase. Furthermore, separate phrases have been found to morph together as a ‘hybrid’ or ‘transitional’ phrase when an individual is in the process of changing song type (Cholewiak *et al*., 2013; Darling *et al*., 2014; Garland *et al*., 2017). In their study, Garland *et al*. (2017) examined a dataset of more than 9,300 recorded phrases in the South Pacific Ocean. They discovered that during revolution years, when a new song was adopted, individuals would insert a "hybrid" phrase between two different song types as they transitioned to the new song.

The next level of the hierarchical organisation is the theme in which a phrase type is repeated multiple times (Payne & McVay, 1971). There are different types of themes which Payne and Payne (1983) described as static themes, shifting themes and un-patterned themes. As their names indicate static themes display repetitions of identical phrase types, shifting themes change as phrases are repeated at progressive levels of duration or frequency and lastly un-patterned themes may have poor organisation of units and phrases (Payne, 1985). Lastly, a particular sequence of different themes forms the top level of the hierarchy: the song itself (Payne & McVay, 1971). An individual humpback whale can perform a display of this song for many hours, repeating a complete song many times without interruption in what is called a song bout. Winn and Winn (1978) documented the longest recorded song bout in which a male sang for 22 hours with only brief pauses at the surface. Each complete sequence of themes (or a song) varies between less than ten minutes to over half an hour long (Payne & McVay, 1971; Winn & Winn, 1978) however more recent quantitative studies have found an upper limit of 16.7 minutes (Suzuki *et al.*, 2006). Lastly, a song 'type' is a distinct sequence of themes sung by a particular population at a particular time.

This structured hierarchy of humpback whale song is generally agreed upon through the research community and has persisted to the present day (Au *et al.*, 2006; Cholewiak *et al.*, 2013; Green *et al.*, 2011; Lamoni *et al.*, 2023). It also seems that song types persist over time in distinct populations and can be used as an aid in determining whale stocks (Garland *et al.*, 2015; Payne & Guinee, 1983). However, while the structure remains relatively constant, and song types can be indicative of whole populations, the content of the songs is constantly changing. Long-term monitoring of humpback whale breeding populations has revealed that song conformity of singing males within a population is not only remarkably high but also that songs undergo gradual evolution over time, rather than remaining static displays with fixed content (Payne, 1983; Payne, 1985). This has led to a conundrum between population conformity and constant gradual evolution, how this achieved and why. The changes to the song can happen gradually in which embellishments might be made to the song by an individual that are then adopted by the group or population.

Payne and McVay's (1971) findings captured the attention of the scientific community and the public, raising awareness about the vocal and communicative abilities of these magnificent creatures. Since then, researchers have focused on deciphering the intricate structure and temporal patterns of the songs, as well as examining the potential social and reproductive functions they serve within humpback whale populations. We now know that humpback whales produce a vocal display called 'song' thought to be a sexually selected display as all sexed singers have been male and the song is over elaborate for the information it contains (Glockner, 1983, Darling *et al*., 2006; Smith *et al*., 2008; Herman *et al*., 2011). Further evidence of a sexual display is that song is predominantly on the breeding grounds. Alternatively, some authors have suggested that humpback whale songs have a territorial function, serving to establish and defend feeding or breeding territories (Darling & Berube, 2001; Darling *et al*. 2006). For example, Darling and Berube (2001) observed that lone non-singing males approached singing males. The subsequent interruption of singing by non-singing males has been interpreted in different ways. On the one hand, Cholewiak (2013) examined the movement patterns and song dynamics of 13 singers in Mexico. Cholewiak (2013) found that singers increased the rate at which they switched phrase type when in the presence of other singing males and interpreted this as competitive behaviour. On the other hand, song may act as a warning or boundary marker to deter other individuals or groups from encroaching on their preferred areas. Observations from Tyack (1983) and Frankel *et al*., (1995) have found that singing humpback males tend to separate.

Furthermore, humpback whale songs have been speculated to play a role in establishing social bonds and maintaining group cohesion. The synchronised singing behaviour within a population suggests a form of social interaction and cooperation and Darling *et al.,* (2006) have speculated that song may serve as a "real time measure of male association to ensure reciprocity" (Darling *et al*., 2006) however, this idea has been severely disputed due to the vast array of variability within individual song transmission making it unlikely song could serves individual recognition (Herman, 2017). It is important to note that these hypotheses are not mutually exclusive, and multiple functions of humpback whale songs may coexist (Herman, 2017). This shows further similarities to the function of bird songs which have been shown to have multiple purposes (Garland & McGregor, 2020). Further research is needed to gain a comprehensive understanding of the true purpose(s) of humpback whale song.

Studies have also explored the geographic variations in humpback whale songs, revealing distinct regional dialects and cultural differences among populations. These variations have shed light on the unique vocal traditions and social dynamics of different humpback whale populations. Outside of the South Pacific Ocean, humpback whale songs exhibit a high degree of similarity across entire ocean basins. For instance, in the North Pacific Ocean, songs have been found to be similar across different locations at the same time, such as between Japan, Hawaii, and Mexico (Cerchio *et al*., 2001; Helweg & Herman, 1994). Similarly, in the Atlantic Ocean, songs have been observed to change gradually and slowly at the scale of the entire ocean basin (Payne, 1985). In the North Atlantic, humpback whales breed in low-latitude areas located in the western and eastern Atlantic (see Figure 1.3). They migrate to these breeding grounds by following the Antillean Island Chain and around the Cape Verdes, respectively. Satellite telemetry tags and mark-recapture efforts on whale tail markings have helped map their migration routes (Kennedy *et al*., 2014). Western breeding individuals have been found to migrate to feeding grounds across the North Atlantic, including areas in north-eastern United States, eastern Canada, Western Greenland, while eastern breeding individuals migrate to feeding grounds in northern Norway and Iceland (Kennedy *et al*., 2014). Research on humpback whale singing patterns, similar to the findings in the South Pacific, as described below, has provided insights into population connectivity (Garland *et al*., 2015). For example, Schall *et al*., (2021) analysed passive acoustic data from 2011 to 2018 from 13 recording positions in the Atlantic sector of the Southern Ocean (ASSO), a known feeding ground, and found multiple song types present.

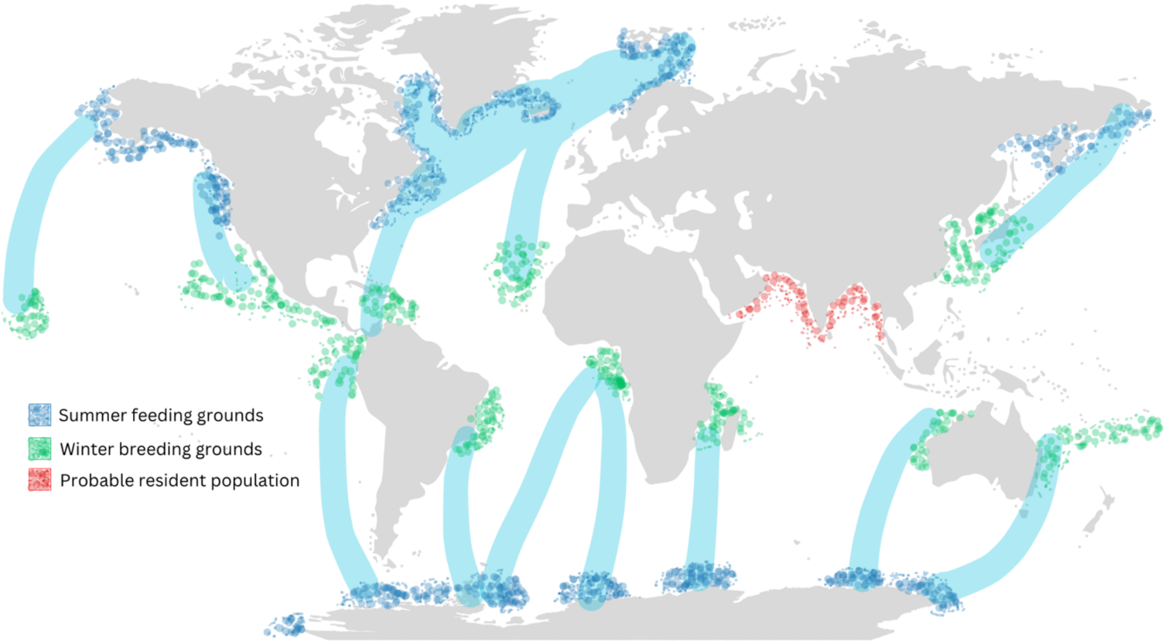

Figure 1.3: The long migration of the humpback whale. Summer and winter relates to seasons in the northern hemisphere. This map illustrates the migratory routes of humpback whales in both the Northern and Southern Hemispheres. Known breeding grounds are highlighted in green, while feeding grounds are highlighted in blue. The figure provides a comprehensive visual representation of the extensive migratory patterns undertaken by humpback whales, emphasising the crucial areas for reproduction and nourishment. Adapted from Riccardo Pravettoni's figure from GRID Arendal, a UNEP partner and non-profit environmental communications centre (https://www.grida.no/resources/7650).

The gradual cultural evolution of songs happens in oceans all over the world, however something else is happening in the South Pacific Ocean. Humpback whales undergo an annual migration from high latitude feeding grounds to low latitude breeding locations and display strong fidelity to their natal breeding grounds (Garrigue *et al*., 2011). The International Whaling Commission recognises six breeding subpopulations in the South Pacific, progressing from west to east: Eastern Australia, New Caledonia, Tonga, American Samoa, The Cook Islands, and French Polynesia. These subpopulations constitute an interconnected metapopulation, wherein several distinct subpopulations collectively form the overall regional South Pacific population, with limited interchange between them (Garland *et al*., 2015). The population in this region is categorised as 'Endangered' (Childerhouse *et al*., 2008). Researchers have a particular interest in studying the transmission of song in the South Pacific Ocean due to the occurrence of song "revolutions," wherein a population abandons its current song in favour of a new and entirely different song type (Garland *et al*., 2011; Noad *et al*., 2000). These song types have been observed to radiate eastward across the South Pacific. For instance, the song from Eastern Australia propagated all the way to French Polynesia within a span of two years (Garland *et al*., 2011). More recent analyses have confirmed that song continues to spread eastward across the entire South Pacific, from French Polynesia to Ecuador (Schulze *et al*., 2022). Many aspects of this remarkable pattern of song revolutions remain poorly understood, including the precise mechanisms of song transmission, which necessitate individuals from different breeding populations coming into acoustic contact. Acoustic contact may occur through shared feeding grounds or migration routes, or individuals may visit different breeding grounds within or between breeding seasons (Noad *et al*., 2000). Recent research has found that song can be heard on feeding grounds, as well as on migratory pathways and that these areas may allow acoustic contact between different breeding populations (Narganes Homfeldt *et al*., 2022; Owen *et al*., 2019; Schall *et al*., 2021). For example, Owen *et al*., (2019) compared song recordings made off Raoul Island in the Kermedecs and recordings made at each of the breeding grounds across the western and central south pacific (eastern Australia to French Polynesia of the same year. Owen *et al*., (2019) found similarities in song themes at the Kermedecs from multiple breeding populations. This finding suggests the Kermedecs may be a migratory stopover for individuals from multiple breeding locations and may facilitate the eastward spread of song types in the South Pacific.

While there is variability in how songs evolve between different oceans, recent research has delved into the individual variability within humpback whale songs, uncovering evidence of individually distinctive patterns and signatures within the larger context of song conformity. These findings have deepened our understanding of how humpback whales use vocalisations as potential means of individual advertisement and potentially as a mechanism for sexual selection (Lamoni *et al*., 2023). For example, Lamoni *et al*., (2023) examined songs from 25 humpback whale singers belonging to the eastern Australian population, including two distinct song types from 2002 and 2003. They quantified the variability at different levels of the song hierarchy and found that inter-individual variability was present across all hierarchical levels of the song structure, indicating heterogeneity among individuals within the population. Furthermore, the study revealed the existence of distinct and individually specific patterns of song production, with clear structural differences between the two song types. These findings suggest that humpback whale males are capable of producing individually distinctive patterns within the framework of song conformity. These distinctive patterns may serve as an advertisement to females, conveying individual qualities and potentially playing a role in sexual selection. Furthermore, Mcloughlin *et al.*, (2018) utilised agent-based models to understand the role of individuals in song evolution. By modelling the migratory patterns of humpback whales alongside sound transmission loss and including possible learning biases, this study was able to determine the need for production errors by individuals to facilitate the gradual evolution of songs.

Although much research has focused on investigating broad-scale changes in humpback whale songs at the higher levels of the song hierarchy (song types and theme) (Garland *et al.*, 2011; Noad *et al.*, 2000; Owen *et al.*, 2019), less attention has been given to the fine-scale evolution of song units. Magnúsdóttir *et al.*, (2019) investigated humpback whale singing behaviour off Northeast Iceland between 2008 and 2009. Their study focused on song unit types defined using fully quantitative techniques. Such investigations into the intricate intricacies of humpback whale vocalizations set the stage for a deeper exploration of vocal production learning in these majestic marine mammals.

1.3 Vocal Learning and Humpback whale song

The idea of vocal learning in humpback whales has been a subject of debate among researchers, with differing viewpoints on whether these whales acquire and modify their songs through auditory experience. Vocal learning refers to the ability of an animal to learn new vocalisations or modify existing ones. In the case of humpback whales, several arguments have been put forth both in favour of and against the idea of vocal learning.

Supporters of vocal learning note that humpback whales within a population converge on a particular song type, resulting in individuals singing the same song at the same time. This pattern of population convergence is reminiscent of cultural evolution observed in bird songs and supports the idea of vocal learning. Furthermore, supporters point out the complexity and hierarchical structure of humpback whale songs, consisting of units, phrases, and themes, imply that these songs are not solely innate but are learned through imitation and practice (Janik & Knörnschild, 2021; Tyack, 2020). This view asserts that humpback whale song units (a unit being the smallest continuous sound to the human ear) are learned as well as the song sequence itself and I refer to this viewpoint as the Vocal Learning Hypothesis.

However, there are also arguments against vocal learning in humpback whales. Some researchers argue that humpback whale songs are innate rather than learned. They propose that the songs are genetically determined and represent a fixed pattern of behaviour. Additionally, while cultural transmission is observed in humpback whales, there is limited direct evidence to demonstrate individual learning of songs. Tracking the learning process of specific songs and establishing a clear cause-effect relationship between social interactions and song acquisition prove challenging. For example, the sonar hypothesis of humpback whale song suggests that the intricate and diverse vocalisations of humpback whales serve as a form of acoustic sonar (Frazer & Mercado, 2000; Mercado III, 2018). According to this hypothesis, the whales use their songs to navigate and gather information about their surroundings, similar to how bats use echolocation. The hypothesis proposes that the unique structure and characteristics of humpback whale songs, including the melodic patterns and complex sequences, enable the whales to gather detailed information about the underwater environment however this idea has received little support (Au *et al*., 2001). Cerchio *et al*., (2013) examined all levels of the song hierarchy in songs recorded in Mexico and Hawaii and found that 21 variables changed significantly and synchronously in both locations. They argued that this gradual change may be due to a set of rules derived by an innate template. Mercado and Perazio (2021) also argued that songs of unconnected populations have changed in similar ways, however when this study is closely explored it seems the results depend on visual appraisal of particular subsets of the datasets which make the conclusions unreliable. The presence of similar songs or similar changes in songs among separate populations may contradict the notion of vocal learning. However, recent evidence suggests that populations previously assumed to lack acoustic communication actually come into contact during migration or while sharing feeding areas as described above (Narganes Homfeldt *et al*., 2022; Owen *et al*., 2019; Schall *et al*., 2021). Additionally, according to Garland and McGregor (2020), the central focus of humpback whale song research lies in the arrangement of song units into distinct sequences, suggesting that these units might originate from a universal repertoire. In contrast to vocal production learning, this perspective suggests that sequence learning, which involves acquiring complex arrangements, is the primary form of learning underlying humpback whale songs rather than vocal production learning. Despite these researchers (Garland & McGregor, 2020; Cerchio *et al.*, 2013; Mercado III, 2018) holding differing perspectives and degrees of scepticism regarding vocal learning at the unit level (or its existence altogether), they collectively propose that humpback whale song units could stem from an innate repertoire or catalogue of units and I refer to this viewpoint as the Internal Unit Hypothesis.

In conclusion, the question of whether humpback whales vocally learn their songs remains an ongoing research topic with varying perspectives. What adds further complexity to this is that there are also varying views on how vocal learning should be assessed as outlined above. While arguments supporting vocal learning emphasise cultural transmission and complex song structures, the evidence is not conclusive. The lack of direct evidence for learning add complexity to the debate. To enhance our comprehension of the vocal learning capabilities of this wide-ranging mammal, empirical studies focusing on humpback whale song unit types are essential.

1.4 Cumulative Cultural Evolution and Humpback whale song

While the ongoing debate revolves around determining the specific level of the song that undergoes vocal learning (if at all), the possibility of humpback whale song serving as an illustration of cumulative cultural evolution (CCE) is also under scrutiny. Cumulative cultural evolution (CCE) refers to the phenomenon where human cultures progressively enhance the complexity and efficiency of their cultural traits over time. It has been considered a defining characteristic that sets humans apart from nonhuman animals (Tomasello, 2000; Tomasello, 1994). However, recent research has revealed evidence of CCE in various species, particularly in relation to the refinement of specific skills or the development of new innovations.

One area of interest in exploring CCE outside of humans is the study of humpback whale song. Allen and colleagues (2018) have proposed that humpback whale song exemplifies CCE due to its increasing complexity over time. In their study, Allen *et al*. examined the song structure of humpback whales off the west and east coasts of Australia over a period of thirteen consecutive years. They observed that the song on the west coast regularly spread to the east coast during "revolutions," while more gradual changes occurred between these events. The researchers found that as the songs evolved between revolutions (typically spanning one to two years), there was an increase in complexity measured by the number of distinct units per phrase and the overall duration of the song (Allen *et al*., 2018). However, during revolution years when old songs were replaced with new ones, complexity was reduced, only to be rebuilt in the periods between revolutions. This increase in complexity is believed to be a result of males embellishing their songs to stand out to potential mates, while reductions in complexity during revolutions may indicate a limitation in the social learning capacity of novel material among humpback whales (Allen *et al*., 2018). In a subsequent study conducted by Allen and colleagues (2022), it was revealed that populations do not necessarily need to reduce complexity in order to effectively learn song patterns. In this study, the quantitative analysis of six distinct song types (2009-2015) transmitted from the east Australian to New Caledonian populations revealed that New Caledonian whales demonstrated a high level of accuracy in learning each song type, irrespective of the complexity of the pattern.

It is inferred that changes made by individual males are incorporated by the larger population, leading to a general conformity in song structure at any given time and subsequent incremental increases in complexity over the lifespan of a song. This pattern suggests a form of cultural transmission and cumulative refinement of humpback whale songs, supporting the notion of CCE in this species. The study conducted by Allen *et al*. (2018) provides compelling evidence for the presence of CCE in humpback whale song, highlighting the dynamic nature of cultural evolution in nonhuman animals. By examining the changes in complexity and the social learning dynamics within whale populations, this research contributes to our understanding of the broader mechanisms underlying cultural evolution beyond human societies.

The cycles of innovation and transmission observed in humpback whale song, which lead to increased complexity, align with the mechanisms described in cumulative cultural evolution (CCE) literature, potentially making humpback whale song a nonhuman example of CCE. However, it raises questions about what constitutes an "improvement" in the song. Is a more complex song inherently "better," or is its significance limited to a specific population and time? To truly consider CCE as a unique human feature, we must clearly define its characteristics and distinguish it from other phenomena. The cycles of innovation and transmission seen in humpback whale song resemble those found in human music and other forms of artistic expression. Just as we question whether a new whale song is "better" than its predecessor, we can also ponder the comparison of the Beatles to Elvis or Beyoncé to Beethoven. Therefore, without a comprehensive understanding of what characterises cumulative cultural traits in human societies, it becomes challenging to comprehend nonhuman cultures and what truly sets us apart from other animals.

1.5 Humpback whales and public engagement

As described above, humpback whale song structure was first published in scientific literature in 1971 with Payne and McVay's foundational study. However, it was the year prior, 1970, the humpback whale made a splash into the turf of the Beatles by singing on vinyl across the globe. In 1970 Roger Payne released a 5-track album called 'Songs of the humpback whale' which went multi-platinum in the US. In 1979 National Geographic included copies of this vinyl album in one of their 1979 issues (National Geographic, 1979). Most importantly, these songs, released across the world captured the heart of a generation and started a global movement against whaling in many parts of the world (Roberts, 2023). People across the world through the 1970s were engaged in protests against whaling and this eventually led to the whaling moratorium to stop whaling in many countries in the world including the UK, USA, France and Australia (IWC, 1982). This whaling moratorium has allowed many species of whales to recover, not least humpback whales themselves which are now classified as of 'Least Concern' on the IUCN Red List after decades as an 'Endangered' species (Stevick *et al*., 2003; IUCN, 2008; Cook *et al*., 2018). This shows what a motivational example whale song can be for engagement in biodiversity issues but also how interesting the general public find whale song to be. Whales, in particular humpback whales, have been used as a flagship species for engaging the general public about conservation concerns and more specifically about animal culture and communication.

Nevertheless, as the world rallied against whaling, it became apparent that equitable participation in STEM (Science, Technology, Engineering, and Mathematics) fields has not been socially and demographically equitable. Individuals from low socio-economic status backgrounds have been observed to achieve lower educational outcomes and have fewer opportunities in pursuing science careers in comparison to their more affluent counterparts (Archer, DeWitt, Osborne *et al*., 2012; Godec *et al*., 2020). Communities with low socioeconomic status often face significant barriers when it comes to accessing and participating in STEM fields. These communities tend to have limited resources, educational opportunities, and support systems that contribute to disparities in STEM engagement (Godec & Watson, 2021). The expenses linked to pursuing STEM education or accessing informal learning opportunities beyond the school setting, such as museums or workshops, can pose a substantial obstacle. This financial burden has the potential to restrict certain demographic groups from gaining exposure to hands-on experiences and practical learning opportunities, which have been demonstrated as pivotal factors contributing to science performance. Bridging the gap in access and opportunities will not only benefit these communities but also contribute to a more diverse, innovative, and inclusive STEM workforce.

1.6 Thesis Overview

This thesis focuses on the cultural evolution of humpback whale song at both broadscale processes and across disciplines (Chapter 2) and at a fine-scale and across different timescales (Chapters 3 and 4) and lastly as a vehicle for public engagement in cultural evolution research (Chapter 5). In Chapter 2 I analyse cumulative cultural evolution in aesthetic cultural products across disciplines and use humpback whale song as a case study of nonhuman CCE. In Chapter 3 I investigate how humpback whale song units may be stored in the brain through analysing how particular song units evolve over a breeding season in the South Pacific Ocean. In Chapter 4 song unit evolution is further explored over two seasons and two locations in the North Atlantic Ocean, where I also report a further confirmation of long-range acoustic links between Scottish waters and the Caribbean breeding grounds. In Chapter 5 I show how humpback song research can be utilised as a public engagement tool within a science centre.

In Chapter 2 a conceptual analysis across three disciplines (biology, musicology and philosophy) is developed to understand whether and how aesthetic cultures fit into the current CCE framework. In philosophy aesthetic attractiveness is taken as aesthetic value because this holds more currency in the philosophy of aesthetics literature. In musicology historical musicology is reviewed to search for an objective way of measuring aesthetic value in music works before investigating how technological advancements in musical production relate to changes in aesthetic value. Lastly, CCE evidence in nonhuman animals is reviewed before utilising humpback whale song as a nonhuman CCE case study.

In Chapter 3 a fine-scale acoustic analysis is performed on humpback whale song recordings collected in the Cook Islands, South Pacific Ocean in the 2019 breeding season. I attempt to infer the cognitive processes underlying song learning by conducting a detailed examination of unit changes. I track the evolution of a unit type within one song type across the breeding season in different theme types within the same song. This tracking in different theme types helps to illuminate whether humpback whale song units are selected from an innate template of units or alternatively whether they are learned individually and separately within separate theme types. For instance, if song units originate from an inherent catalogue, then we would anticipate that if they undergo changes, the same unit would change in a consistent manner across all themes in which it is displayed. On the other hand, if the changes in the same units vary across different themes, it indicates the occurrence of vocal production learning.

In Chapter 4, I aim to infer the cognitive processes underlying song learning through a detailed examination of unit changes and explore the scale of acoustic transmission. To achieve this a fine-scale acoustic analysis is conducted on humpback whale song recordings gathered in the eastern Caribbean and Scotland during 2020 and 2021, respectively. The aim is to investigate the connectivity between these two locations and ascertain the potential presence of the same song and population. Additionally, I explore the evolution of a specific humpback whale song unit across two seasons, encompassing both breeding and feeding grounds in the North Atlantic Ocean, building upon the analysis presented in Chapter 3.

Although Chapter 5 and Chapter 6 may differ from the conventional structure of a biology PhD, their inclusion is justified by their importance. These chapters represent the integration of outreach and impact with my research, emphasising the broader societal implications. By recognising the significance of incorporating outreach efforts, they serve as a tangible expression of this belief and highlights the necessity of embracing outreach and impact within our academic endeavours. I conduct two case studies on public engagement practices and evaluation in two locations in Scotland. Chapter 5 involves the development of a whale research exhibition within a science centre. This exhibition showcases eight distinct whale research stations that were operational for four months, providing an opportunity for active public participation. Evaluation methods were devised and implemented to assess the outcomes of the event. However, due to the unexpected closure of this exhibition caused by the COVID-19 pandemic, a second public engagement project was initiated in Chapter 6, as a two-year annual event held outdoors for a single day – this was not focussed on humpback song but on the local development of a BioBlitz type project, due to the logistical constraints imposed by the pandemic. Both types of live events are focused on low socio-economic status communities and are evaluated to determine their short and long-term impacts.

2 Chapter 2: From Beethoven to Beyoncé: Do Changing aesthetic cultures amount to 'cumulative cultural evolution'?

Abstract:

Culture can be defined as "group typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (Laland and Hoppitt, 2003, p. 151). Once thought to be a distinguishing characteristic of humans relative to other animals (Dean et al., 2014) it is now generally accepted to exist more widely, with especially abundant evidence in non-human primates, cetaceans, and birds (Rendell and Whitehead, 2001; Aplin, 2019; Whiten, 2021). More recently, cumulative cultural evolution (CCE) has taken on this distinguishing role (Henrich, 2015; Laland, 2018). CCE, it is argued, allows humans, uniquely, to ratchet up the complexity or efficiency of cultural traits over time. This "ratchet effect" (Tomasello, 1994) gives the capacity to accumulate beneficial modifications over time beyond the capacities of a single individual (Sasaki and Biro, 2017). Mesoudi and Thornton (2018) define a core set of criteria for identifying CCE in humans and non-human animals that places emphasis on some performance measure of traits increasing over time. They suggest this emphasis is also pertinent to cultural products in the aesthetic domain, but is this the case? Music, art and dance evolve over time (Savage, 2019), but can we say they gain beneficial modifications that increase their aesthetic value? Here I bring together perspectives from philosophy, musicology and biology to build a conceptual analysis of this question. I summarise current thinking on cumulative culture and aesthetics across fields to determine how aesthetic culture fits into the concept of CCE. I argue that this concept is problematic to reconcile with dominant views of aesthetics in philosophical analysis and struggles to characterise aesthetic cultures that evolve over time. I suggest that a tension arises from fundamental differences between cultural evolution in aesthetic and technological domains. Furthermore, this tension contributes to current debates between reconstructive and preservative theories of cultural evolution.

2.1 Introduction

Culture can be broadly defined as “group typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information” (Laland and Hoppitt, 2003: p151). Cultures evolve, in the sense that they change over time, and there is vigorous and ongoing debate over the extent to which this cultural evolution can be understood in the same or similar Darwinian framework that underpins our understanding of genetic evolution (Claidière *et al.*, 2014; Mesoudi & Thornton, 2018b; Nettle, 2020). Cultural transmission occurs through different social learning pathways: vertically (parent to offspring), horizontally (between individuals of the same generation) or obliquely (between unrelated individuals of different generations) (Cavalli-Sforza & Feldman, 1981). There is, however, disagreement as to whether this transmission is dominantly preservative or transformative. Of course, preservation and transformation must both be present if culture is to evolve at all (Gabora & Tseng, 2017), but debate about relative importance persists. Cultural evolutionary theorists view cultural transmission as preservative, in which variants are faithfully transmitted between individuals (with some degree of error). On the other hand, cultural attraction theorists argue that cultural transmission is reconstructive, wherein cultural variants are potentially transformed in the context of being reconstructed by the receiver (Acerbi & Mesoudi, 2015; Mesoudi, 2011; Scott-Phillips *et al.*, 2018)

Human life is rich with culture pervading science, technology, customs, beliefs, art, literature and music. Culture was once thought to be a distinguishing characteristic between humans and other animals (Dean *et al.*, 2014) but is now generally accepted to exist outside humans, with evidence in nonhuman primates, cetaceans and birds (Aplin, 2019; Rendell & Whitehead, 2001; Whiten, 2021). Although semantic disagreements persist (Heyes, 2020), there is ample evidence that the content of non-human culture evolves in the sense of changing over time (e.g. (Garland *et al.*, 2011). Despite this evidence from across the animal kingdom, there still appears to be something distinctive about the way human culture builds upon itself over time to increase the performance of our cultural products. This process, referred to as cumulative cultural evolution, or CCE henceforth (Boyd & Richerson, 1996; Tomasello, 2000), has become a primary focus for those trying to understand the differences between human and nonhuman culture, and how human populations collectively improve their cultural toolkits. Humans are able to “ratchet up the complexity or efficiency of cultural traits over time” through this process (Tomasello, 2000; Tomasello, 1994, p. 312).

If CCE is to be a feature of human uniqueness, then we need very clear ideas of what it is, and what it is not (Vaesen & Houkes, 2021). My purpose here is to highlight what we see as an ambiguity in current thinking on the key features of CCE when it comes to cultural traits that are valued primarily or exclusively for their aesthetic properties - what I will term as ‘aesthetic cultural traits’ or ‘aesthetic products’.

Using interdisciplinary perspectives on the philosophy of aesthetics, musicology, cultural evolution, and biology, I show here how the question in my title is not trivial, and that its answer will have important implications for how we think of CCE in humans and non-humans alike, using musical performance and nonhuman animal song as my principal motivating examples. One of my primary goals is to build bridges between a number of disciplines whose interests I see as overlapping on this question. Because of this, some material may be familiar to some readers but new for others, and while I do not pretend to provide comprehensive reviews of each area, I hope most readers interested in this general topic will find something informative from a discipline different to their own background.

Here I begin with an introduction to cultural evolutionary theory and ask how aesthetic cultures may fit into the current framework of CCE. I then examine whether aesthetic attractiveness (in terms of aesthetic value) can be measured sufficiently to enable its incorporation into this framework. I then take an example of an aesthetic culture – music – and explore whether this can improve over time. Finally, I discuss a case study of potential CCE in nonhuman animals – humpback whale song – through the lenses of these arguments. My discussion is born of a realisation that we cannot evaluate whether humpback whale song is CCE without first determining how human aesthetic cultures fit into the CCE framework.

2.2 Cumulative Cultural Evolution (CCE)

Mesoudi and Thornton (2018) sought to define a set of core criteria for CCE in human and nonhuman animals. The core criteria comprise four steps or qualities:

i. that behavioural variation exists;
ii. a behavioural variant is passed onto others by social learning;
iii. that the learned behavioural variant must enhance some measure of performance [my emphasis], and lastly;
iv. that steps i, ii and iii are repeated to create sequential improvement over time.

Recent literature is ambiguous regarding whether Cumulative Technological Culture (CTC) is merely one form of, or is synonymous with, CCE (Miton & Charbonneau, 2018; Osiurak & Reynaud, 2019). Mesoudi and Thornton (2018) sought to clarify the concept of CCE in part due to the diversity of definitions of CCE in the literature. They contemplated 35 definitions, of which eight specified technology in CCE. Mesoudi and Thornton's conception of CCE is not however restricted by definition to the technological domain and could, theoretically, include any cultural trait which meets their core requirements. It is their requirement for improved performance that we focus on here. Examples of a performance measure may be "the efficiency of migratory routes or extractive foraging, the durability and sharpness of cutting tools, or the aesthetic attractiveness of art or dress styles." (Mesoudi and Thornton, 2018: p2; my emphasis; note that Tables 1A and 1B in Appendix 2.1 give further examples of performance measures used in the literature). However, while 'aesthetic attractiveness' is mentioned as a performance measure early in their paper, it is not explored further. My intention here is to pull at this thread, because the interdisciplinary discussions that led to the present analysis suggest it is not straightforward to say that aesthetic 'attractiveness' can increase in a measurable way. In my discussion of this problem, I interpret aesthetic attractiveness to mean 'aesthetic value' as used in literature in the philosophy of aesthetics and focus on that value as the experience of an aesthetic product, in context, by individuals.

I define aesthetic cultural traits as those which are created, transmitted, and consumed because of the intrinsically valuable experiences which sustained appreciation of them affords. Examples of these aesthetic cultural traits are primarily found in the arts, where traditional categories include (but are not confined to) those cultural products (or artworks) found within visual art, sculpture, literature, poetry, music, performance art, theatre, film, dance, and architecture (what we refer to as 'aesthetic products'). I use the term 'aesthetic culture' to refer to cultural activities and products (including events such as musical performances or live theatre) that have been designed to afford aesthetic experience or be objects of aesthetic appreciation. The concept of an 'aesthetic domain' may seem nebulous, as almost any object, activity or process could be experienced aesthetically (as emphasised in the burgeoning 'everyday aesthetics' literature – see (Leddy, 2012; Melchionne, 2013; Saito, 2017), but I use the expression to refer primarily to the examples above, whilst accepting that the concept has a fuzzy boundary and can be applied to non-standard cases. I also note that although there is some philosophical scepticism regarding whether the different arts share properties which would allow them to be united into a single group (Kivy, 1997), I focus on examining aesthetic products as a whole, in the sense defined above.

Some cultural evolutionists maintain that an additional essential criterion of recognising cumulative culture is that no one individual would be able to create the behaviour, skill or knowledge in question on their own, such that the cultural product "is beyond the capacities of a single individual" (Sasaki & Biro, 2017).[1] This is a point of contention within the literature between the 'process' vs 'product' oriented views of cumulative cultural evolution (Reindl *et al*., 2020). Product oriented views assert *as a diagnostic criterion of CCE* that cultural products must be beyond the capacity of a single individual to create *de novo*. On the other hand, process focused views emphasise the processes of iterated innovation and transmission that resulted in a given cultural product. If, for example, a group produces stone tools following a history of repeated learning cycles, as in Mesoudi and Thornton's (2018) core criteria, it is an example of CCE irrespective of whether another individual in a different group at some point develops an identical stone tool *de novo*. A product-oriented definition presents some issues in the aesthetic domain however – anyone can invent a new tune, but would we consider the same sequence of notes differently if it had been produced

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[1] A common example cited as the pinnacle of human cumulative culture, as beyond the capacities of one individual, is when one person stepped on the moon. This feat was a team enterprise including technologies across a range of disciplines, the research for which was carried out over multiple centuries Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews*. https://doi.org/10.1111/brv.12053 .

by a babbling toddler rather than an advanced music student who had been trained in composition and its history? We need not be derailed by this debate here, since both views are reliant on the concept of an 'improvement of performance' (or 'ratcheting'), which forms the central concern of this paper.

We think it is imperative for cultural evolution researchers to interact with disciplines that have existing traditions of thought and study related to the phenomena they are bringing under the cultural evolution lens, so my motivation here was partly to explore via interdisciplinary dialogue what it might mean to talk of cumulative cultural evolution in the aesthetic domain. Has art improved in the way that our capacity to reach celestial bodies has? While surely few would doubt the excellence of both in their respective contexts, is the music of Beyoncé really the product of countless iterations of *performance improving* innovation since the time of Beethoven? A principal reason to undertake this enquiry is that the resolution of this question has important implications for thinking about whether non-humans have elements of CCE, which I address through the example of humpback whale song. Mesoudi and Thornton (2018) are clear that they consider those behaviours transmitted by social learning that are fitness neutral as non-cumulative. They posit examples of first names in humans and changes in birdsong as showing neutral drift as opposed to cumulative evolution (Mesoudi & Thornton, 2018a). But where is the line between 'fitness neutral' and 'aesthetic' to be drawn? If we are unable to determine how aesthetic cultures 'improve' and are therefore cumulative, must we also consider large tracts of aesthetic human cultural products as the result of neutral drift as opposed to any kind of cumulative evolution? A secondary reason is that through my dialogue with researchers across philosophy, musicology and biology I have come to the view that current debates in cultural evolution between advocates of 'traditional' approaches and more recent contributions from supporters of cultural attraction theory might be clarified by considering the way in which CCE might occur and/or differ in the aesthetic domain.

Borrowing terminology from Sterelny (2017) for efficiency, cultural evolutionary theorists of the "Californian" ('traditional') (e.g. (Boyd and Richerson, 1996; Acerbi and Mesoudi, 2015; Mesoudi and Thornton, 2018; Buskell, 2019) and "Parisian" perspectives (e.g. (Claidière *et al.*, 2014; Morin, 2016) agree that humans' ability to live and thrive in a wide variety of ecological conditions is dependent on the accumulation of cultural learning over time, but they disagree about the relative importance of transmission versus construction in that process (Sterelny, 2017):

> ***The Californian perspective*** (sometimes presented as the 'traditional' view) frames cultural transmission as a preservative mechanism in which variants are chosen and faithfully transmitted between individuals (with some error) which creates overall stability in cultural traits across time (Acerbi & Mesoudi, 2015).
>
> ***The Parisian perspective***, specifically cultural attraction theory (CAT), emphasises transformative processes in which cultural variants are reconstructed by the receiving individual. CAT aims to explain cultural variation by way of cultural attractors. Cultural attraction theory includes the concept that some variants are statistically more likely to be reconstructed due to inherent biases within the individuals doing the reconstruction (Morin, 2016).

Proponents of the Californian perspective question the validity of CAT as a separate theory to explain culture (Buskell, 2017a, 2017b, 2019), but Acerbi and Mesoudi (2015) assert that these two theories are not necessarily in contrast to each other, arguing a broad cultural attraction theory may encompass the same processes addressed by cultural evolutionary theory; in contrast CAT proponents defend the distinctness of their framework (Morin, 2016; Scott-Phillips *et al.*, 2018).[2]

Is this debate an unresolvable clash between two fundamentally different views of cultural evolution, or do the different perspectives arise because they are primarily focused on fundamentally different forms of cultural evolution – consistent with Vaesen and Houke (2021) I use the term 'technological' cultural knowledge (e.g. how to build canoes) in the Californian case, as opposed to forms of culture that operate more exclusively in the

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[2] See Sterelny Sterelny, K. (2017). Cultural evolution in California and Paris. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*. https://doi.org/10.1016/j.shpsc.2016.12.005 for a more in-depth analysis of the agreements and disagreements between these two perspectives of thought in cultural evolutionary research.

aesthetic domain (e.g. heraldic symbols)? I will argue that appreciating the fundamental differences of what it means to talk about CCE in technological and aesthetic cultural contexts lends support to Acerbi and Mesoudi's (2015) assertion that these schools can co-exist, since their ideas originate in fundamentally different types of cultural evolution. In the 'technical' realm, it is unproblematic to think about ratchetting improvements, and to those improvements being transmitted, and tested against an external environment. In the aesthetic domain however, psychological processes like cultural attraction will increase in influence, as the form of the cultural products is not tested against an external environment, but more by the experience of viewing or listening to them, and the responses evoked therein. Here, the aesthetic process has much more in common with the transformative accounts of CAT, but as I shall see, it is more problematic to think about an aesthetic 'ratchet'.

2.3 Can aesthetic value improve cumulatively?

Mesoudi and Thornton (2018) propose 'aesthetic attractiveness' as one measure of performance that could show cumulative improvement. Their prospect of measuring aesthetic attractiveness intersects with topics in philosophical aesthetics – specifically, the subjectivity of taste – which I discuss in this section. I interpret 'aesthetic attractiveness' here as 'aesthetic value', since the latter has more currency in the aesthetics literature. However, the conclusion I motivate, that aesthetic value may lack the objectivity needed to be a good proxy for the improvement that is a core criterion of cumulative cultural evolution, is equally applicable to 'aesthetic attractiveness'.

What, then, is 'aesthetic value'? The most common view in the philosophical aesthetics literature states that an object has aesthetic value or disvalue by virtue of, and in proportion to, the quality of the aesthetic experience it can produce in spectators who meet standard viewing (or listening, tasting, smelling, and so forth) conditions (Beardsley, 1969; Stecker, 2010; Watkins & Schevill, 1974). Standard viewing conditions specify minimum conditions which a percipient (a person who is able to perceive things) must meet for her aesthetic experience of an object to be representative of the calibre of aesthetic experiences which that object can produce. Examples of standard viewing conditions include having functioning sensory and cognitive capacities, having art historical or contextual knowledge, as appropriate, about the work or object (or performance) to which they are attending (such as the knowledge of a painting's provenance and the ability to classify it in the correct genre), and having experience of suitable comparators[3].

According to this view, hereafter 'the standard model', an artwork or aesthetic product which consistently produces enriching, satisfying or rewarding aesthetic experiences is aesthetically valuable for doing so. Conversely, a work which elicits dull, onerous or nauseating aesthetic experiences thereby has aesthetic disvalue. The standard model casts aesthetic value as a kind of instrumental, rather than final, value (where instrumental value is the value something has a means to an end, and final value is autotelic; the value something has as an end or 'for its own sake'): aesthetically valuable objects are valuable because they are means to aesthetic experiences.

This raises the issue of what makes an experience 'aesthetic'. Aesthetic experiences vary in their duration, intensity and character. Some are brief moments of fleeting pleasure in which we savour a sumptuous quality we chance upon in our surroundings: the fragrant scent of a plant, or the undulating peal of church bells. Other aesthetic experiences are not so pleasant: we may feel repulsed, oppressed, distressed, indignant or frustrated. Think, for example, of a formulaic pop song played *ad nauseum*, or the decomposing carcass of a bird. Francis Bacon, the painter, alludes to aesthetic experience having a restorative effect in the following:

> 'If I go to the National Gallery and I look at one of the great paintings that excite me [...] the painting unlocks all kinds of valves of sensation within me which return me to life more violently' (David Sylvester, 1987, p. 141)

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[3] Walton's 'Categories of Art' Walton, K. L. (1970). Categories of Art. *The Philosophical Review*. https://doi.org/10.2307/2183933 contains useful suggestions about which qualities aesthetic experiences of artworks should be directed at.

The intensity of some aesthetic experiences can displace the sense we have of ourselves as experiencing subjects who are apart from the observed world. These experiences may acquire a quasi-spiritual or quasi-religious character. Ralph Waldo Emerson describes one such experience in the following:

> 'I see the spectacle of morning from the hilltop over against my house, from daybreak to sunrise, with emotion which an angel might share … the active enchantment reaches my dust, and I dilate and conspire with the morning wind'(Emerson, 2003, p. 43)

Attempts by philosophers efforts to explain what makes these experiences 'aesthetic' can be situated in four camps: (i) the content-oriented approach which characterises aesthetic experiences in terms of the qualities at which they are directed (see (Carroll 2002, 2006, 2012, 2016); (ii) the axiological approach which treats aesthetic experiences as being of final, and not just instrumental value (Iseminger; Stecker, 2001); (iii) affect-oriented approaches, which characterise aesthetic experience in terms of a distinctive affective state, set of affective states or a type of pleasure (Beardsley, 1969)Beardsley 1969); and (iv) attitudinal accounts, which explain aesthetic experience by reference to an 'aesthetic' attitude or a way of allocating attention (see Bullough 2008; Stolnitz 1960; Nanay 2016, 2018). Hybrid positions which combine several of these approaches are also possible.

We now have a rough outline of what Watkins and Shelley (2012) describe as the 'dominant' view of aesthetic value[4]. Thomas Munro expresses it in the following:

> 'Works of art as products – pictures, poems, and sonatas – can be good only instrumentally, as means to good experience in someone at some time […] No work of art or "objective" quality in art (such as unity or balance) can be good in itself […] It has aesthetic value as a means to good aesthetic experience' (Munro).

Monroe Beardsley puts it in slightly different terms:

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[4] The standard model is not without its detractors, such as Sharpe Sharpe, R. (2000). The empiricist theory of artistic value. *The Journal of Aesthetics and Art Criticism*, *58*(4), 321-332. and Watkins and Shelley Watkins, M., & Shelley, J. (2012). Response-dependence about aesthetic value. *Pacific Philosophical Quarterly*, *93*(3), 338-352. , though neither give a positive account of what might replace it.

> '"X has aesthetic value" means "X has the capacity to produce an aesthetic experience of a fairly great magnitude[5] (such an experience having value)"' (Beardsley).

More recently, here is Robert Stecker:

> 'Aesthetic value comes in two varieties. There is the intrinsic value of aesthetic experiences themselves by which I just mean that they are valuable in themselves. There is the instrumental value of objects capable of delivering aesthetic experience to those who understand them'(Stecker, 2010) (Stecker).[6]

If aesthetic value is to be a proxy for cumulative improvement, as Mesoudi and Thornton suggest, then we need to be able to measure it in some way. The standard model gives us a rough sense that this would involve examining the quality of aesthetic experiences an object affords a subject who meets standard viewing conditions. However, it is unclear how much consensus there could be about aesthetic value which is measured in this way. A given object may afford different aesthetic experiences for different people depending on their tastes and preferences (which have themselves many inputs including from the individual's expertise, cultural background and the context in which an object is presented – see Figure 1). Consider Death Metal music. A piece of Death Metal may provide an intensely satisfying

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[5] 'Magnitude' is Beardsley's term for the collective effect which three inter-related factors have on the character of an experience. The factors are: (i) how *unified* – 'coherent' and 'complete' – the experience is; (ii) how *intense* the experience is; and (iii) how *complex* the experience is (i.e. 'the range or diversity of the distinct elements that it brings together into its unity') Beardsley, M. C. (1969). Aesthetic Experience Regained. *The Journal of Aesthetics and Art Criticism*. https://doi.org/10.2307/428903 ibid., Dickie, G. (1965). Beardsley's Phantom Aesthetic Experience. *The Journal of Philosophy*. https://doi.org/10.2307/2023490 , Dickie, G. (1974). Beardsley's Theory of Aesthetic Experience. *Journal of Aesthetic Education*. https://doi.org/10.2307/3332129 .

[6] Other proponents of the standard model, or a variant of it, include: Ross Ross, D. E. (1994). Modernist impulses in the human sciences, 1870–1930. This volume grew out of 2 international conferences:" The Life Sciences, the Social Sciences, and Modernity" held in Bellagio, Italy, May 1990 and" The Modernist Impulse in the Life and Social Sciences" held at the Ctr for Interdisciplinary Studies at U Bielefeld, Germany, Nov 1991., ; Lewis (1946); Dickie (1988); Levinson (1992; 1996); and Goldman (1995; 2006). See Forsey Forsey, J. (2017). Aesthetic experience, Aesthetic value. *Estetika: The European Journal of Aesthetics*, *54*(2), 175-188. for a critique of Stecker.

aesthetic experience for one person and a torturous and unpleasant aesthetic experience for another. The amount of aesthetic value or disvalue the piece has would therefore seem to depend on *whose* aesthetic experience we study.

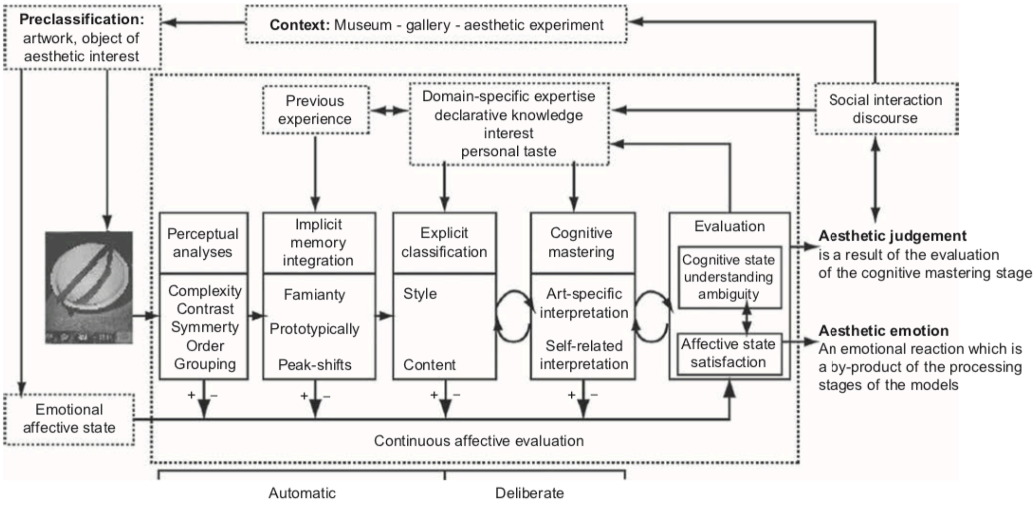

Figure 4: Taken from Leder et al., 2004: A model of aesthetic appreciation and aesthetic judgement

If, as the standard model implies, the aesthetic value of objects derives from our aesthetic *experiences* of them, and those experiences vary, then we may have to index measurements of aesthetic value to individual percipients. Quite how much consensus or divergence there is amongst aesthetic experiences could be established through empirical research (by, for example, conducting surveys). It seems at least probable that we could identify trends that indicate which artworks provide high quality aesthetic experiences and which do not. What remains unclear is how much consensus would be needed in order for measurements of aesthetic value to be a good proxy for the improvement as a criterion for CCE.

Clearly, an argument for classifying a behaviour as CCE would seem, at least, less compelling if there is a lack of consensus about whether the products of that behaviour had improved by a measure of performance. To this concern, I can offer four responses that warrant further consideration:

1. accept that measurements of aesthetic value vary relative to the tastes and preferences of individual percipients and accept that that putative cases of CCE which advert to aesthetic value are on shaky foundations; (indeed, some implicitly take this approach by focusing specifically on “cumulative technological culture” as the explanandum (Osiurak & Reynaud, 2019);
2. argue against relativism, which David Hume famously does[7] (see Hume, 1995), though not without facing considerable challenges (Kivy, 1997; Levinson, 2002; Shusterman, 1999);
3. argue that there is too little consensus about aesthetic value to justify using measurements of it as a proxy for cultural fitness; or
4. argue against the standard model of aesthetic value and in favour of an alternative which is less vulnerable to objections from relativism (though it is unclear what such an alternative would look like).

In summary, the standard model provides a framework within which aesthetic value can be empirically investigated; we can measure the aesthetic experiences of people who satisfy standard viewing conditions and, in doing so, learn how aesthetically valuable the objects of their experiences are. However, it remains to be seen how much intersubjective validity measurements of aesthetic value gathered in this way could have. CCE requires a ‘ratcheting’ of improvements in some measure of performance over time. But how much intersubjective validity do these measures of performance need? Further research could establish just how objective a measure of performance needs to be for CCE and just how much or little consensus there is among our aesthetic experiences.

2.4 Does music improve over time?

Moving from general considerations of improvement in aesthetic value, I now consider how concepts of improvement and progress have been deployed in a highly significant area of human aesthetic culture – music. Mesoudi and Thornton (2018) do not expand upon their

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[7] "Under some or other of these imperfections, the generality of men labour; and hence a true judge in the finer arts is observed, even during the most polished ages, to be so rare a character: Strong sense, united to delicate sentiment, improved by practice, perfected by comparison, and cleared of all prejudice, can alone entitle critics to this valuable character; and the joint verdict of such, wherever they are to be found, is the true standard of taste and beauty." (Hume, 1874 – 1875)

identification of ‘aesthetic attractiveness of art’ as a possible measure of performance. Contrastingly, Mesoudi (2011) posits that the sort of change seen in the aesthetic aspects of music is not a matter of improvement but is better captured by the notion of cultural drift which is the result of the random copying of cultural variants. I investigate this tension now, firstly looking at how ‘progress’ (including the sense of increasing aesthetic value) has been theorised in historical musicology and ethnomusicology. I consider technical advancements and other developments which some authors argue lead to ‘local’ improvements in aesthetic value. Lastly, I review empirical studies utilising large digital datasets.

In 1788 Johann Nikolaus Forkel, a founding figure in modern historical musicology, invoked a striking image of an octopus (Dahlhaus, 1987). He used this image to capture his vision of the teleological development of “the arts and sciences [which] only grow to *perfection* gradually”, in “stepwise *progression* from the simple to the complex” (my emphasis)[7]. Nearly two hundred years later in an essay on ‘Progress and the avant garde’, musicologist Carl Dahlhaus (1987) referred back to Forkel’s octopus to illustrate “the paradox of the idea of progress”. This paradox arises when we take a particular view on musical change: that music is inexorably developing through a series of ‘stages’, becoming more complex and, in some sense, improving. Although this idea has not survived detailed examination of the world’s musical cultures (Nettl, 2006), it seemed like a certainty to Forkel, no doubt nurtured by living in the optimistic Enlightenment, and continued to be a common implicit assumption and explicit declaration well into the twentieth century, by which time it was being illegitimately backed up by misapplied arguments taken uncritically from Darwinian evolutionary theory (Mundy, 2006, 2014).

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[7] There is no straightforward or standardly accepted definition of musical complexity, evidenced by the fact that the standard encyclopedia of music, ‘Grove Music Online’, contains no entry for the term. However, I note here that ‘complex’, as antonym of ‘simple’, is often used informally to describe either an overall impression or various dimensions of music, such as melody, harmony, rhythm, timbre and structure, from at least two points of view: those of the performer and the listener. Naturally, this indexes performance skills and listener familiarity and preferences, and can never be entirely objective. Here Beardsley’s characterization of the complexity of an aesthetic experience (already cited above) as “the range or diversity of the distinct elements that it brings together into its unity” seems to be a reasonable description of the term’s application to musical works by writers in historical musicology such as Forkel, and for the main part this is how I use it in this section of my paper (the exceptions are for the corpus studies cited below by Parmer and Ahn (2019) and Percino (2006), which use information-theoretic measures).

[8] “Ce qu’on appelle en général *progrès* n’est que *transformation*.”

This assumption of progress – or growth – towards perfection runs counter to a second commonly-held intuition: that the acknowledged masterpieces of a particular style or period are not superseded by subsequent works. Stravinsky's 'Rite of Spring' is no higher in aesthetic value than Beethoven's 'Eroica', Radiohead's 'Kid A' no improvement on The Beatles' 'Abbey Road'. As Dahlhaus puts it, it would "be blindly presumptuous to ascribe a higher rank to the musical present than to the past". In this context he cites music historian François-Joseph Fétis, who appealed to the view that the goal of music is emotion, and wrote against the prevailing mood of his day that "in general what we call *progress* is only *transformation*…" (1835, my translation).[8] 'Change rather than progress' with respect to aesthetic value is currently the conventional view in musicology.

However, there may be progressive development in various aspects of musical *means* and 'language'. Such improvements in the technological means (or means of production) through which musical works are produced and performed have occurred and are generally gradual (e.g. the nineteenth century expansion of the Western orchestra both in size and variety of instruments) but some are customarily viewed as revolutionary (e.g. the rapid uptake of staff notation in Gregorian Chant, or the introduction of digital production to popular music).

Regarding musical language, the discovery of harmony has often regarded as a key stage in the development of music (Benzon, 1993; Gilbert, 1920; Spencer, 1890), enabling wholly new domains of aesthetic experience. We might also listen to those composers and musicologists who have seen progress in terms of the development of a musical language, or in the way of *thinking through music*, as the addressing of certain 'technical puzzles' (Adorno, 2020). Dahlhaus describes this process with respect to the music of Stockhausen:

> 'difficulties which at first seemed insoluble provided the stimulus for works at a second level on which earlier problems were solved. Admittedly, others arose in their stead, but these in turn urged musical thinking onwards. This seems to suggest that musical development in a restricted sphere, that of compositional technique, shares certain traits with the progress of a scholarly discipline' (1987: 20).

However, importantly, we should strongly resist the idea that there is any single or privileged musical language. Even within Western Art Music (WAM), the past century has arguably seen the end of the so-called ‘common practice period’, a strong and largely successful challenge to the hegemony of musical modernism, and the emergence and spread of multiple and very disparate styles (new complexity, minimalism, neoclassicism, neoromanticism, spectral, etc.). If there is ‘progress’ within a language it is severely local (e.g., we might think of how Schoenberg’s serialism with respect to pitch was broadened into ‘total serialism’ in the works of Boulez and Stockhausen), and certainly cannot be measured in any absolute terms. Returning to my question: “Does music improve over time?”, it is surely undeniable that gradual and sometimes ratchetting, in the sense of being very unlikely to be reversed, development of this kind result in changes in aesthetic experience and hence aesthetic value. Nonetheless, the history of the rise and fall of classical and popular musical styles, and the changes in popularity of individual artists, demonstrates the wide range of the evaluation of such changes and offers no support for global or unilineal increase in aesthetic value.

In comparative musicology and ethnomusicology, progress was problematised from the mid-1920s onwards, particularly after World War II (Mundy, 2006). An example of this rejection is found in Curt Sach’s posthumously published ‘The Wellsprings of Music’ (Sachs) in which he describes progress as a ‘dangerous slogan’, and writes that “[w]e no longer believe in a neat evolution from low to high, a constant development from unassuming simplicity towards an ever growing complication”. He criticises the internal contradictions of teleological views of musical history with the telling point that their adherents frequently held up an earlier period as offering the most perfect music. Leonard B. Meyer echoes Sachs in his ‘Music, The Arts, And Ideas’ (Meyer), in which “the demise of the idea of progress” in music is seen as part of a wider social and historical movement. Meyer argues that “[w]ith the development of historical musicology and ethnomusicology, the notion of stylistic progress has to all intents been given up.” Nonetheless Sachs still recognises a form of limited progress, in which each period sets “for art a temporary goal of its own”, a goal which may require the acquisition of new techniques and new means of expression. Sachs finds musical progress in the early development of opera, and the changing treatment of recitatives from Peri to Monteverdi. “Progress exists at best within a limited span; as to the total of art, there is no progress, no regress, but simply otherness.”

Meyer (Meyer) offers perhaps the most systematic and comprehensive account of stylistic change in general, which although focused on the history of WAM is broad enough to include other musics. Alongside the ‘apparently random’ changes that have been the focus of some contemporary modelling studies (Bentley *et al*., 2007) and which I discuss below, Meyer also discusses ‘mutational change’. This is particularly relevant to us because such revolutionary changes (such as the discovery of linear perspective in the visual arts, serialism in music, or the invention of new aesthetic goals) are said to give rise to “permanent and fundamental alteration” in the ‘fundamental presuppositions’ or ‘premises’ of a style. In their irreversible effects such paradigm shifts resemble the operation of Tomasello’s ratchet and could be linked to Sachs’s views on limited aesthetic progress. Once new premises have been established, artists work to explore the new realm of aesthetic possibilities offered by the new technological means, musical forms, or aesthetic goals. Meyer argues that the resulting period of intra-stylistic change is best captured by a model where change is predominantly driven internally rather than externally and is typically (though not inevitably) associated with a growth in complexity and reduction in informational redundancy.

Turning from historical musicology to the empirical sciences, the development of computational techniques in the field of Music Information Retrieval (Lartillot *et al*., 2008; Schedl *et al*., 2014), coupled with the assembling of large digital archives of recorded music and databases such as the Million Song Dataset (Bertin-Mahieux *et al*., 2011), has made it more straightforward to pose testable scientific hypotheses on various aspects of the cultural evolution of musical styles (Brand *et al*., 2019). Although it is true that some published studies using ‘evolution’ in their title either do not use concepts or tools informed by evolutionary biology, instead they indicate a quantitative analysis of temporal trends and patterns (e.g., Serrà *et al*., 2012); or use biological measures of population change (such as diversity and disparity) without attempting to account for their causes (Mauch *et al*., 2015), there is also a significant body of research addressing whether such changes can be better explained through cultural drift alone (resulting from random copying) or when coupled with transmission or psychological bias (the term used to capture the effects of listener preferences, whether determined by musical features, desire for novelty, or social pressure to conform) (Acerbi & Mesoudi, 2015).

To raise the possibility that trends in musical cultures may be explained without reference to listener preferences is in some ways to question the very possibility of aesthetic progress and seems to strike at the notion of meaningful agency on the part of both music creators and audiences. Yet support for this possibility has arisen from corpus studies into the ability of a random copying model versus models incorporating transmission biases to predict observed turnover rates of songs in album and internet charts (Acerbi and Bentley, 2014; Bentley *et al*., 2007), turnover rates in the frequency of use of drum samples (Youngblood, 2019), and the dependence of the changing emotional content of lyrics on content and model biases (Brand *et al*., 2019). This research suggests that chart trends can predominantly be explained through cultural drift, with some evidence for conformity bias for specialist genres (Acerbi & Bentley, 2014; Youngblood, 2019), and a content bias for negative lyrics (Brand *et al*., 2019).

On the other hand, the rather unintuitive conclusion that chart success is mainly the upshot of random copying and has little to do either with its aesthetic value or with the content bias of the listener (i.e., a preference based on aesthetic experience), is challenged by other work which shows that success can be well-predicted through acoustic properties (Interiano *et al*., 2018), and is influenced by various measures of musical complexity (Parmer and Ahn, 2019; Percino *et al*., 2014). Moreover, moving outside the realm of Western pop music, Nakamura & Kaneko (Nakamura & Kaneko) have demonstrated that trends in dissonance across four centuries in Western classical music can be reproduced in a simple evolutionary model excluding random copying, in which creators learn from the past and evaluators make selections based on novelty and style conformity; and further, that this simple model successfully predicted changes in an unrelated genre.

Finally, another perspective on this debate is provided by the results of the 'DarwinTunes' experiment reported by MacCallum and colleagues (2012). Here, a 'population' of short melodic loops, with successive generations being generated through modelled random mutation and reproduction, was allowed to evolve under the pressure of selection governed by listener preference. Once again, a balance is struck between cultural drift and psychological bias. It is striking that harmonic and rhythmic properties of the loops approached those commonly considered aesthetically pleasing in Western pop music: i.e., it appears that listeners chose tunes based on aesthetic grounds rather than at random. It is difficult to compare the different contexts offered by this experiment and the corpus studies into real-world music-buying habits described above, but the results of MacCallum *et al*. (2012) are consistent with iterated learning experiments showing that learning biases in the copying of drum patterns leads quickly to 'rhythmic universals' (Ravignani *et al*., 2016). Together these studies may offer comfort for those seeking to hold on to a notion of agency. In a comment on the DarwinTunes experiment from the perspective of the 'Parisian' perspective of cultural evolution, Claidière and colleagues (2014) emphasised the importance of guided transformative processes rather than random mutation in the evolution of 'real music'. To us, this points to the need to take into account the makers of music as well as its audience, and the combined message is that creation and choice may after all be a driving force in cultural evolution. I note that in the artificial context of the 'DarwinTunes' experiment the proxy of mean listener preference is used, and as I have unpacked in my philosophical analysis of aesthetic value above it is unclear whether preference can equate to a measurement of aesthetic value. It is also difficult to extrapolate from the results of this experiment context to the way in which the world's diverse musics have altered over time.

Over the course of the last hundred years, historical musicology and ethnomusicology have come to the conclusion that any notion of global aesthetic progress is dead in the water, inescapably bound up with discredited social Darwinist notions of cultures evolving toward some idealised Western pinnacle. Nonetheless, in addition to undeniable technical and technological advancements, there are some strictly limited and local cases in which we might speak of improvement: Dahlhaus's advances in 'musical thinking' within a specific musical language, Sachs's temporary progress towards particular aesthetic goals requiring the development of new techniques, and Meyer's exploration of the possibility space of a new style. Empirical support for these limited cases may come from the corpus studies discussed above, which have demonstrated an increase in instrumental complexity associated with the growth of new popular music styles (Percino *et al*., 2014), and have confirmed the increased use of dissonant harmony in the history of WAM (Nakamura & Kaneko, 2019). However, the quest for, l*et al*one the identification of, a culture-independent measure of global 'aesthetic value' has long been abandoned in musicology, and the empirical studies cited have instead used proxies of chart success or listener preferences. Aesthetic goals, when considered at all, are seen to be learned, set and evaluated from within particular musical cultures. Each musical culture can and perhaps should be thought of as a distinct stem of a constantly diversifying evolutionary bush rather than steps on a ladder. Adopting this perspective, who is to judge the relative merits of the musical productions of a Beethoven and a Beyoncé?

2.5 Is Cumulative Cultural Evolution unique to humans?

While students of philosophy and musicology may be familiar with the preceding content, it may not be so obvious why it could, as I argue now, be relevant to debate at the interface of human and nonhuman animal cultural evolution. If CCE is to be somehow diagnostic of human uniqueness, then there will inevitably be great interest in understanding whether anything like it occurs in non-humans. Some have challenged the claim that CCE is unique to humans. For example, Hunt and Gray (2003) posited tool manufacture in New Caledonian crows (*Corvus moneduloides*) as CCE. A variety of cultural behaviours in primates have also been postulated as cumulative in character from nutcracking behaviour in chimpanzees to eye-poking in capuchin monkeys (Cebinae) (Perry, 2011), More recently, Jesmer *et al*., (2018) have shown evidence for the CCE of migration routes in relocated populations of both bighorn sheep (*Ovis canadensis*) and moose (*Alces alces*). Individuals from a population of bighorn sheep that had been established in the environment for over 200 hundred years were found to have double the efficiency in their migration route compared to individuals of a population that had only been established for up to 35 years. This was due to a longer history of repeated cycles of innovation (in movement decisions) and learning, very similar to Mesoudi and Thornton's (Mesoudi & Thornton) core criteria, in the longer established populations.

Further provocative evidence for CCE in nonhuman animals comes from experiments in homing pigeons (*Columba livia*) (Sasaki & Biro, 2018). This study found that chains (‘generations’) of pairs in which information was pooled between multiple individuals over five iterations (or ‘generations’) created routes that were eventually more efficient than the two control chains consisting of solo fliers or pairs that stayed the same. The authors argued from this that collective intelligence in animal groups can initiate CCE (Figure 2). Finally, observational evidence from the cultural evolution of humpback whale song has also been proposed as a contender for nonhuman CCE (Allen *et al*., 2018), and I explore this in more detail below.

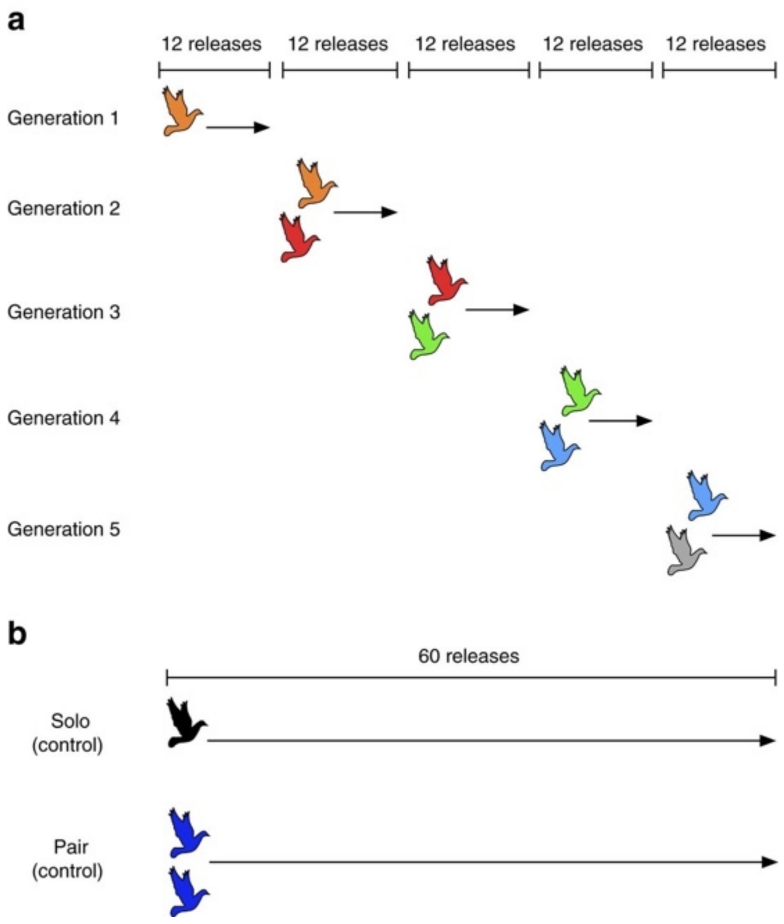

Figure 5: From Sasaki and Biro (2018): "Homing flight release protocols. (a) Experimental group; (b) control groups. In each chain of the experimental group, a single pigeon (orange) was first released from the same site repeatedly 12 times, then partnered with a naive pigeon (red) and flown as a pair a further 12 times. The first bird was then replaced by a third bird (green) and this new pair (red þ green) was also released 12 times. This procedure continued until the fifth-generation bird (grey) was added and flown a final 12 times. In the control groups (b), single pigeons and fixed pairs were released the same number of times as the total flown by the experimental group (60 flights). All three treatment groups contained 10 independent replicates (chains, solo birds or pairs)."

These examples are however open to critical scrutiny due to lack of direct evidence of both social learning and innovation (Dean *et al*., 2014; Whiten, 2018). Arguably, Sasaki & Biro's (Sasaki & Biro) is the most convincing study from this perspective, but the trait it focuses on, a navigational route, could in theory be improved readily by a practicing individual without social input. From a product-focused perspective on CCE, it is not out of the question in most of non-human examples that an individual could learn to produce the documented trait improvements asocially (Tennie *et al*., 2020), and from this perspective the migration route example is arguably strongest. Finally, all these cases focus on the refinement of a particular skill rather than an entirely new innovation or recombination (Whiten, 2018).

2.5.1 Humpback whale song case study

The roots of my enquiry into the tension between CCE and change in aesthetic cultures was that its resolution has important implications for thinking about whether non-humans have elements of CCE, and in particular, whether humpback whale song should be considered an example, as suggested by Allen and colleagues (2018).

Some of the strongest evidence for nonhuman culture is found in the complex songs of humpback whales (*Megaptera novaeangliae)* (Garland *et al*., 2011; Payne, 1985). Male humpback whales produce a vocal sexual display called 'song' during the breeding season. Song is a long, stereotyped acoustic signal with a hierarchical structure, such that each song is composed of a set of themes, each theme is composed of repeated phrases and each phrase is composed of a stereotyped sequence of units (Payne & McVay, 1971; Suzuki *et al*., 2006). All male humpback whales of each breeding population sing the same song at any given time. The speed of changes to a song that spread across a population indicates that song sequences are socially learned (Janik & Slater, 1998; Tyack & Sayigh, 1997). Generally, each song changes gradually with all singers of the same population updating their song resulting in the maintenance of similarity across the population (Payne, 1985; Payne & Guinee, 1983). The transmission of song in the South Pacific Ocean is of particular interest to researchers due to the occurrence of song 'revolutions' in which a population discards a current song type in favour of a new, and completely different song type (Garland *et al*., 2011; Noad *et al*., 2000). Song types have been found to radiate eastward across the South Pacific Ocean. For example, the song of Eastern Australia was transmitted eastward all the way to French Polynesia in two years (Garland *et al*., 2011).

Allen *et al*. (2018) examined the song structure of humpback whales off the west and east coasts of Australia over thirteen consecutive years. The west coast song regularly spread to the east coast during 'revolutions', but songs underwent more gradual changes in between these events. Allen *et al*. (2018) found that the complexity of songs, measured as the number of distinct units per phrase and overall song duration, increased as a song evolved between these revolution events (typically over one to two years). However, as old songs were replaced with new songs during revolution years complexity was reduced, only to build up again between revolutions (Figure 3). It is thought that an increase in complexity may represent embellishment by males wishing to stand out to females and that reductions in complexity during revolutions may indicate a limit to the social learning capacity of novel material in humpback whales (Allen *et al.*, 2018). Due to the conformity in general song structure at any one time it can be assumed that changes by individual males are incorporated by the population at large and then further built upon to create this incremental increase in complexity over a song's lifetime.

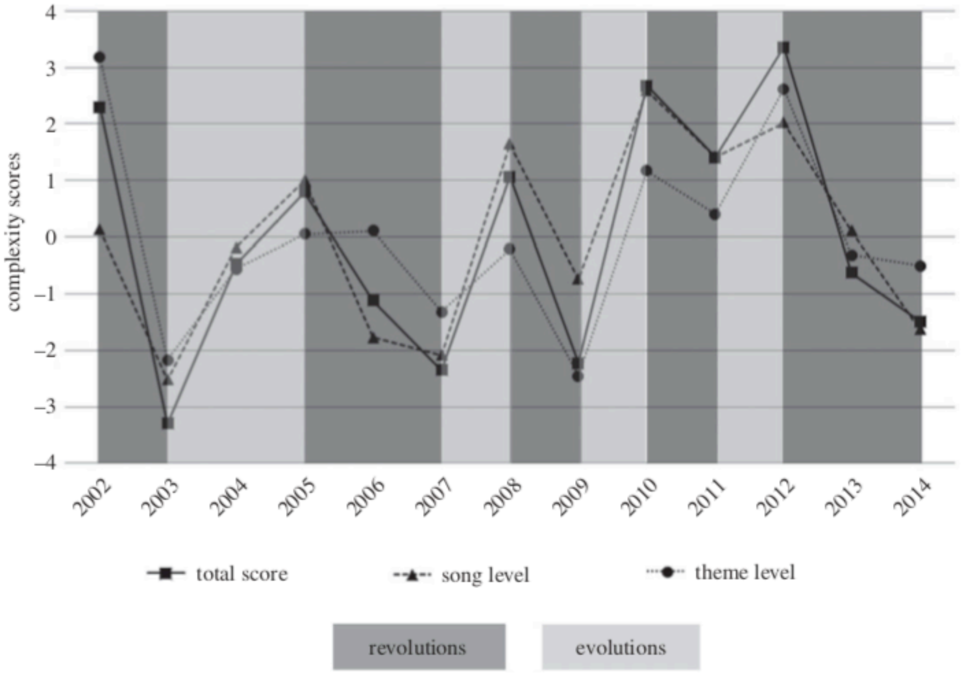

Figure 6: Taken from Allen et al., 2018: "Song complexity scores for each year (2002 – 2014) representing complexity at the (i) song-level, (ii) theme-level, and (iii) total complexity. Revolution and evolution transitions are demarcated."

These cycles of innovation and transmission that produce an increase in complexity mirror the mechanisms described in CCE literature and makes humpback whale song a potential nonhuman example of CCE. But in what sense has the song 'improved'? Is the more complex song 'better'? Or is the actual content selectively neutral (borrowing a genetic fitness term for the fitness of cultural traits), only significant within a specific population at a specific time? These questions are also relevant to ongoing debate over the evolution of aesthetics in nonhuman animals (Prum, 2018). While I do not mean to uncritically compare the experience of humpbacks hearing a song to human aesthetic experiences, it does seem legitimate to ask what basis, if any, do we have to differentiate between 'fitness neutral' evolution of song in this example, and change in human aesthetic products?

2.6 Technological and aesthetic cultures evolve in different ways

While I do not wish to equate human music with humpback whale song, I do wish to point out that when humpback whale song is examined through the lens of cumulative cultural evolution, the secondary questions posed about improvement in performance are similar to those of aesthetic value (or aesthetic attractiveness) in human aesthetic culture. Humpback whale song in at least some populations increases in complexity through cultural evolution, akin to some changes in musical styles (Allen *et al*., 2018; Percino *et al*., 2014). However, this increase in complexity is reduced when song revolutions occur, which would seem contrary to the ratchet effect, or sequential improvement central to the CCE framework. As with the cultural evolution of human art forms, we cannot uncritically equate change (in this case an increase in complexity) with an improvement in performance. There are iterations of embellishment, upon which each individual learns and incorporates changes or additions into their own repertoire, after which the same individual may add further embellishments/changes/additions. In a similar manner, the core processes of learning, innovation, and transmission are present in aesthetic cultural products. Consequently, the key question arises: do we widen our definition of CCE (potentially dropping or weakening one of Mesoudi and Thornton's core criteria) to encapsulate both aesthetic cultural products in humans and strengthen the case for nonhuman CCE (e.g. humpback whale song)? Or, if we cannot show that the human aesthetic cultural products improve in any measurable way, do we exclude them both from the CCE framework (Osiurak & Reynaud, 2019)?

We have focussed on aesthetic value as the metric by which aesthetic products might or might not be said to improve, but some authors consider advancements in the means of production that create an aesthetic product to qualify as an improvement within the aesthetic domain (Tinits & Sobchuk, 2020). I argue in contrast that while the means of production may be an input of consideration to the overall aesthetic value of an aesthetic product, the means of production cannot solely determine improvement in the aesthetic value or experience of an aesthetic product. Instead, the means of production are cultural traits within the technological domain. The contrasting view from a contemporary study by Tinits and Sobchuk (2020) depends upon the philosophical stance of Becker (Becker), a sociologist who argues that art is better understood as a collective activity than as a collection of artworks. According to Tinits and Sobchuk (2020) this means that the mechanisms behind the production of a painting cannot be sharply distinguished from the painting itself (where 'painting' could be replaced by a piece of music, a film, a book, etc). Tinits and Sobchuk (2020) describe cumulative cultural evolution in the aesthetic domain by pointing towards the increase in complexity in the structure of production crews behind films. However, the process by which an aesthetic value arises from the interactions between a product and a specific percipient is complex. Undoubtedly, contextual factors about the process of production (for example knowledge of the circumstances of the production, or the artist's statements of intent, or a film directors influences) could be important inputs to both the aesthetic experience and the ultimate aesthetic judgement of a given product (Leder *et al.*, 2004). To us, this means that relationship between CCE in production methods and resultant aesthetic values is also likely complex and unlikely to follow simple correlations. Tinits and Sobchuk (2020) present their study as showing CCE in an aesthetic domain, but they are focused on the means of production (in this case the film industry), which is, at least partially, distinct from the aesthetic value of the final product (the film). In my view, they have shown that the means of production of aesthetic traits can evolve by the process of CCE (traits belonging in the technological domain), rather than showing CCE in the aesthetic traits themselves. Similarly, the nineteenth century expansion of the Western orchestra both in size and variety of instruments would not automatically mean an increase in aesthetic value or attractiveness of the aesthetic products created through such an expansion.

A theory related to Becker's is held of music by sociologist Christopher Small, who prioritises performance over the musical 'work', and defines 'musicking' as the participation in any capacity whatsoever in a musical performance (Small). Musicking is just one aspect of a society's ritual activities which articulate its (ideal) social relationships, and a participant's aesthetic pleasure in a performance arises when its musical gestures successfully articulate or affirm these relationships in a way which meshes with the participant's own view of them. Aesthetic judgments and value, for Small, thus refer implicitly to the society that has given rise to the performance being judged. If the degree of pleasure is related to the degree of fit between performance and participant, it seems highly unlikely that aesthetic value can increase in the open-ended way implied by Tinits and Sobchuk. Our stance is supported somewhat by Yang *et al*.'s (2019) suggestion that aesthetic experiences do vary across cultures, as aesthetic judgements varied between participants with different cultural backgrounds, with aesthetic judgements more positive when participants viewed visual art from their own culture.

Such detailed analyses of the relationship between the technological and aesthetic domains of cultural evolution can, in my view, help clarify current debates in cultural evolution between advocates of Californian cultural evolution theory and more recent contributions from supporters of the Parisian cultural attraction theory. I have analysed above the ways in which cultural change might differ between technical and aesthetic domains. How might my treatment lead to additional understanding of why Parisian-perspective cultural attraction and Californian-perspective cultural evolution can co-exist? I propose that they are accounts of cultural change that are directed at different types of fitness landscape. In the technological domain, the Californian perspective works well because a problem, once defined, is essentially static – for example: "produce using available materials a human powered craft for navigating sheltered waters in the Arctic" – and solutions can then be objectively compared. In this domain, discussing cumulative cultural evolution in the context of improving performance is relatively unproblematic.

In contrast, within the aesthetic domain, the 'problem' – maximising aesthetic value – can never be static because the target, the aesthetic value judgements of the percipient, is always moving. Tastes are changing, and sub-groups branch toward radically different and sometimes fundamentally incompatible judgements of value, such that solutions cannot be objectively compared, and can in fact be described as arbitrary with respect to any criterion that does not reside within a human mind. Here, the value of 'solutions', i.e. aesthetic products, is defined as much by the characteristics of the audience as by the nature of the solution, which is why the notion of cultural attractors, features of particular groups of minds at particular times, can be valuable as a tool for explaining cultural change in this domain[9]. I should therefore expect from the arguments I have laid out that fundamentally different principles could govern cultural changes in the two domains, and as a result be mindful of the problems of confusing or conflating the two. Inevitably there are going to be cases where the contrast is not clear cut, but in general I suggest that recognition of this contrast between aesthetic and technical domains provides a conceptual framework in which both Parisian and Californian perspectives on cultural change can and should co-exist.

My paper brings together thought from biology, musicology and philosophy with the aim of disentangling the implications of applying the idea of improvement in performance that is critical to the concept of CCE to the cultural evolution of aesthetic attractiveness or value. My overall conclusion is that this is clearly not a trivial task and requires more attention than has been previously allocated in the CCE literature, which has been predominantly technological in focus (Vaesen & Houkes, 2021). Depending on the philosophical stance taken, this task may even prove impossible. Through a philosopher's lens I have examined the nature of aesthetic value and whether it can be measured in any meaningful way, and from the perspective of musicology I have examined a long tradition of thought about whether the aesthetic value of a specific example, music, can progress. Both views find that the answer is not straightforward and importantly that the answer we choose has potentially important repercussions for how we treat an array of cultural phenomena both in humans and other animals. Lastly, I have discussed a nonhuman animal case study to evaluate the repercussions of my findings on particular cases of nonhuman animal culture. I hope that my paper opens up new avenues of discussion about CCE within the aesthetic domain and that this is just the beginning of a fruitful discussion between disciplines.

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[9] While Scott-Phillips et al. Scott-Phillips, T., Blancke, S., & Heintz, C. (2018). Four misunderstandings about cultural attraction. In. discuss "ecological attractors" within the context of cultural attraction, this seems to us a flawed conflation of two fundamentally different domains of cultural change.

The question remains though as to whether cultural change in the aesthetic domain can ever be meaningfully described as cumulative, if there cannot be unambiguous consensus on the nature of what is accumulating? The answer matters. If it is no, which from the perspective of the philosophy of aesthetics is arguably the supported position, and the one I lean toward, cultural change in the arbitrary form of animal signals must be excluded – humpback whale song is not, from this perspective, an example of cumulative cultural evolution. The perhaps uncomfortable extension however is that large swathes of human cultural production in the aesthetic domain must also be moved out of the cumulative box, including Mesoudi and Thornton's (Mesoudi & Thornton) last example of "the aesthetic attractiveness of art". In contrast, if the answer is yes, then Mesoudi and Thornton's original examples all stand, but we have no basis for saying that humpback whale song does not also show cumulative cultural evolution, and the philosophical issues raised above become a more serious problem for this account of CCE. I do not pretend to answer this question here definitively, rather my goal has been to articulate it, and the consequences of choosing each answer, and I hope to have clarified how, in my view, accounts of cumulative cultural evolution are currently resting on the horns of a dilemma when it comes to the aesthetic domain.

Chapter 2 Appendices

Appendix 2.1: Examples of 'improvements' in literature as taken from Mesoudi & Thornton's supplementary material A: Human, B: Non-human

A: HUMAN

Study / species	**Improvement**
Caldwell & Millen 2008	Yes – Towers got higher and planes flew farther
Mesoudi 2008	Yes – Arrowheads scores increased
Kirby, Cornish & Smith 2008	Yes – Increases in learnability of languages
Beppu & Griffith 2009	No
Wisdom & Goldstone 2010	Yes – Increase in team performance
Derex, Godelle & Raymond 2013	Yes – Fishing nets scores increased
Wasielewski 2014	Yes – Performance of clay and reed devices increased
Kempe & Mesoudi 2014	Yes – Number of pieces solved increased
Muthukrishna *et al*. 2014	Image editing task: Yes – Image editing skills increased. Knot tying task: No – Participants could only do worse than the initial demonstrator
Derex & Boyd 2015	Yes – New tools and high score totems were produced
Zwirner & Thornton 2015	Yes – More efficient baskets were produced

Derex & Boyd 2016	Yes – New active ingredients were produced and remedies scores got improved
McGuigan *et al*. 2017	Yes – New and higher rewards were obtained
Fay *et al*. 2018	Yes – Reproduction accuracy increased

B: NON-HUMAN ANMAL

Study/ species	**Improvement**
Sasaki & Biro 2017 – homing pigeons (Experimental)	Yes
Fehér *et al*. 2009 – zebra fnches (Experimental)	Yes – vocal learning
Claidière *et al*. 2014 – Guinea baboons (Experimental)	Partly – Improvements in individual performance (correctly remembered blocks) across transmission chains, but better performance does not provide any functional benefts to the individual
Dean *et al*. 2012 – chimpanzees and capuchin monkeys, compared to human children (Experimental)	No – Animals typically failed to obtain more desirable rewards (NB there is no evidence that more desirable rewards had greater nutritional value)
Marshall- Pescini & Whiten 2008 – chimpanzees (Experimental)	No – Asocial learning of probing by one individual only; no social learning of probing
Price *et al*. 2009 – chimpanzees (Experimental)	Yes – in some conditions, food rewards could only be accessed by putting together components to make a longer tool
Yamamoto *et al* 2013 – chimpanzees (Experimental)	Yes – Some individuals switched to a more effective technique after observing demonstrators (sucking)
Vale *et al* 2017 – chimpanzees (Experimental)	Yes – Learning a more efficient technique following observation of a trained demonstrator (though some individuals also learned to modify tools in the absence of a demonstrator)
Davis *et al* 2016 – chimpanzees (Experimental)	Yes – Some individuals, forced by experimental design to use a highly inefficient method switched to a more efficient (faster) method after observing demonstrators
Kendal *et al* 2009 – nine- spined sticklebacks (experimental)	Yes – switching to the rich patch provides foraging returns
Schofeld *et al* 2017 – Japanese macaques (Observational)	No – But novel behaviours (e.g. digging pools to wash food) argued to build on previous socially learned behaviours
Hunt & Gray 2003 New Caledonian crows (Observational)	No – No evidence that different tools differ in their efficacy
Filatova *et al*. 2013 – Killer whales (Observational)	No – Vocalisations do not become "better" in any functional sense. There may be cultural change (e,g, through processes analogous to drift), but not CCE according to our 57definition.

Boesch 2003; Sanz *et al*. 2010 and others – wild chimpanzees (Observational)	No – No direct evidence that supposedly complex tools are more effective than simpler tools
Perry *et al*. 2011 – wild capuchin monkeys (Observational)	No – no evidence that new behaviours provide fitness benefits

3 Chapter 3: Fine-scale evolution of humpback whale song in the Cook Islands

Abstract:

This chapter examines temporal change in humpback whale song units at a fine scale, aiming to unravel the interplay between individual learning processes and cultural evolutionary processes. Ethical constraints in studying humpback whale songs prompt indirect approaches, and for this I focussed on the ‘groan’ unit in the Cook Islands in a single song and season. Employing a methodology encompassing theme analysis, fine-scale unit analysis, and automated measurements from custom code built on previous humpback song research, the study facilitated the investigation of 1717 humpback whale song units from a single breeding season. Results indicate overall stability in the ‘groan’ meta-unit, challenging the hypothesis of ongoing vocal production learning at the unit level. Alternative factors like signal quality, coarticulation, and exhaustion are explored with limited impact. The findings contribute to understanding humpback whale vocalisations, paving the way for future comparative studies with birds and offering insights into the cognitive learning mechanisms underlying song. The ambiguity in song unit evolution suggests the need for longer-term datasets to unravel the intricacies of humpback whale vocalisations and their potential connections to social calls.

3.1 Introduction

There has long been consistent research interest in the development, learning and production of vocal sequences in animals, not least because of the broad programme to understand the evolution and usage of human vocal language. There are behavioural, neural and genetic similarities between the way that human infants acquire speech and songbirds learn song characteristics (Kuhl, 2003; Moorman *et al*., 2011). Bird song research has generated a substantial body of literature that delves into the intricate relationship between individual learning processes and cultural evolutionary processes. This extensive literature has explored various aspects of bird song, including its complexity, cultural evolution, population differentiation, and the mechanisms underlying vocal learning biases (Read & Weary, 1992; Williams & Lachlan, 2021; Lachlan & Feldman, 2003). For instance, Williams &

Lachlan (2022) and Lachlan & Feldman (2003) have contributed to this field, shedding light on the cultural evolution of bird songs and the coevolution of cultural signals and genes encoding learning preferences (Williams & Lachlan, 2022; Lachlan & Feldman, 2003; Lachlan, 2018). Furthermore, the study of bird song has provided insights into the process of cultural evolution, such as the development of song dialects in different bird species and the impact of environmental factors on song learning (Luther & Baptista (Luther & Baptista, 2010; MacDougall-Shackleton & MacDougall-Shackleton, 2001). Additionally, the literature has highlighted the significance of sensory experiences during development in shaping vocal learning biases in birds, emphasising the role of social learning and genetic variation in bird song structure (James *et al*., 2020; Lahti *et al*., 2011; Chen & Meliza, 2019). Overall, the extensive literature on bird song serves as a rich resource for understanding the interplay between individual learning processes and cultural evolutionary processes in avian vocalizations. Beyond birds, Zandberg et al., (2012) have provided insights from a global cultural evolutionary model of humpback whale song, demonstrating the broader applicability of cultural transmission and evolution studies across species (Zandberg et al., 2021). Nonetheless, our understanding of song learning and production in humpbacks is far behind these similar efforts in birds. This is partly because we obviously cannot experiment on whales in the same way as birds, however we can use indirect approaches to try to unpick what we can about underlying learning processes. Observations of patterns and evolution of humpback whale song can help us unpick how songs are being learned. For example, Garland *et al*., (2017) found that humpback whales learn songs in segments through analysing rare occurrences of song hybridisation events (where new songs are spliced with an existing song). An indirect approach may also be applied when investigating how humpback whale song units are learned and produced.

One of the most influential voices in the field of bird song learning has been that of ornithologist Peter Marler. Marler (1997) proposed three foundational models for understanding song learning in birds, each offering a unique perspective on the intricate processes that shape avian vocalisations. The first model, often referred to as the "The Sensorimotor model" aligns with Marler's concept of genuine song learning. It posits that birds are capable of acquiring any song type when exposed to an appropriate model during the critical phase of their development. Under this model, there is an assumption that birds start with a blank slate, with no prior knowledge of a predefined template, and have the capacity to learn diverse song types. The second model, known as “Learning based on selection”, echoes Marler’s work on innate templates. It suggests that birds come equipped with some prior knowledge of the song they are expected to learn. This knowledge may include a species-specific song type or a basic framework for their song. The learning process under this model involves modifying and fine-tuning this pre-existing template to align with the desired song type. The third model, Marler’s “Memorisation by instruction followed by selection in production” offers a nuanced perspective by highlighting the temporal dynamics of song learning. It suggests that there are specific phases during a bird’s development when learning is most effective. These sensitive periods are characterised by the interplay of innate and learned components in song acquisition, reflecting a balance between the rigidity of templates and the flexibility of learning.

Vocal production learning is “the ability to modify the structure of vocalisations as a result of hearing those of conspecifics or sometimes other species, either live or from a recording” (Janik, 2000). Vocal production learning has been studied extensively in birds and is evident in all species of songbirds (oscines) studied so far, alongside some patchy distribution in other bird orders such as hummingbirds (Apodiformes) and parrots (Psittaciformes). The evidence in mammals is sparser with examples in humans, bats, cetaceans, pinnipeds and nonhuman apes with a few instances of species in other orders such as naked mole-rats, pygmy goats and common house mice (Janik & Knörnschild, 2021).

However, all vocal production learning is not made equal. Rather than using a binary label to document a species as a vocal learner or not, vocal production learning has been argued to exist on a continuum, on which an ascension in vocal learning capability is accompanied by increasing cognitive demands (Arriaga & Jarvis, 2013; Janik & Knörnschild, 2021). The ‘continuum hypothesis’ ranks species by their capability from vocal non-learners, through limited and moderate vocal learners to complex vocal learners. This spectrum view was adopted in the most recent revision of Janik and Slater’s original 1997 definition of vocal production learning (Janik & Knörnschild, 2021). The field has opened up to a broader range of species with a variety of capabilities to enable more fruitful comparative studies into the mechanisms that enable learned vocal modification. On the lower end of this continuum a species may exhibit vocal convergence in which innate acoustic signals of individuals that interact more frequently produce calls that are more similar to each other over time (Janik & Knörnschild, 2021). Moderate vocal learning can be exemplified by the ability to acquire novel species-specific call types (or song types). Complex vocal learning is defined by Tyack (2020) as “the need to hear a sound to form a learned auditory template before the animal can form a vocalisation that matches the template”.

Tyack (2020) distinguishes between two forms of vocal production learning that he calls ‘limited vocal learning’ and ‘complex vocal learning’ where the former may involve fine-tuning an inherited motor pattern and the latter involves matching a learned template. Tyack (2020) distinguishes between two forms of vocal production learning (from now on vocal learning). There are several limited forms of vocal learning that have been found to be widespread in the animal kingdom. Tyack (2020) defines limited vocal learning as “limited vocal learning as the ability to fine-tune acoustic features of species-specific vocalisations that can develop in the absence of auditory input because innate motor programmes can generate the species-specific pattern.”. On the other hand, complex vocal learning is much less widespread and is reliant on matching a learned template and is defined by “by the need to hear a sound to form a learned auditory template before the animal can develop a vocalisation that matches the template”. Tyack (2020) asserts that there is a need to distinguish between limited and complex vocal production learning because limited vocal learning has a broad taxonomic distribution while complex vocal learning has only been detected in songbirds and humans so far. Tyack (2020) asserts that limited and complex vocal learning are underpinned by different neural pathways in the brain.

In captivity, experiments by Abraham *et al*., (2018) have shown evidence of vocal imitation of novel conspecific and human speech sounds in killer whales (*Orcinus orca*). In the wild, some of the most convincing evidence for vocal production learning in cetaceans comes from the analysis of two call types shared across different pods of killer whales (*Orca orcinus*) and. In this study one shared call type was found to change structure over a 12-year period in both pods in a similar way, while another call type did not change (Deecke *et al*., 2000). These parallel gradual changes in this call type were evaluated to be due to vocal production learning between members of different pods (Janik & Knörnschild, 2021). Janik and Knornschild (2021) compare this evidence in wild killer whales to the observations of humpback whale song evolution in the Northern hemisphere and propose humpback song as an example of vocal production learning. For these reasons, Tyack (2020) also postulated humpback whale song evolution as an example of complex vocal learning.

It is important to understand whether humpback whale song units (a unit being the smallest continuous sound to the human ear) are derived from an innate universal repertoire or whether each unit is subject to complex vocal learning (as defined by Tyack 2020). While ultimately, we still don't know the answer, there are two main suggestions about how humpback whales come to produce their song units. One is the hypothesis that I term the Vocal Learning Hypothesis in which the units themselves are learned as well as the song sequence. The authors advocating the Vocal Learning Hypothesis point out that song units are known to be highly variable, and evolve over time, which if correct would place song unit learning into the category of complex vocal production learning (Janik & Knörnschild, 2021; Tyack, 2020). For a wide variety of sound types to change in unison or for a new song type to be learned from another population, it is thought that this must be further evidence of vocal production learning in humpback whales (Janik and Knornschild, 2021; Tyack, 2020). Tyack (2020) went so far to assert "if not complex vocal learning, how else would such observations arise?".

However, in contrast, some authors assert that humpback whales may have a species typical repertoire of essentially fixed song units at birth and instead that it is the mixing of units unto unique sequences that is the primary focus of learning and song change (Garland, 2020). This brings us to the second hypothesis, the Internal Unit Hypothesis, in which song units are thought to be relatively fixed and innate, and instead it is only the sequences of units that are learned. The hypothesis that I term The Internal Unit Hypothesis asserts there to be a genetically inherited species-specific worldwide repertoire and it is therefore the arrangement of these units into themes (or phrases/sequences) that are evolving, and learned (Garland & McGregor, 2020). In contrast to vocal production learning then, this view posits that the primary form of learning underlying humpback song is sequence learning (to develop complex displays). Researchers supporting the Internal Unit Hypothesis agree that there may be a worldwide song unit repertoire and therefore the possibility of a finite number of song unit types (Cerchio *et al*., 2001; Garland & McGregor, 2020). The Internal Unit Hypothesis would imply an innate template for each unit and would be supported if isolated populations were found to produce repertoires of song units that are similar to those of other populations they are not in acoustic contact with.

The Internal Unit Hypothesis is also supported by Cerchio *et al*'s (2000) study in which 44 variables (spanning the song hierarchy) were measured in humpback songs recorded in Hawaii and Mexico. Cerchio *et al*., (2000) found that 21 variables changed significantly over a 12-week period in which the structure of units and phrases changed synchronously in each area with no interaction of region. They proposed that, rather than cultural transmission, the gradual change of sound features may be due to rules derived from an innate template. This idea is further reiterated by a study from Mercado and Perazio (2021) in which they argue that acoustically isolated humpback populations (recorded in different locations and separated by decades) produced songs in 'acoustically comparable cycles' which they suggest may be due to universal production templates. However, when this study is closely explored it seems the results depend on visual appraisal of particular subsets of the datasets. Furthermore, it is difficult to follow Mercado and Perazio's argument that leads them to their conclusion that song evolution is not due to cultural transmission.

Garland & MacGregor (2020) state that "it is the arrangement and rearrangement of units into distinct, stereotyped patterns that is the major focus of humpback whale song research" rather than the evolution of units themselves. Garland *et al*., (2017) suggested that humpback whale songs are learned in segments and there is a "switch when similar rule" at both the unit and phrase level such that new phrases are switched with the most similar existing phrase when a song replacement occurs. Furthermore, some song units have also been observed outside of the song display in social interactions (Dunlop *et al*., 2007). In support of the idea that at least some sound units could be largely innate, social sounds of humpbacks have been found to be highly stable over decades within the South east Alaskan feeding ground (Fournet *et al*., 2018) and this opens the question whether the song units derived from social calls are also highly stable. Therefore, there may be important connections between song unit repertoires and social call repertoires that are yet to be investigated.

Humpback whale song is commonly cited as an example of complex vocal learning (the need to hear a sound to form a learned auditory template before the animal can form a vocalisation that matches the template) and it is important that species are chosen carefully for comparative studies (Janik & Knörnschild, 2021). However, there seems to be ambiguity in the literature at what level of the humpback whale song hierarchy is subject to vocal learning. Humpback whale acoustic research is performed by passively recording songs and analysing changes over time. It is not possible or ethical to record songs in an experimental setting. Therefore, to indirectly investigate how humpback whale song units may be stored in the brain this study aims to utilise particular instances of song units that are displayed in more than one theme type within the same song. This study aims to further our understanding through a unit level analysis in which a unit is tracked across different theme types within a particular population's song, in this case the population that breeds around the Cook Islands in the South Pacific Ocean. My analysis approach takes influence from Deeke *et al*., (2000)'s study of killer whale vocalisations. Deeke *et al*. (2000) followed the evolution of a shared call type in different matrilines to determine acoustic contact. Similarly, this study will track one unit type across different theme types to elucidate whether units are derived from the same or different templates. This study has instead taken a shared unit type (call type) between different phrase types (matrilines in Deeke *et al.*) to assess whether the unit type could be stored as one template but used in different phrase types. Concurrent change but with no overall divergence between unit types in separate themes would be compelling evidence for a unit that is stored as a single template.

In this chapter, I will examine the first hypothesis, which proposes that song units change in independent directions, "The Vocal Production Learning" Hypothesis. This hypothesis aligns most closely with Marler's sensorimotor model which suggests that there is no a priori knowledge of a predefined template, and song learning involves a high degree of flexibility and adaptability. The second hypothesis, the "Internal Template Model" focusing on the parallel changes in song units across different themes, is akin to Marler's Learning based on selection model. It suggests that birds possess knowledge of a template, which is modifiable, allowing them to make coordinated changes in their songs. This hypothesis implies that there is some pre-existing structure that guides song learning.

If humpback whales are selecting song units from a species-wide repertoire, and each unit type was a discrete memory item, then we would expect the same units to evolve in the same way, regardless of what theme in the song it is displayed in, or indeed not evolve at all. On the other hand, if a humpback is learning each sound at the level of the phrase type (repeated in each theme), then we may expect units to evolve differently, and as such the unit may appear similar but is actually drawn from a different acoustic representations or templates in the brain. We could then presume the units to be produced from new learned templates to which the individual matches their own acoustic signal.

Here I track the evolution of a unit type within one song type to help elucidate how humpback song units may be learned and thus illuminate whether humpback song units are selected from an innate template of units (supporting the Internal Unit Hypothesis) or alternatively whether they are learned individually and separately within separate theme types (supporting the Vocal Production Hypothesis).

Furthermore, I investigate whether other potential factors may be contributing to changes in unit structure over time. Firstly, I determine whether Signal to Noise ratio has any discernible impact on the robust measurements obtained Iskarous *et al*. (2013). Secondly, coarticulation of unit types is explored (d'Alessandro & Fougeron, 2021). Coarticulation in the context of bioacoustics refers to the phenomenon where the acoustic properties or characteristics of one sound unit, such as a vocalisation or signal, are influenced by the characteristics of the preceding or following sound unit (James *et al*., 2020). It suggests that there is a dynamic interaction between successive acoustic elements, potentially affecting their properties, such as frequency, duration, or amplitude. Secondly, I investigate potential coarticulation between unit types. Lastly, exhaustion in repeated signals was investigated. In the field of bioacoustics, exhaustion refers to a phenomenon where animals, particularly during extended periods of vocalisation or communication, may experience a decline in the quality, intensity, or characteristics of their acoustic signals. This decline is often associated with physical fatigue or limitations in the animal's physiological capacity to maintain consistent vocalisations. Humpback whale songs serve as a compelling example of this, as they are characterised by their repetitiveness and complexity.

3.2 Methodology

3.2.1 Data collection

Acoustic recordings of humpback whale songs were made off Rarotonga in the Cook Islands (GPS: S21’ 12.357 W159’ 44.602) during the Austral winter and humpback breeding season (deployed 05/08/19 and retrieved 13/10/19) (Figure 3.1 and 3.2). The recordings were made using a bottom moored autonomous acoustic recorder (Ocean Instruments SoundTrap (ST 300, STD). The SoundTrap was set to a duty cycle to record for thirty minutes in every two hours over the duration of the deployment, at a sampling rate of 24 kHz. All recordings were audited manually (visually, using Raven Pro, and aurally scanning the data for signs of humpback whale song presence). Positive humpback whale song recordings were categorised on a four-point quality scale based on signal to noise ratio (a representative sample from each quality scale is included in Appendix 3.1). High quality recordings (assigned ‘GOOD’ or ‘BEST’ quality) were those recordings that clearly showed all frequencies of each unit of the song above any background noise. GOOD and BEST quality recordings enabled transcription and measurements to be taken at the unit level to enable fine-scale analysis of units over the season. An overview of the complete methodology can be view in Figure 3.3.

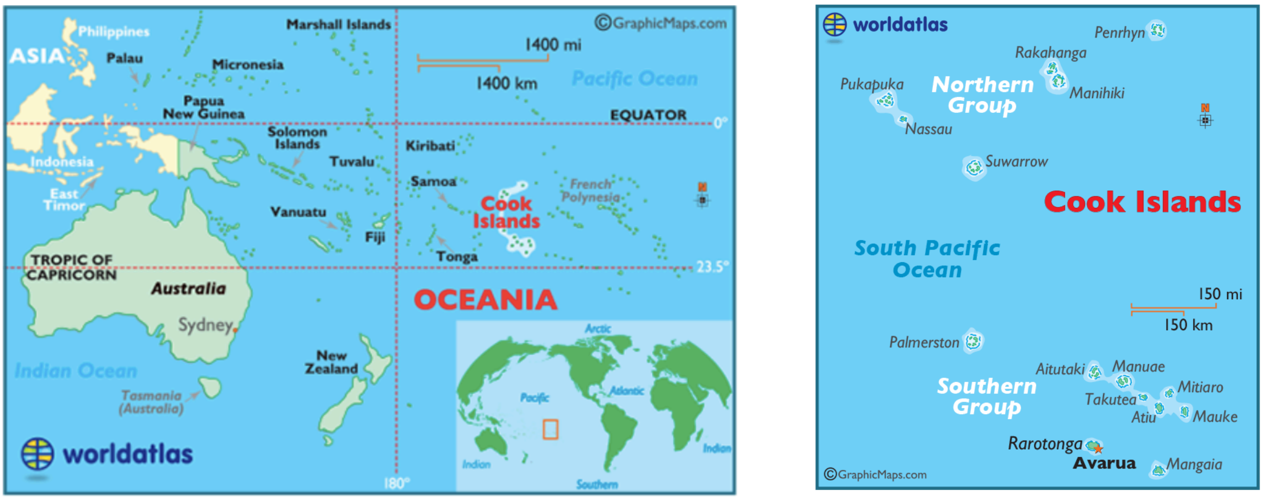


Figure 3.1: a. Location of the Cook Islands in the South Pacific Ocean and b. The Cook Islands showing the Northern and Southern Island groups (Image freely available from WorldAtlas.com)

▲

Figure 3.2: The location of the Soundtrap deployment to the north east of Rarotonga in the Cook Islands at GPS: S21’ 12.357 W159’ 44.602)

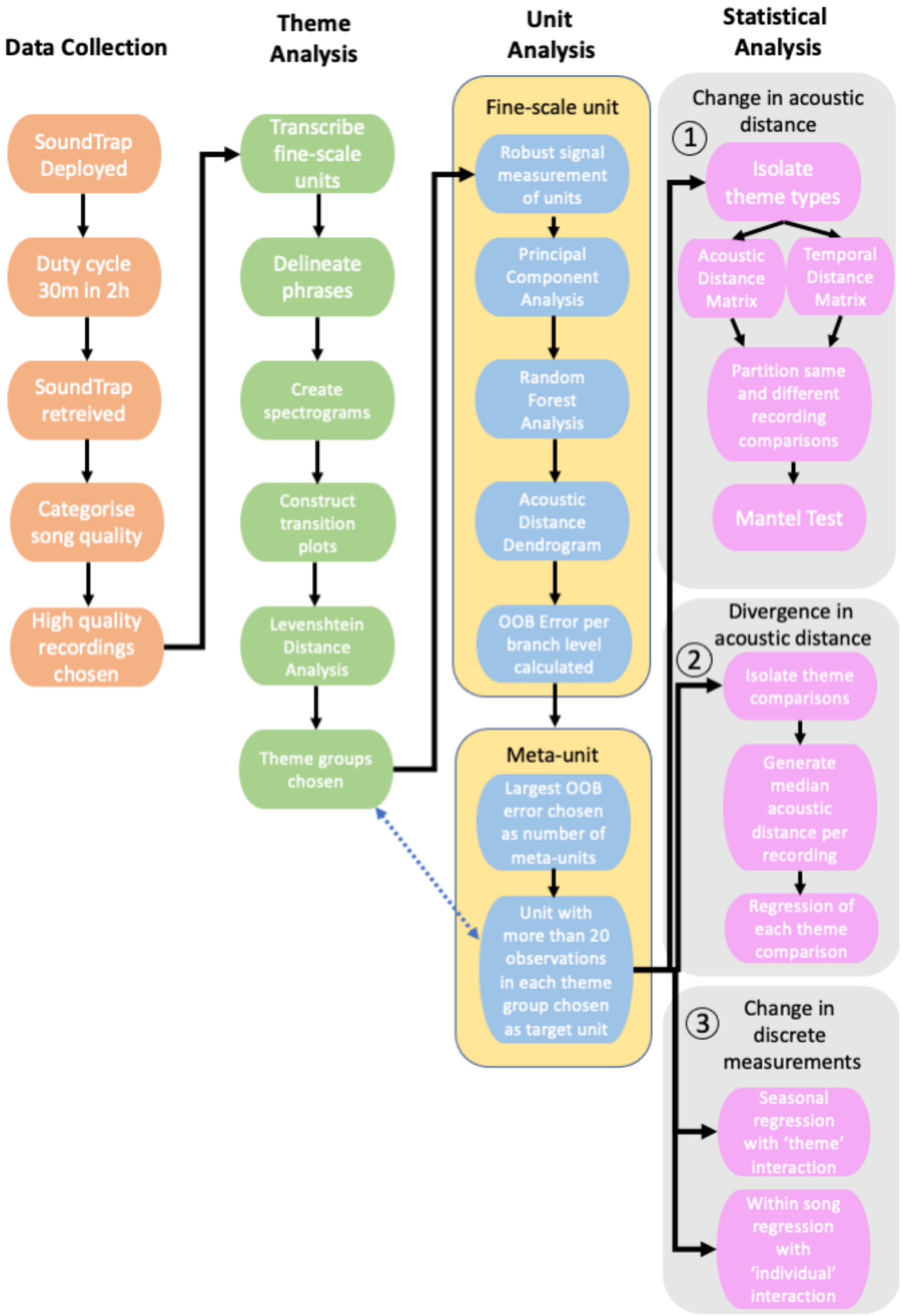


Figure 3.3: Overview of analysis process

3.2.2 Theme level analysis

Spectrograms were viewed in Raven (Version 1.6) and a preset spectrogram view was applied (FFT: 2048, Brightness: 65, Contrast: 63, 512-point hop size) displaying approximately 10 seconds of song from 0 - 5 kHz on a 23-inch screen. Song recordings were transcribed first at the unit level. Each unit (the smallest continuous sound to the human ear) was transcribed (assigned a representative name) by a human classifier based on the visual and aural qualities of the sound following methodology from previous humpback whale song research (Garland *et al.*, 2011; Noad *et al.*, 2000; Payne & Payne, 1983). The unit names were descriptive to allow fast recognition of a unit (e.g. ‘whistle’, ‘groan’) and were based primarily on the peak frequency of the unit, and subsequently on other characteristics such as duration, frequency trend and broadband frequency structure (see Appendix 3.2 for table unit categories). Each unit name was given a shorthand code, for example a moan assigned the code ‘m’, a modulated moan assigned ‘mm’ and so on (See Appendix 3.3 for a complete list of unit names and codes). A unit catalogue was created in which a representative unit of each type was added to a PowerPoint file alongside all other unit types to enable rapid comparison of dozens of units (both visually and acoustically)(Please see this online link). This unit catalogue reduced subjectivity of unit classification during the transcription phase (a protocol for how to create these short acoustic and visual samples is provided in Appendix 3.4).

Phrases were delineated by firstly identifying the longest gap in a series of units and then observing whether the delineated sequence of units between these longer gaps was repeated in such a way that ‘hanging units’ at the end of a theme were minimised. ‘Hanging units’ are units that do not fit into a repetitive phrase sequence and are therefore conspicuously left over after multiple phrase renditions (Cholewiak *et al.*, 2013). The gap between units is generally found to be regular within a phrase and longer between phrases (Garland *et al.*, 2017). Clear patterns of units were identified from the song spectrogram and each pattern was allocated to a phrase type.

Small changes to a phrase sequence, for example the substitution of one unit for another unit, created similar phrase types within a theme. These similar phrase types were denoted as a ‘b’ version of the original phrase type, for example phrase 1a and phrase 1b are very similar (e.g. phrase 1a was lb lb cr lb cr ls(p) while phrase 1b was lb lb lb ls(p)). A transitional phrase was defined as a phrase which takes the start of the preceding and end of the following theme. A transitional phrase is typically produced when the individual is moving to their next theme in a song (Payne, 1985). Transitional phrases were removed from further analysis for consistency with existing literature (Garland *et al*., 2011; Garland *et al*., 2013; Garland, Rendell, Lilley, *et al*., 2017; Noad *et al*., 2000). Spectrograms of each theme (including 'b' themes) were created in R using the 'warbleR' package (FFT = 2048, Hop Length = 75).

The order of themes was plotted using transition plots in which all theme types (including b themes) were visualised in a cycle (see e.g. Figure 4 in Cholewiak *et al*., 2012). Transition plots visualise song structure and performance consistency within and between individuals. A transition plot was created for each recording and only complete song cycles were included to construct the transition plots.

All phrases identified by a human observer were then entered into a Levenshtein distance analysis (LDA) to verify the relationship of phrase and theme categorisation described above. The LD (or string edit distance) is a metric for comparing humpback whale song sequences which has been used in previous research to understand song similarity at different levels within the song hierarchy (Garland *et al*., 2015). The Levenshtein distance (LD) is a similarity measurement that calculates the minimum number of insertions (i), deletions (d), and substitutions (s) needed to transform one string of data into another. Humpback songs and phrases often have different string lengths therefore the LD is divided by the maximum string length and then subtracted from 1 to normalise the LD in creation of the Levenshtein Similarity Index (LSI) (Equation 3.1).

$$LSI(a,b) = 1 - \frac{LD(a,b)}{\max\,[length(a), lengthL(b)]} \qquad \text{Equation 3.1}$$

Here a string was a typical sequence of units (i.e. a phrase). I created a representative phrase string (called the set median string) across all of the recordings. The median string is the string with the smallest distance from all others in the set. Levenshtein distance analyses were carried out in R Studio (Version 1.4.1106) using the 'leven' package (Garland and Lilley, 2015). The resulting pairwise similarity coefficients were then visualised as dendrograms constructed using hierarchical cluster analysis. Each cluster of phrase types in these dendrograms was reduced to one theme type and then labelled with a colour name for ease of reference. These broadly inclusive theme types allowed us to track evolution of units across the season because theme phrase sequences may also evolve over the season (e.g. 1a evolving into 1b and so on). As a further test of how well each dendrogram represented the data, the Cophenetic Correlation Coefficient (CCC) was also calculated. A CCC score of over 0.8 is considered a good representation of the groups present within original the data. Dendrograms were subjected to bootstrapping to assess the robustness of identified themes, aligning with established methodologies from prior humpback whale song research (Garland *et al*., 2015).

3.2.3 Unit level analysis

The sample rate of 24kHz and FFT size of 2048 meant that each frequency bin encompassed 11 Hz, setting the upper limit of frequency resolution. Robust signal measurements were generated from manual box selections around song units (for harmonic tonal sounds, around the fundamental frequency component) using Raven Pro (v1.6.1) (see Table 3.1 for a complete list of the robust measurements used). Here the term 'robust' refers to energy-based rather than selection-based measurements. Unlike selection-based measurements, which rely entirely on the time and frequency endpoints of the selection as manually entered, robust measurements are based on energy sums in the time or frequency domain over the selection so therefore small changes in the borders of the selection rectangle should have little effect on the computed measurement values (Charif, Strickman and Waack, 2010). Due to the analysis focusing on the fine-scale evolution of units over time, it was important that measurements were repeatable and robust, and included the complete dataset, rather than only measuring a subset which has been the standard practice for previous broadscale humpback song research (Noad *et al*., 2000; Garland *et al*., 2011; Garland *et al*., 2017). I made a number of methodological efficiencies over previous measurements in earlier humpback whale song research - partly informed by them doing that work – which enabled measurements to be taken of my complete dataset rather than taking only a sub-sample of the highest quality units. For context, in previous humpback song research the start and end frequencies of units are usually taken by careful point measurements through placing the cursor onto what is perceived to be the beginning of the unit as implied by the signal to noise ratio of the call. This is time-consuming and could be open to observer error. Similarly, the duration of each unit is commonly measured by carefully applying the selection box to each unit so that the start and end of the selection box matches with the perceived start and end of the unit as implied by the SNR. Again, this can be time consuming and open to observer bias. To avoid the above problems, a robust measurement (Dur90) was used in place of duration as defined by the placement of the box selection. Start and End frequencies were calculated using custom MATLAB code. Start Frequency utilised the robust measurement 'Time 5%' (the point in time that divides the selection into two time intervals containing 5% and 95% of the energy in the selection). The first 5% of the energy of the selection was assigned to one clip and then a power spectrum of that section of the selection was estimated using custom MATLAB code, from which peak frequency was located (see Figure 3.4). This technique was also used to estimate the end frequency (utilising the time at which 95% of the energy in the selection window was cumulatively obtained through to the end of the selection). The Start Frequency was the peak frequency between 'Begin Time' (as defined by the start of the selection box) to the robust measurement 'Time 5%' (the point in time that divides the selection into two time intervals containing 5% and 95% of the energy in the selection). The End Frequency was the peak frequency between Time 95% (the point in time that divides the selection into two separate time intervals containing 95% and 5% of the energy in the selection) and 'End Time' (as defined by the end of the selection box) (The custom MATLAB code to produce start and end frequency automatically is available at this link: https://figshare.com/s/f65314c391b6769311ae). A subset of units was subjected to measurements using both the manual traditional method and the new method, allowing for a comparison to assess the consistency between the two approaches (Figure 3.5).

Table 3.1: Measurements made on each song unit (including description of each measurement)

ABBREVIATIONS OF DESCRIPTORS	MEASUREMENT TYPE	DESCRIPTORS	UNITS
PEAK FREQ	Based on spectrogram values as computed by the Power Spectral Density	The frequency at which Max Power/ Peak Power occurs within the selection. If Max Power/ Peak Power occurs at more than one time and/or frequency, the lowest frequency at Max Time at which Max Power/ Peak Power occurs.	Hz
FREQ 5%	Robust signal measurement	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection. The computation of this measurement is similar to that of Center Frequency, except that the summed energy has to exceed 5% of the total energy instead of 50%.	Hz
FREQ 95%	Robust signal measurement	The frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection. The computation of this measurement is similar to that of Center Frequency, except that the summed energy has to exceed 95% of the total energy instead of 50%.	Hz
BW 90%	Robust signal measurement	The difference between the 5% and 95% frequencies	Hz
DUR 90%	Robust signal measurement	The difference between the 5% and 95% times.	s
TIME 5%	Robust signal measurement	The point in time that divides the selection into two time intervals containing 5% and 95% of the energy in the selection. The computation of this measurement is similar to that of Center Time, except that the summed energy has to exceed 5% of the total energy instead of 50%	s
TIME 95%	Robust signal measurement	The point in time that divides the selection into two time intervals containing 95% and 5% of the energy in the selection. The computation of this measurement is similar to that of Center Time, except that the summed energy has to exceed 95% of the total energy instead of 50%	s
START FREQ	Computed from Raven Robust measurements using custom MATLAB code (https://figshare.com/s/f65314c391b6769311ae)	The peak frequency in the first 5% energy of the unit.	Hz

END FREQ	Computed from Raven Robust measurements using custom MATLAB code (https://figshare.com/s/f65314c391b6769311ae	The peak frequency in the last 5% energy of the unit.	Hz
FREQ TREND	Derived from automatic measurements described above	Start Freq divided by End Freq A value >1 indicates that the sound decreases in frequency and a value <1 indicates the sound increases in frequency from the start to the end of the sound.	Hz/Hz

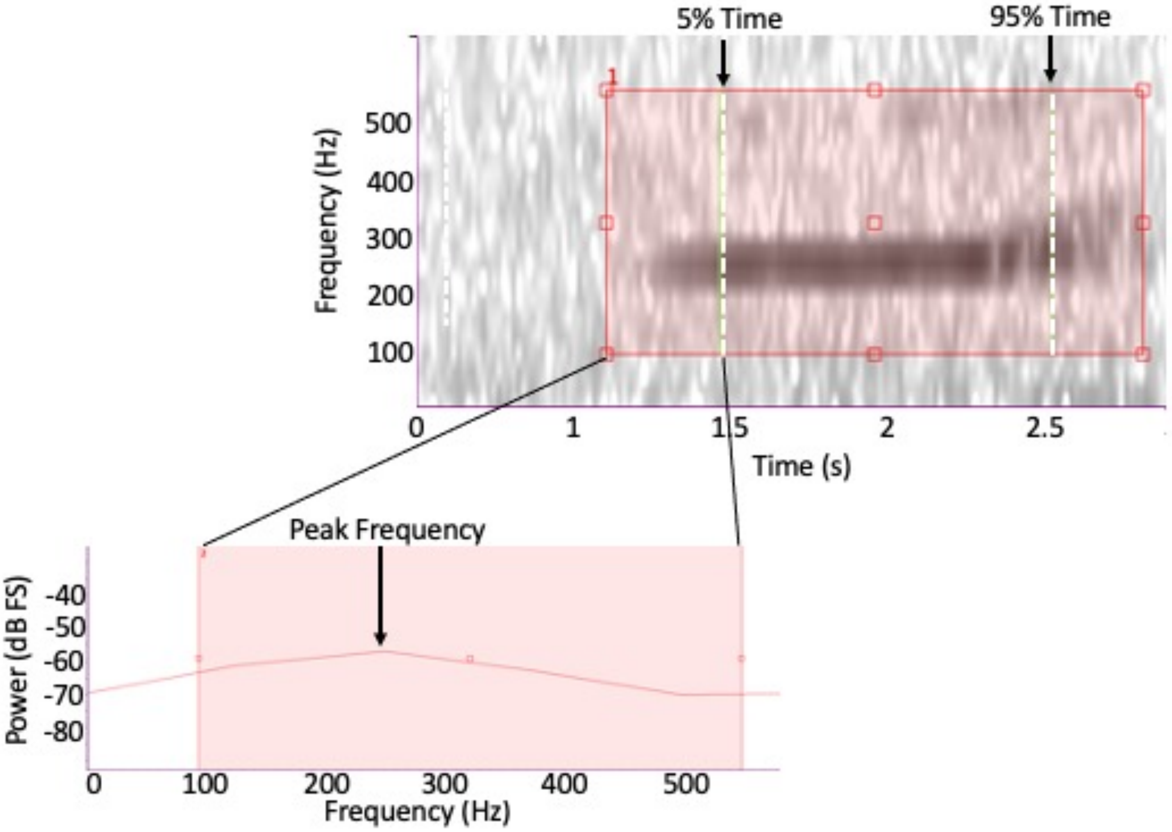


Figure 3.4: Start Frequency utilised the robust measurement 'Time 5%' (the point in time that divides the selection into two time intervals containing 5% and 95% of the energy in the selection). The first 5% of the energy of the selection was assigned to one clip and then a power spectrum of that section of the selection was estimated using custom MATLAB code, from which peak frequency was located.

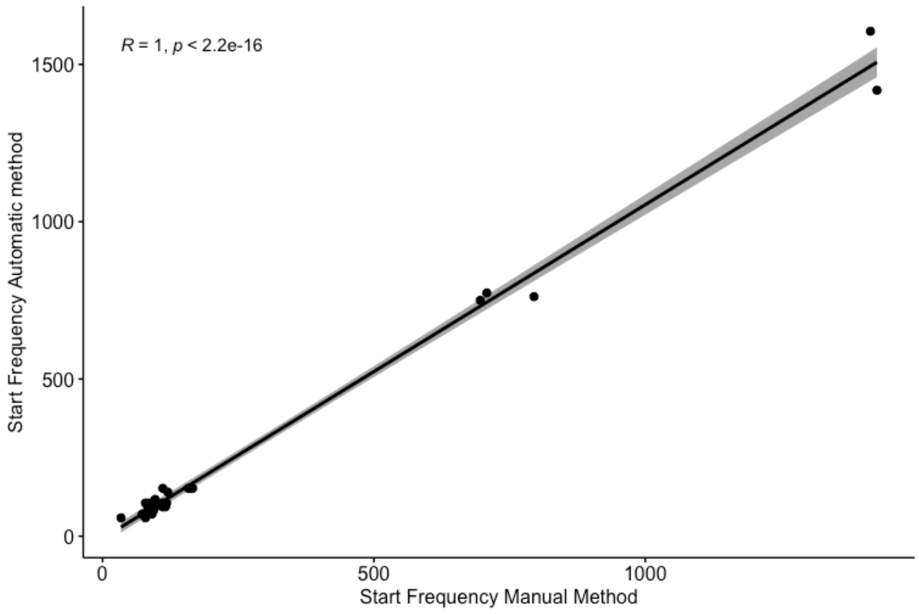


Figure 3.5. Correlation test of standard and automatic Start Frequency measurements. A Pearson correlation coefficient was computed to assess the linear relationship between the manual method and automatic method of obtaining the Start Frequency. The methods were highly correlated, R(28) = 1, p < 0.001).

The mean, median and standard deviation of each measurement for each unit type was calculated. In order to test if the measurements taken in Raven Pro 1.3 could explain the human classification of units, a principal component analysis (PCA) was conducted. A heat map of variable importance was also computed to examine the relative importance of each measurement type to the delineation of each unit type. Heat maps provide a means to concurrently visualise groupings of samples (i.e. unit types) and features (i.e. measurement types). Initially, a hierarchical clustering analysis is performed on both the rows and columns of the data matrix. Subsequently, the columns or rows of the data matrix are rearranged based on the outcomes of the hierarchical clustering, which positions similar observations in close proximity. This reordering places blocks of "high" and "low" values in close proximity within the data matrix. To facilitate visualisation, a colour scheme is applied, and the resulting data matrix is presented. By employing this visualization technique, it becomes possible to identify variables that exhibit distinct characteristics for each sample cluster.

All units were input to a random forest analysis to check consistency of the qualitative classification, following previous research that has utilised random forest analysis to determine the robustness of their unit categories (Garland et al., 2017; Tolkova et al., 2017; Fournet et al., 2018). A random forest consists of a large number of decision trees across which the outcome with the most votes becomes the model's prediction. The random forest analysis was set to 500 trees initially as a large number of trees enables more reliable estimates of out-of-bag (OOB) error. The OOB error is a measure of accuracy of the model derived from testing a sample of data that was not used to the train the model (termed OOB) on the model itself. The number of trees (ntree) and number of variables considered at each split (mtry) was varied to find the best fit as determined by the lowest OOB error.

The analysis aimed to track unit types that occurred in different theme contexts to test the hypothesis of whether or not units evolved differently in different theme contexts. The original transcription of the song data created a fine-scale unit library. Unfortunately, this fine-scale unit library meant that if a unit type evolved into other 'types' during any song change then this unit evolution couldn't be tracked within a continuous measurement series. To avoid missing this potentially significant unit evolution unit types were recombined into larger unit categories, for example, "short" and "long" modulated moans were combined into "modulated moans". To achieve this quantitively values for each measurement of each unit type were calculated. All mean measurements were standardised and then the Euclidean distance was calculated between each fine-scale unit type. Utilising the 'hclust' package in R, the Euclidean distances were then clustered via both the average-linkage method and Ward2 method to create comparative dendrograms. These dendrograms allowed us to view each fine-scale unit type as an end-node. The two linkage methods (Average and Ward2) were compared by calculating the cophenetic correlation coefficient (CCC) to determine the best fit with the original Euclidean distances. The linkage method with the highest CCC and therefore the best fit with the original Euclidean distances was chosen to perform the rest of the analysis.

This dendrogram was then cut into successively smaller number of groups (such that the number of fine-scale units per group increased) as determined by the branches within the dendrogram. As the number of groups decreased the number of fine-scale units within each group increased so that the total number of fine-scale units was held constant. For example, if the if the total number of fine-scale units was 45 we therefore began with 45 'branches' and then the next step was to combine the most similar two branches, as defined by their placement on the dendrogram, so that we then had 44 branches. The next step was then to combine the next most similar two branches so that we had 43 branches. This process was repeated until there remained only one branch containing the complete 45 unit types.

Random forest models were created for each number of branches. The random forest model with the lowest error rate was 18.3% (ntree 600, mtry = 4) was applied in a loop to an average-linkage dendrogram of the 45 units. The out of bag error (OOB error) for each iteration was plotted. Conspicuous jumps in OOB error indicated that the number of fine-scale units being allocated to the wrong group significantly increased at this point. The number of branches present before each large jump was investigated through examining the dendrograms with this number of branches. For example, if there was a large jump in OOB error when the number of groups increased from four to five then a dendrogram with four groups was taken forward. If there was another large jump in OOB error between 16 and 17 groups, then a dendrogram with 10 groups was also examined. I wanted to choose a number of groups which allowed fine-scale units to be brought together to allow their evolution to be tracked across the season but that also did not lump very different units together. I sought a balance between neither being too lumpy nor too splitty and used my knowledge of each fine-scale unit type and the fine-scale unit catalogue to make this judgement.

When the number of groups was chosen, the number of observations within each group was counted across theme type and recording. Units with more than 100 observations in each theme type were considered for further analysis. Fine-scale units outside of the chosen group that were obviously derived from any of the fine-scale units in the chosen group were added to this group too. This judgement was made based on examination of cluster plots, which showed that fine-scale units that had been placed on a different branch due to a change in length or modulation were close in acoustic space (see Appendix 3.10). For example, if an “ascending modulated moan” was within the target group then the "long ascending modulated moan” fine-scale unit type was also added to the group. Again, this was to encapsulate any song evolution that may occur. This process created a final group of multiple fine-scale units termed a ‘meta-unit’ which was named the ‘Groan’ unit.

3.2.4 Alternative Hypotheses: SNR, Coarticulation and Exhaustion

To further explore potential factors contributing to changes in the units over the duration of season three recordings that might affect the measures I am using to characterise units, I conducted additional analyses. My objective was to investigate whether the Signal to Noise ratio (SNR) of the acoustic files had any discernible impact on the start and end frequencies obtained through the custom MATLAB code, as well as whether the robust measurement 'Duration90' was influenced by SNR. In this analysis, I employed the 'SNRNISTQuick' robust measurement in Raven to assess the SNR within each unit selection. For each recording, I calculated the average SNR, average start frequency, average end frequency, and average Duration90 for all classified 'groan’ units. Subsequently, I performed Pearson correlation tests to examine the relationships between SNR and each of these measurements. These additional analyses allowed me to explore potential associations between acoustic file quality (as reflected in SNR) and the characteristics of the groan units.

Coarticulation in the context of bioacoustics occurs when the acoustic properties or characteristics of one sound unit, such as a vocalisation or signal, are influenced by the characteristics of the preceding or following sound unit. To explore the potential coarticulation between the peak frequency of the groan unit and that of the preceding unit, I conducted a linear regression analysis. In this analysis, I employed a linear model where the response variable was Peak frequency of focal unit and the explanatory variable was peak frequency of the preceding unit and the model included an interaction term of preceding unit type. To ensure the robustness of my findings, preceding unit types with limited observations (fewer than 50 instances) were excluded from the analysis.

Lastly, exhaustion in repeated signals was investigated within one theme type. In the field of bioacoustics, exhaustion is where animals, particularly during extended periods of vocalisation or communication, may experience a decline in the quality, intensity, or characteristics of their acoustic signals. To investigate the potential occurrence of exhaustion in humpback whale song displays, I focused on a distinct theme type within the songs and isolated the groan unit for analysis. To assess the presence of exhaustion, I examined the variations in peak frequency within this unit over the course of the song. For each recording, I calculated the average peak frequency over the first rendition of groan units appearing within the selected theme type, as well as the average peak frequency for the last rendition. Additionally, I determined the population's overall average peak frequency. To gauge the magnitude of change in peak frequency, I computed the absolute differences between the peak frequency of the first rendition and the overall population average, as well as between the peak frequency of the last rendition and the overall population average for each recording. To statistically evaluate whether there was a significant change in peak frequency from the first to the last rendition and whether this change was moving towards the population average, I conducted a t-test on these calculated differences. If exhaustion were happening, I would expect the t-test to convey a significant change in peak frequency from the first to last rendition. This analysis allowed me to explore potential evidence of exhaustion within the humpback whale song display.

3.2.5 Statistical Analysis of Unit Change over Time

Each theme type was isolated from the dataset and firstly an acoustic distance matrix was generated across all recordings in which element i,j for each theme type is the acoustic distance between unit observations i and j. The acoustic distance was calculated using Euclidean distance utilising the following eight measurements: “PEAK FREQ” “FREQ 5%", "FREQ 95%”, “BW 90%”, "DUR 90%”, “TIME 5%”, “TIME 95%”, “START FREQ”, “END FREQ”, “FREQ TREND”. Secondly, a temporal distance matrix was created in which element i,j was the time difference between the occurrence of units i and j (in seconds), measured from the 5% point on the cumulative energy of the unit. For each theme the data were partitioned into those comparisons that were within the same recording and those comparisons across different recordings, which allowed analysis of variation both within and between individuals. Different recordings were likely to be from different individuals due to a sampling strategy which chose recordings with at least 48 hours between them. This is in line with previous published research (Garland *et al*., 2017; Lamoni *et al*., 2023) which assumes that humpback whale individuals are unlikely to stay close enough to a recorder to collect good quality song over two days. As a result of this, different song bouts or recordings separated by at least 48 hours will be referred to as the songs of different individuals in the remainder of this thesis.

In the domain of humpback whale song research, the prevailing view posits that individuals within populations are intricately interconnected, creating a unified network where individual whales influence one another, leading to the development of a communal song that maintains conformity throughout the season (Garland *et al*., 2017). This perspective implies that treating different song recordings as distinct individuals enables the exclusion of social network or temporal associations as causes for song similarity. Individuals within the breeding population display transient behaviours, constantly moving and entering or departing at varying times (Derville *et al*., 2019; Schall *et al*., 2022). Consequently, the likelihood of a robust spatial or temporal network between singing male humpback whales is reduced within a breeding population. This notion is substantiated by the findings of Darling *et al*. (2022), whose research demonstrates high mobility among individuals, exemplified by their attendance at both Mexican and Hawaiian breeding grounds within the same winter season.

A symmetrical matrix was required for input into a Mantel test. A Mantel test was chosen to analyse for change of acoustic structure over time because this test allows input of distances in time and space (here defined as acoustic space). A Mantel test is a statistical test of the correlation between two matrices. Mantel 'R' values can fall within a range between -1 to 1. A Mantel R value of -1 suggests a strong negative correlation, 0 suggests no relationship at all and 1 suggests a strong positive relationship. In this case the first matrix was the matrix of Euclidean acoustic distances between all possible unit pairs in the study. The second matrix was the temporal distances between all possible unit pairs in the study. To generate a symmetrical matrix of the partitioned observations partitioned datasets required to be a length equal to a triangle number to fulfil the conditions of R function 'symMat' in which a symmetrical matrix is a square matrix that is equal to its transpose i.e. a symmetric matrix has symmetry along its diagonal such that m[row][col] always equals m[col] for all cells of the matrix to be occupied a triangle number must be utilised. A triangular number T_n is a figurative number that can be represented in the form of an equilateral triangular grid of elements such that every subsequent row contains an element more than the previous one (Weistein, 2002). To achieve this, the closest triangle number below the number of observations within each vector was identified and a random sample equal to this triangle number was derived from the vector. To check for any effect of sampling error on the mantel output a random sample was applied 10,000 times to each partitioned dataset. The frequencies of observations were plotted and checked for normal distribution and no sampling effect was found for any of the randomly sampled vectors. A Mantel test, from the R Package 'vegan' based on Pearson's product-moment correlation with 999 permutations was applied to each dataset using R code "mantel(acousticMATRIX, timeMATRIX, method= "pearson", permutations=999)". The Mantel test was against the null hypothesis that there was no correlation between unit acoustic similarity and time between recordings - this null hypothesis would mean units were not changing detectably over the sampled period. If units are changing we expect a consistent relationship in which acoustic distance increases with the passage of more time between recordings.

To investigate whether the groan meta-unit (defined above as a group of fine-scale units) changes in different ways in different theme types each comparison between pairs of observations derived from different theme types (either Red – Blue, Blue – Green and Red – Green) were isolated from the dataset. Summary statistics were generated for each theme comparison and the median acoustic distances between each theme pair within each recording were analysed with a linear regression of form "lm(median ~ Time) [see this link for complete R code: https://figshare.com/s/fa4e30b02877d8693e8c].

Table 3.2: Recording and exact time since first recording (in days)

Recording	Days since start of season
2019-08-26 08:12:44	0.0
2019-08-31 14:12:44	5.3
2019-09-02 14:12:44	7.3
2019-09-05 22:12:44	10.6
2019-09-15 06:12:44	20.0

Violin plots of each regression were generated directly from the above models using the R function 'violinplotter' (v3.0.1, Paril, 2022) to visualise the distribution of the data and variation of the mean (acoustic distance between theme types was grouped by time since the start of the season). Under this analysis I expected the coefficient for 'Time' to be significantly different from zero, and further I expected that distance would change at different rates in the three models if similar units were evolving independently in the two themes. If so, I would interpret different rate in change as suggesting that the units used in the different themes, despite being the same unit type, had independent change trajectories over time and were unlikely to be drawn from the same cognitive or neural representation when produced.

Discrete acoustic measurements

A linear regression with interaction of theme type (Orange, Indigo, Violet) was applied to the median in the form of ‘lm(median ~ TimeDays * theme, data = measurement type)’. To test whether units in different theme types were changing in different ways across the season and an interaction term was added. Interaction plots were generated using ‘interact plot’ in the ‘interactions’ package (v1.1.5, Long, 2021). Under this analysis, significant interaction terms would provide an explicit test of different trajectories of acoustic change across different themes, this is arguably more robust than fitting individual models.

To determine how each acoustic measurement type changed within song sessions the robust measurement ‘Time5s’ was standardised from start of each recording. Time5s was converted from seconds to minutes for easy interpretation of output plots. Themes were analysed independently. For the Orange and Indigo themes, recording 27/02/20 was removed due to only one iteration of the orange and indigo themes being captured in this song recording (all other recordings had at least X such iterations). A linear regression with interaction term ‘Recording’ in the following form was applied to each theme type dataset: “lm(MeasurementType ~ Time5__s_ * Recording, data = ThemeType)”. The interaction term allowed testing of whether units in different individuals (recordings) were changing in different ways across their song sessions. Visual inspection of the model of the untransformed data showed that data from some measurement types required some transformation in order to accommodate the large positive residuals and produce a better fit of the model. For each measurement type a model utilising raw values and a model utilising log-transformed values was fitted. The resultant Q-Q plots were inspected and the model with the best residual pattern was selected as the model for that measurement type.

For each measurement type a table of how each individual changed their display of each unit in each theme type (positively, negatively or No Significant Change) was created through examining the interaction term outputs of the regressions for each individual in each theme.

3.3 Results

3.3.1 Data Collection

The SoundTrap successfully made 830 30-minute recordings equating to 415 hours of audio data. 108 (13%) recordings were found to have humpback whale song present. Of thirteen recordings allocated to at least 'GOOD' quality level, six were chosen for fine-scale analysis across the season separated by at least two days to increase the likelihood that each recording was from a separate individual (Table 3.3). The high-quality recordings chosen spanned a time frame from 26/08/19 to 15/09/19 within the total deployment period between 05/08/19 to 13/10/19 and provide a range of times to explore song evolution within the peak singing period within the breeding season. Two songs types were identified in the six recordings, of which one was dominant (present in five recordings). More than one song type has been documented in the same year at the Cook Islands in previous years (e.g. see Garland *et al*., 2011) leading to speculation that this site may be a breeding location and a migratory corridor for individuals returning to other breeding locations. The presence of two distinct song types within a single season provides additional support for the hypothesis that this site may serve as a migratory corridor. However, it is worth noting that only one recording of song type 2 was identified, suggesting that it may be an anomalous occurrence, possibly attributed to an aberrant male. Spectrograms showcasing the themes of the second song type can be found in Appendix 3.5 for further examination. The dominant song (named SONG 1) was chosen for further analysis. An example of this song's theme structure is presented in Figure 1. A transition plot for each recording can be found in Appendix 3.7.

Table 3.3: Recordings chosen for analysis

Recording ID	Date	Length (minutes)	Song Type	Number of song cycles	Themes present (without transitional themes)
2608	26/08/2019	30	1	2	1a, 2a, 2b, 2c, 3a, 3c, 3b,
3108	31/08/2019	30	1	3	1a, 2a, 2b, 3a, 3b, 3c,
0209	02/09/2019	30	1	2	1a, 2a, 2b, 3a, 3b
0509	05/09/2019	30	1	1	1d, 2a, 2b, 3a

0909	09/09/2019	30	2	5	4, 5, 6, 7, 8a, 8b
1509	15/09/2019	30	1	4	1b, 1c, 2a, 2b, 2c, 3b

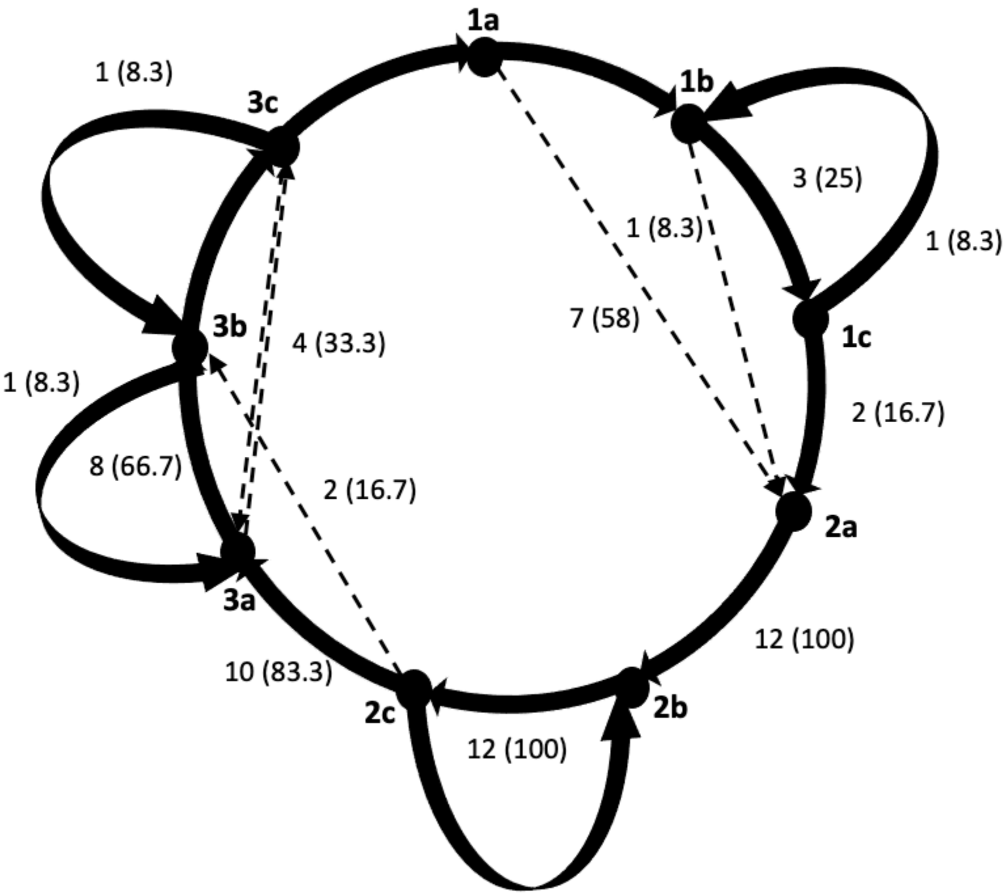


Figure 3.3: Transition diagram for all Song 1 complete song cycles. 12 song cycles present. The first number is the number of cycles in which the transition occurs and the second number is the percentage of the 12 cycles.

3.3.2 Theme analysis: how is Song 1 structured into different theme types?

Song 1 was composed of three core themes, evidenced by the Levenshtein analysis and dendrogram outputs, which supported the qualitative classification of three core themes with 3-4 theme variants within each (Figure 3.3; see Appendix 3.6 for complete spectrograms of the core themes). The theme composition was supported by both the weighted (Figure 3.4) and unweighted (see Appendix 3.8) analyses. All spectrograms of each core theme variant can be viewed in Appendix 3.6. Each core theme type was given a colour name: Red (theme 1a, 1b, 1c, 1d), Blue (theme 3a, 3b, 3c) or Green (theme 2a, 2b, 2c) (see Figure 3.4).

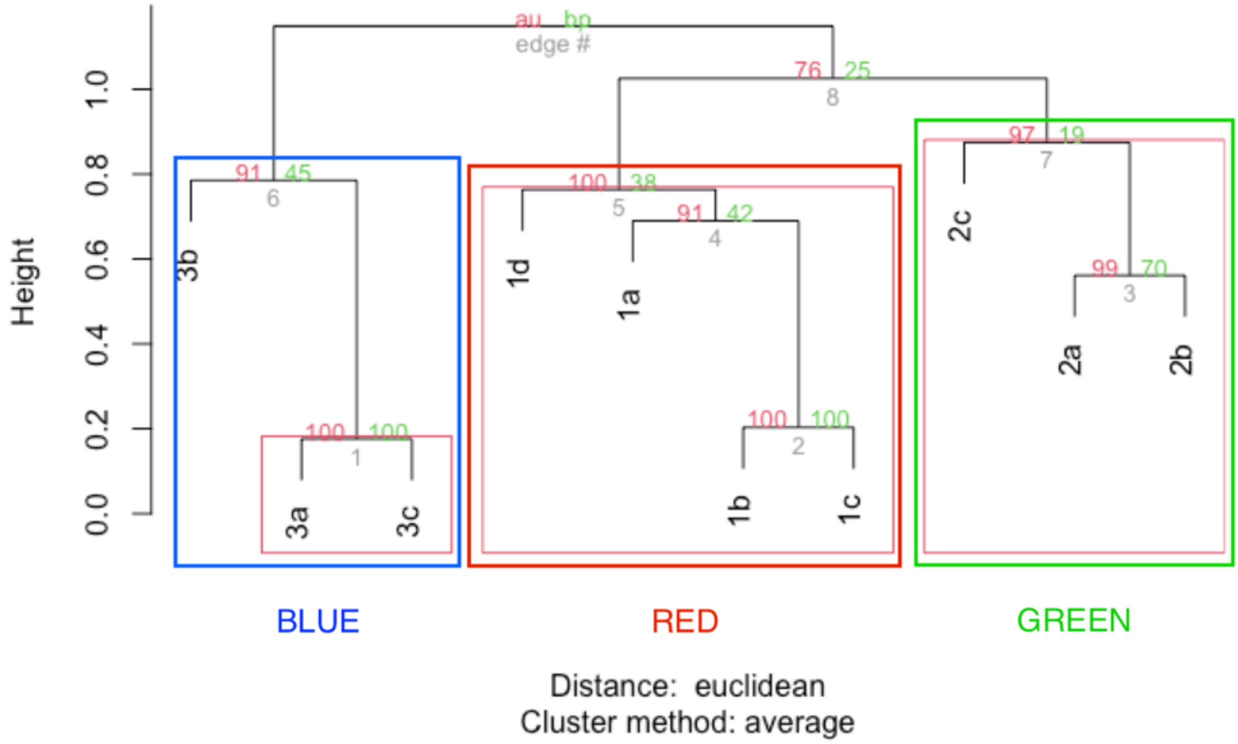


Figure 3.4: Weighted dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Cook Islands 2019 Song 1 (CCC = 0.802). A CCC score of over 0.8 is considered a good representation of the groups present within the data. Branches with high bootstrap values (AU significance P > 95% and bootstrap probability significance P > 70%) are strongly supported by the data, whereas lower values suggest uncertainty in their division.

3.3.3 Unit analysis: What fine-scale and broad-scale unit types are present in Song 1?

Transcription of SONG 1 identified 45 units (Appendix 3.9, 3.10). The random forest models applied to each branch level in the unit dendrogram revealed two clear jumps in out-of-bag error (at 4 and 16 groups) (Figure 3.5). My visual inspection of the groupings revealed that the dendrogram with 16 groups of fine-scale units more realistically represented variation in the unit types (Figure 3.6 and see Appendix 3.10 for a comparison of 4 and 16 groups). Of these 16 meta-unit types, one was able to be tracked over all three core themes (red, blue and red) (see Table 3.4) and across the season (Table 3.5). This meta-unit – named the ‘groan’ unit – was therefore chosen for further analysis. The additional units “long moan", "long groan", "long ascending modulated moan", "long moan (pulsated)” were added to this meta-unit because they were simply longer versions of fine-scale units within the groan group and could represent evolution of the unit over the season or within song sessions (Figure 3.7 and see Appendix 3.11 for complete list of original unit types committed to the meta-unit ‘Groan’). In the fine-scale unit analysis groans are distinguished from moans by having a lower peak frequency (fine-scale ‘groans’ exhibit a peak frequency below 250 Hz and fine-scale ‘moans’ exhibit a peak frequency between 250 and 500 Hz). In total 1717 observations were analysed in the final analysis.

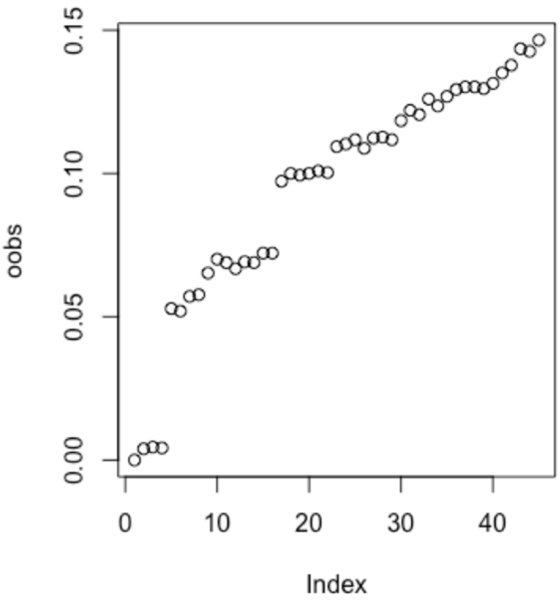


Figure 3.5: The plot of OOB error scores per number of unit groups revealed two jumps in OOB error at four and sixteen groups. The number of groups was how many categories the total 45 fine-scale units were split into. A large jump in OOB meant that more unit observations were incorrectly assigned to a group. The OOB error score for 4 groups was just over 1% and the OOB error score for 16 groups was 7.5%.

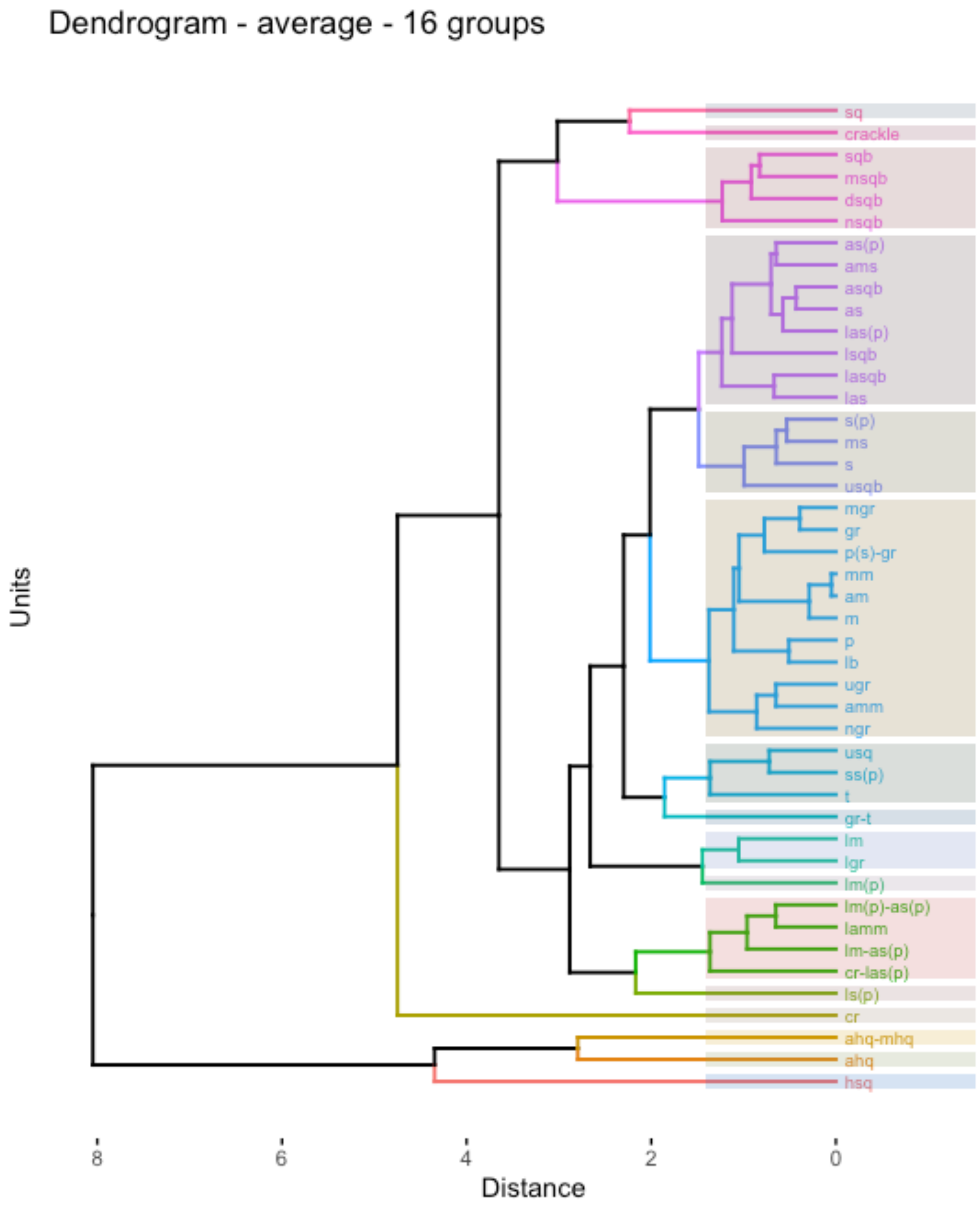


Figure 3.6: Average linkage dendrograms partitioned into 16 groups. The dark blue group in the middle of the dendrogram represents the meta-unit 'groan'.

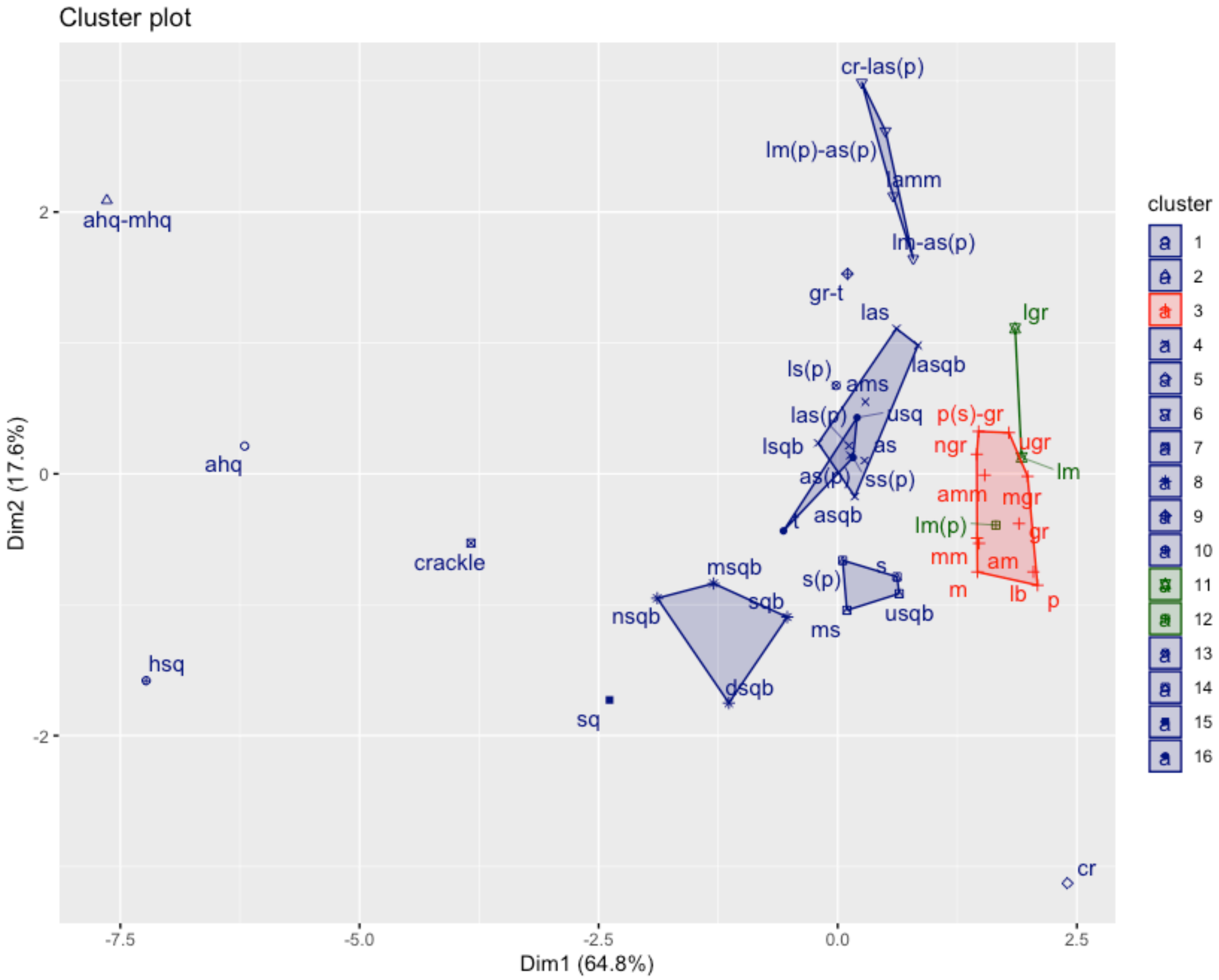


Figure 3.7: Cluster plot visualising the song units partitioned into 16 groups. Cluster 3 (red cluster) represents the meta-unit 'groan'. The longer versions of these units were also included in the analysis and can be seen to overlap with this group (see groups 11 and 12 in green).

Table 3.4: Number of observations of meta-unit groan in each core theme

Theme	Recording				
	260819 CI	310819 CI	020919 CI	050919 CI	150919 CI
Red	81	107	33	20	84
Green	56	65	79	147	80
Blue	198	169	198	252	148

Table 3.5: Number of observations in new unit categories

Theme	**Meta-unit type**													
	groan	fifteen	fourteen	shriek	thirteen	four	two	three	twelve	sixteen	five	nine	one	trumpet
red	325	0	0	21	148	10	6	0	0	0	71	13	1	1
green	427	5	3	73	0	0	0	16	0	7	0	8	257	38
blue	965	0	0	1	0	0	0	0	34	0	0	1	14	495

3.3.3.1 Seasonal change: do units change and if so, do the same unit types change in the same way in different themes?

Original outputs revealed that four specific unit observations were causing severe outliers in acoustic similarity measure. All four observations were from the red theme and related to two fine-scale unit types due to one measurement type displaying an error in the original dataset. These observations were identified and removed from the analysis. All removed datapoints and reasons for removal are listed in Appendix 3.12.

Across the season no change in acoustic distance was found in the blue theme while in the red and green themes significant but small magnitude correlations between acoustic distance and time were detected (Red: Mantel statistic R: 0.031, p = 0.001 (Figure 3.8); Green: Mantel statistic R: 0.006, p = 0.018) (see Appendix 3.13 for all Mantel test summaries over the season).The divergence test did not detect any aggregate acoustic change over the season between units produced in the context of different theme pairs, for any pair of themes (Figure 3.9, see Appendix 3.14 for complete divergence outputs). Of all the discrete measurements ‘End Frequency’ was the only measurement found to be changing in a statistically significant and different way across theme types (F = 14.252, p <0.05) (Figure 3.8). End Frequency was found to increase over the season with significant differences between theme types in which the red theme type increased and the blue theme type showed a weak decrease while the green theme type did not change (Figure 3.9). Other discrete measurements did not show any significant change between theme types across the season (see Appendix 3.15 for complete outputs).

Table 3.6: Model Summary of 'End Frequency' regression

Predictors	*Estimates*	*CI*	*s.e*	*t*	*p*
(Intercept)	127.030+	-15.823, 269.883	63.149	2.012	0.075
TimeDays	**14.252***	1.088, 27.415	5.819	2.449	0.037
Theme: green	**269.462***	67.438, 471.487	89.306	3.017	0.015
Theme: blue	173.198+	-28.826, 375.223	89.306	1.939	0.084
Timedays x themegreen	-14.570	-33.186, 4.045	8.229	-1.771	
Timedays x themeblue	-16.867+	-35.483, 1.749	8.229	-2.050	0.110
Observations	15				
R^2	0.610				

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

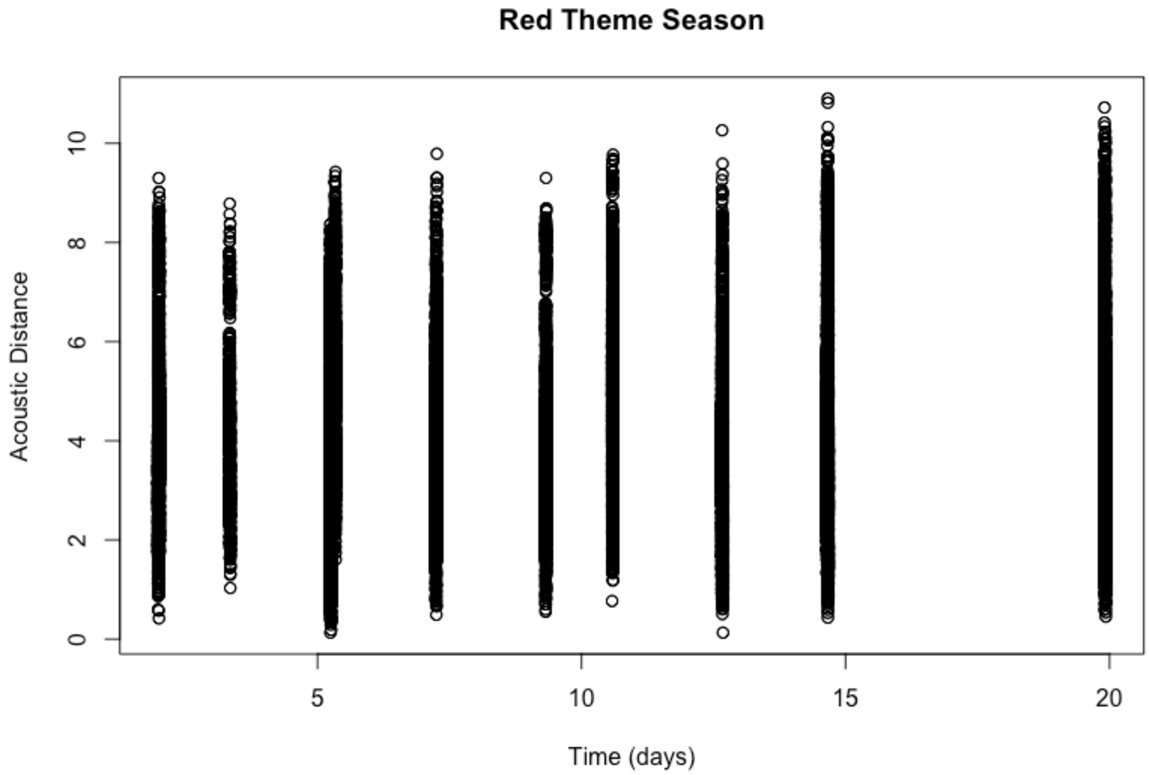


Figure 3.8: Red Theme Season: Acoustic Distance over time – over season. Although weak, there are some points occurring at higher points later in the season which suggests that at least some productions of that unit are getting a bit more different. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.03116, p value = 0.001). However, this change was negligible being close to 0. In other words when units became further apart in time across the recording they did not become noticeably dissimilar in structure.

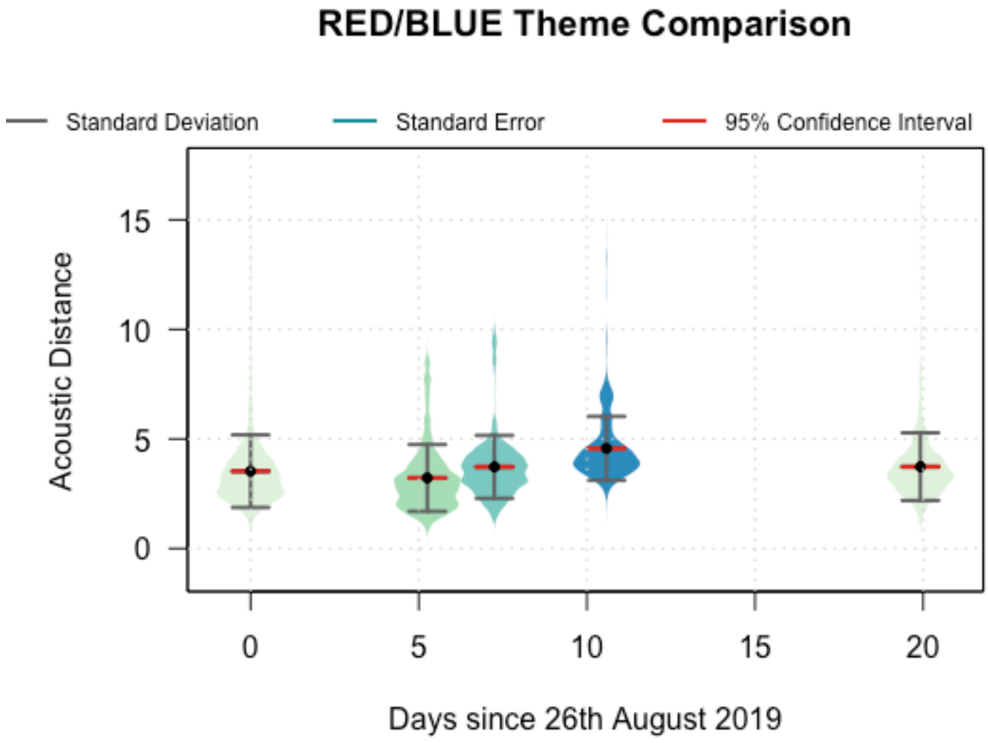


Figure 3.9: Red/Blue Theme Comparison over season - The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryRedBlueComp1) Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant (R^2 = 0.1444, F(1, 3) = 0.5062, p = 0.5281).

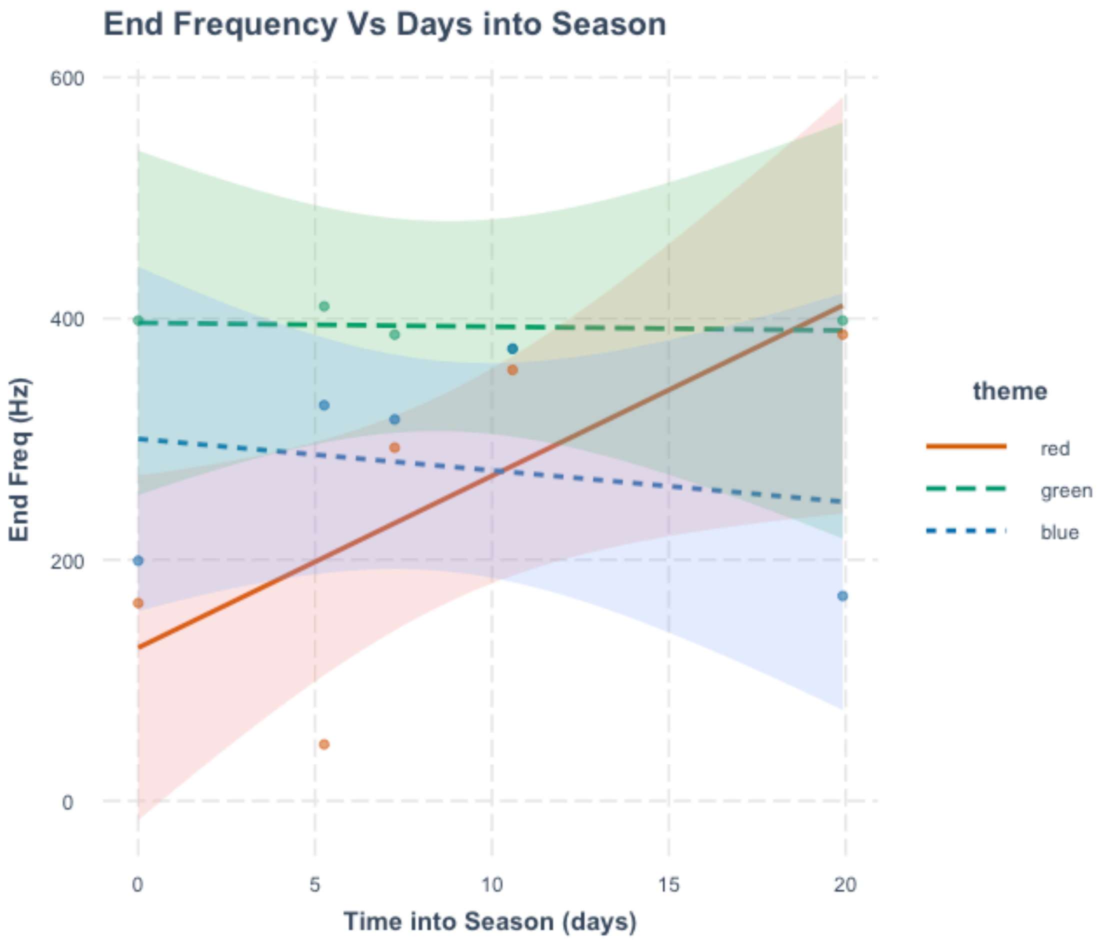


Figure 3.10: End frequency over season: End frequency was found to increase over the season with significant differences between theme types in which the red theme type increased and the blue theme type showed a weak decrease while the green theme type stayed the same. The red theme increased End Frequency by 14.252 Hz per day while the blue theme type showed a slight decrease in End Frequency and the green theme type remained the same.

3.3.3.2 Within song session change: do units change, and if so, do the same unit types change in the same way in different themes?

Within song sessions acoustic change was detected across individuals with idiosyncratic variation. Individuals changed their groan units in different ways across theme types at both the level of overall acoustic change (Euclidean distance) (Table 3.7 for Mantel outputs and Appendix 3.17 for individual-theme mantel plots) and also within discrete measurement types e.g. Peak Frequency (Figure 3.11, 3.12 and 3.13, and Appendix 3.16 for complete outputs across all discrete measurements). For example, a significant change in overall acoustic distance was found in all of the themes of individual 2608 (Table 3.7) however, significant acoustic change was found in only one or two themes of the three total themes in the remaining four individuals (Table 3.7). Discrete measurements also displayed this variability in groan unit change across themes and individuals within song sessions. For example, individual 2608 increased Peak Frequency of their groans in the red theme while they decreased the Peak Frequency of their groans in the blue and green themes (Table 3.8). Similarly, individual 1509 changed their groan unit in different ways in different themes, decreasing Peak Frequency of their groans within the red theme and increasing Peak Frequency in blue and green theme types (see Appendix 3.16 for complete outputs for discrete measurements within song sessions).

Table 3.7: Euclidean Distance – Individual and Theme split Mantel tests

	Mantel	Sig	Mantel	Sig	Mantel	Sig
THEME	Red		Blue		Green	
2608	**0.1107**	0.001**	**0.1654**	0.001**	**0.2805**	0.001**
3108	-0.02776	0.999	**0.02884**	0.001**	-0.02284	0.928
0209	**0.06242**	0.016*	-0.0323	1	0.009096	0.24
0509	**0.5903**	0.001**	**0.03102**	0.001**	**0.04153**	0.001**
1509	-0.005071	0.662	**0.05633**	0.001**	**0.1171**	0.001**

Peak Frequency Over Time within recording

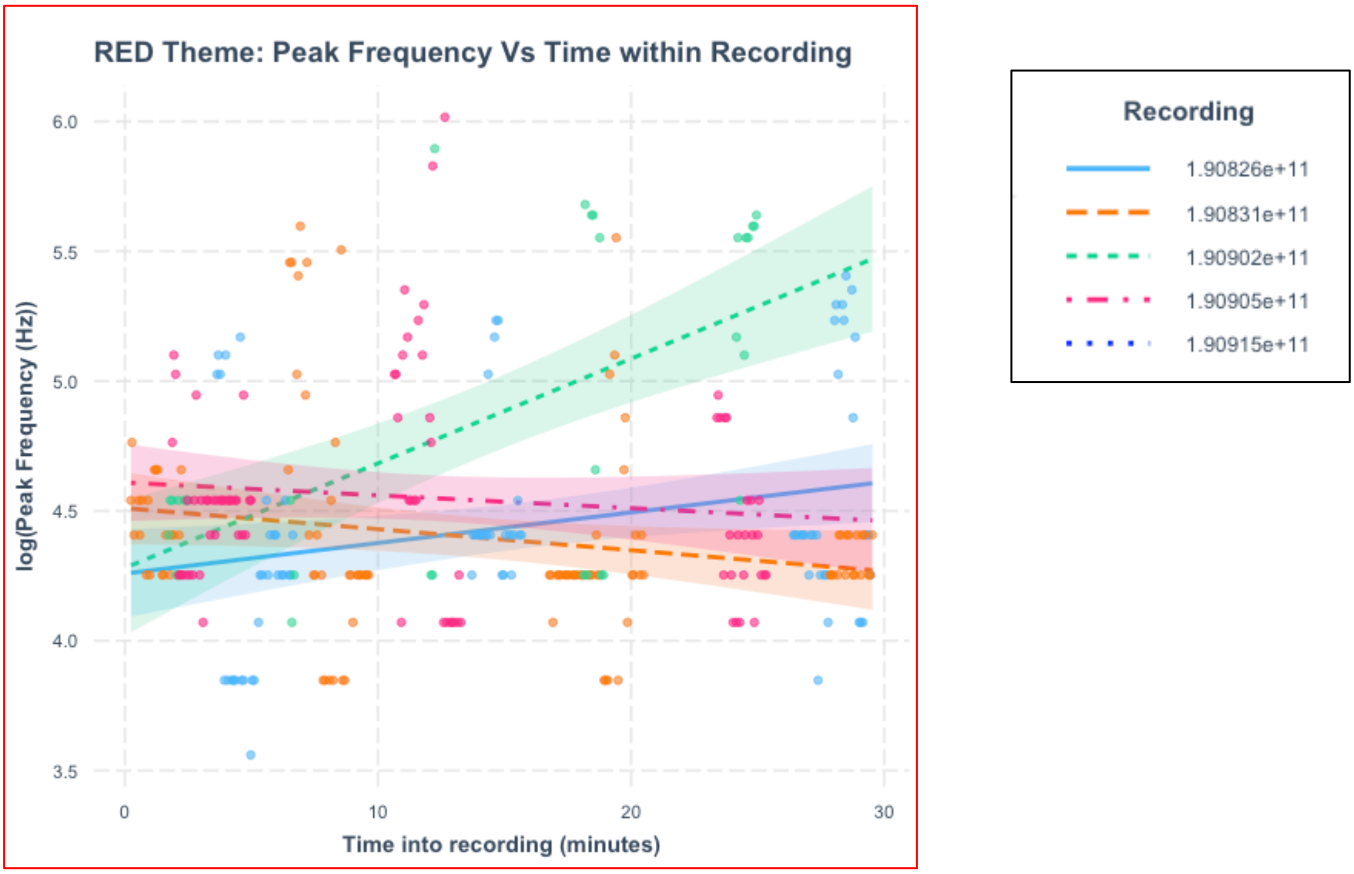


Figure 3.11: All four individuals were significantly changing the peak frequency of the groan unit over time in the red theme. Two individuals (26, 02) increased their peak frequency while two individuals (31, 15) decreased their peak frequency. 26 and 02 started off with a similar frequency and while both increased in frequency over the duration of their song session – 02 increased at faster rate. The red points denote the recording 15/09/19 in this plot.

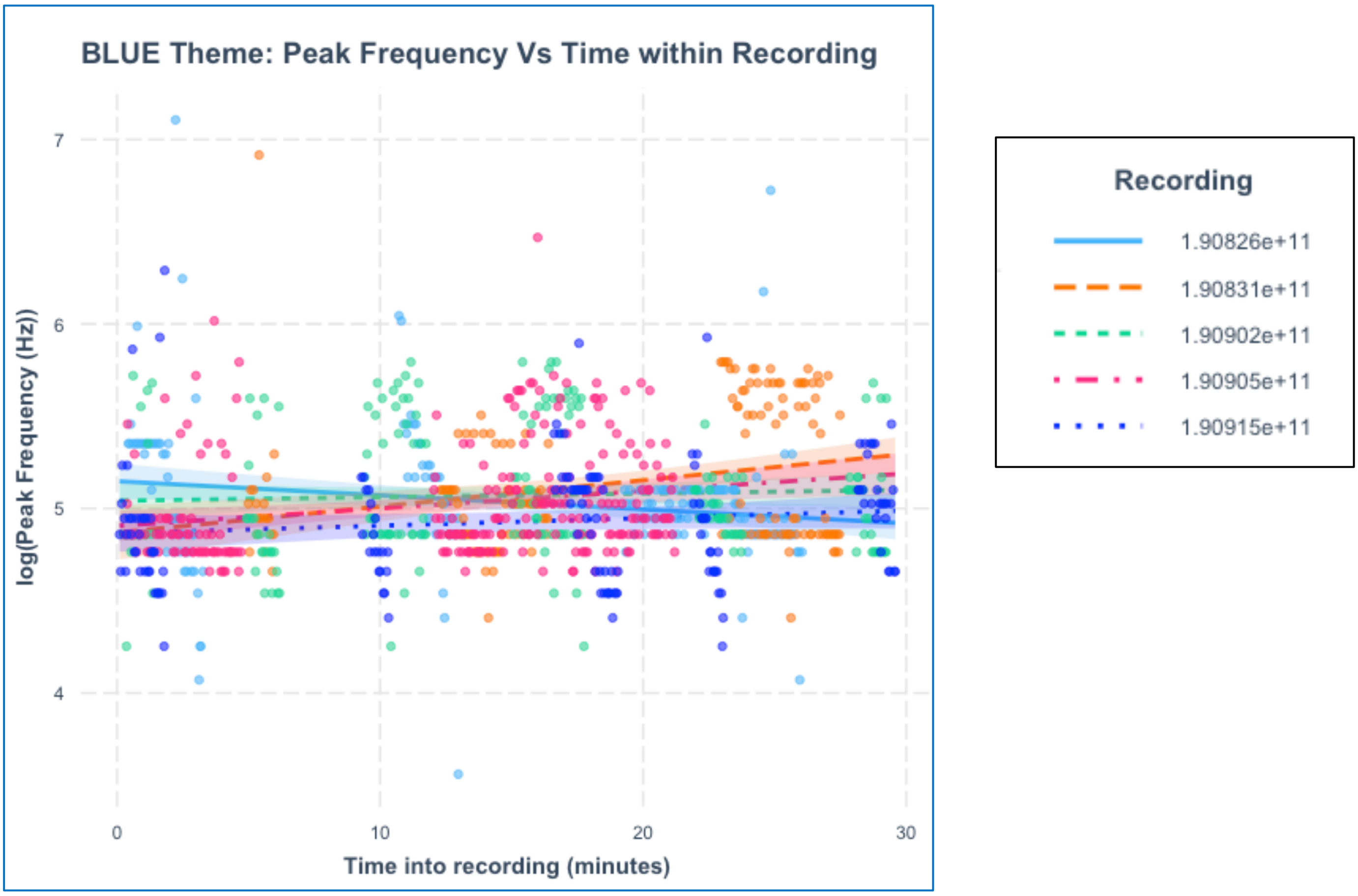


Figure 3.12: Significant difference in trend between individuals within song sessions. One individual (26) is decreasing their peak frequency – while the other 4 individuals are increasing their peak frequency.

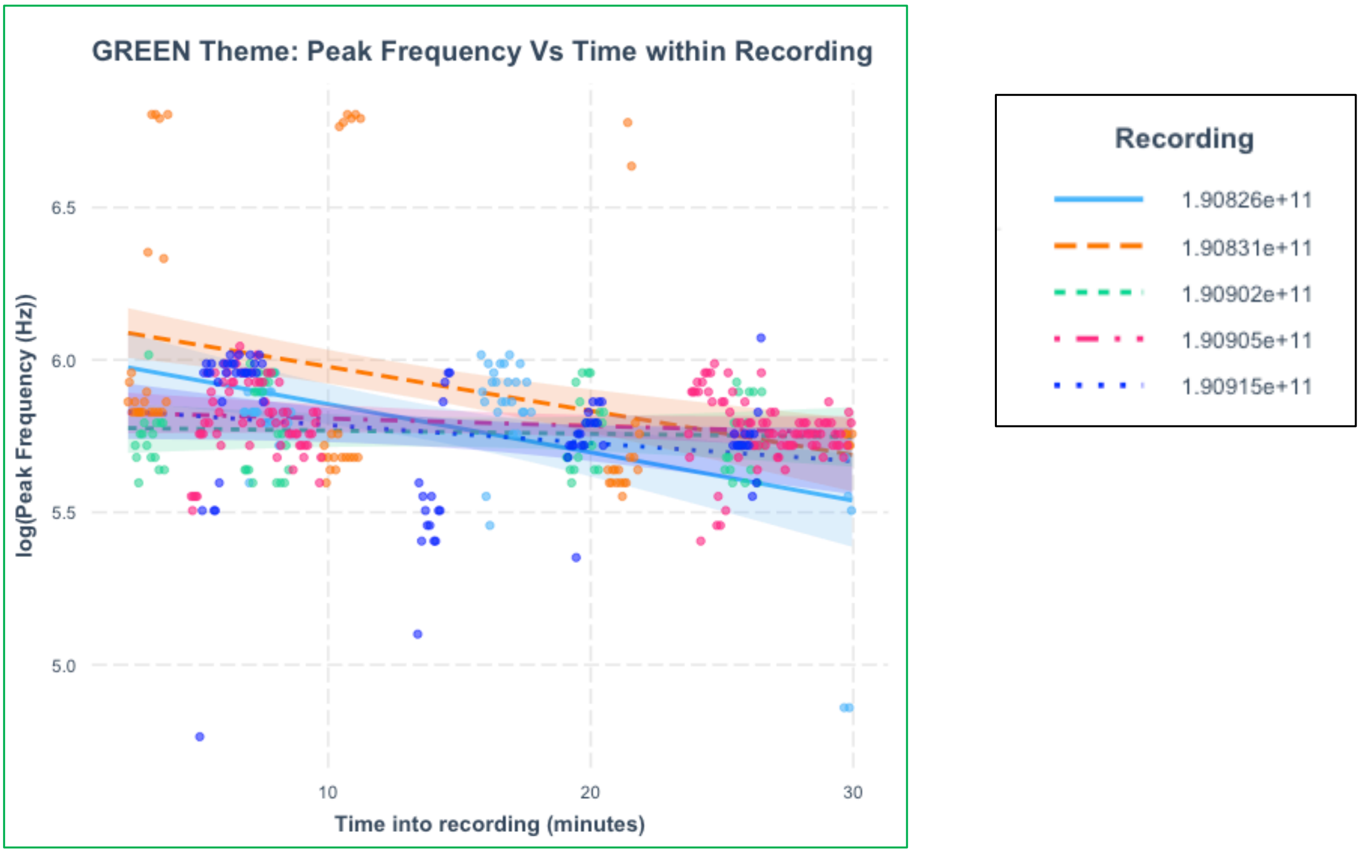


Figure 3.13: Significant difference in trend between individuals within song sessions. 26 and 31 decreasing in the same way while 02, 05 and 15 decreasing at much lower rate.

Table 3.8: Model outputs for Peak frequency per theme for the time x individual term. Stars denote significance level.

ID	RED	BLUE	GREEN	Does the same individual change their groans in different ways in different themes?
26	+0.012*	-0.008**	-0.016***	Yes
31	-0.020	+0.022	-0.167+	Yes
02	+0.029	+0.010*	**+0.015****	Yes
05	NA	**+0.017*****	**+0.013****	No
15	**-0.017***	**+0.012****	**+0.010+**	Yes

3.3.3.3 Alternative Hypotheses

The additional explorations of possible change in unit structure over time due to signal quality as quantified by Signal to Noise Ratio, coarticulation or exhaustion did not yield any consistent effects and are therefore unlikely to affect the main analysis interpretation (please see Appendix 3.20 for full results).

3.4 Discussion

My study aimed to better understand whether humpback song units are selected from an innate template of units (and thus may create new complex displays through usage learning, but are not themselves subject to production learning) or alternatively whether they are learned in the context of specific phrases (and therefore subject to vocal production learning that should be detectable through independent changes in the same unit types occurring in different phrases). This study looked for evidence of change in acoustic structure of one unit type (named 'groan') at two timescales, within individual song sessions and more widely across that span of the breeding season for which recordings were available.

At the seasonal level this groan meta-unit type appeared to be generally stable, with some very small changes in aggregate acoustic distance, over the time-scale we analysed. The groan unit in one theme had no change over the season while the other themes had evidence of very limited changes. The divergence tests also showed that there was no significant divergence of the unit in different theme types as the season progressed. This general stability over the season would support a species-specific unit repertoire, agreeing with Cerchio *et al.*, (2001), Garland & McGregor (2020) and Mercado (2021) who have all suggested that song units may be derived from fixed innate templates. While, in general, stability was found, two of the themes did show statistically significant changes over the season. From our relatively small dataset we can see that comparisons made later in the season were more different from the beginning of the season. These small changes suggest that some productions of this unit are changing as the season goes on. While we can statistically detect changes in these two theme types, there is also a lot of variation around these points such that it is unclear whether an observer would be able to distinguish between early season and late season examples of this unit. The Mantel correlation statistics obtained for these two themes, while statistically significant, were close to zero which indicates a very weak correlation between time and acoustic structure (Legendre, 2016). This suggests the changes are very subtle and unlikely to represent qualitative song change.

When considering individual acoustic measures, the discrete measurement type 'End Frequency' was found to significantly increase over the season in the red theme but did not in the Blue or Green themes. This would indicate that the 'groan' unit is changing in a different way dependent on the phrase type the unit is present in which would indicate divergent trajectories of the same unit type between theme types. However, it is important to note that only one of the eight discrete measurements showed significant differences in trend between theme types.

My study did not detect concurrent change in the same unit rather we detected overall stability at the level of the season. In their study of killer whale vocalisations, Deeke *et al*. (2000) detected that one shared call type was changing in the same way in different matrilines. From this finding of concurrent change which led to no further divergence they could support acoustic contact between the matrilines. This study has instead taken a shared unit type (call type) between different phrase types (matrilines) to assess whether the unit type could be stored as one template but used in different phrase types. Concurrent change but with no overall divergence between unit types in separate themes would be compelling evidence for a unit that is stored as a single template. However, our study found that, over the time period analysed (20 days) there was no divergence between phrase types but also generally no change, or extremely small change, across all of the theme types across the season. It is possible that further evolution may have been detected at longer timescales than we covered over the period when whales are singing in the study area. The timescale analysed in this study was constrained by the quality of recordings derived in the overall deployment period of the breeding season of 3 months.

Unfortunately, multiple individuals were not sampled at the same time point within the season, therefore variation between individuals and variation due to change over the season is somewhat confounded. This is the case for much of humpback research to date and it is generally accepted that as the season progresses all humpbacks update their song to match the current song version (Cerchio *et al*., 2001). It is therefore assumed that changes between individuals collected at different points in the season would also reflect overall changes made to the song at a population level and the methodology of this study is reliant on this assumption. However, data is lacking to confirm synchronous change, in particularly at the hierarchical level of the unit. Further research could aim to record multiple individuals at the same time point to confirm that humpbacks are keeping up with the song changes at all level of the song hierarchy, especially as research has traditionally focused on song evolution in which the cyclical repetitions of themes or phrases are investigated (Payne and McVay, 1971). To achieve this much larger datasets would be required in which multiple individuals are recorded within the same time block (e.g. a day, a week) to track these fine-scale changes and to examine differences between individuals. Humpback whale song research is currently hampered by the difficulty to collect many high-quality song recordings within a short space of time. This could be improved by installing more passive acoustic recorders (such as SoundTraps) in one area or by deploying DTags on multiple individuals as has been utilised in humpback non-song research (unfortunately both with a high cost to the researcher) (Stimpert *et al*., 2011; Videsen *et al*., 2017).

While across the season there appeared to be generally overall stability in the groan unit, relatively more variability was detected within song sessions. Change within the song session was detected in two ways. Firstly, there was variation across individuals as to how they changed the groan unit within the same theme within discrete measurement types. For example, Individual 02's groan peak frequency in the red theme became significantly more different from groans produced by Individuals 05 and 31 groan in the red theme as their song bouts progressed over a 30-minute period (Figure 3.9 and Table 3.7). Not only did their groan units become more different as their song bouts progressed but they also changed in contrasting ways (02 increasing their peak frequency and 05 and 31 decreasing). Secondly, individuals changed the groan unit in different ways in different theme types within their own song display. For example, Individual 15's groan in the red theme significantly increased in peak frequency over the song session while groans from their blue and green themes decreased in peak Frequency. We would expect that if the unit comes from the same template then even within the same song session (presented by the same individual) the unit would change in the same way so that units presented in different themes got no more different from each other. Contrarily, we observed that most individuals change their groan unit in different ways in separate themes. Detecting divergent change of the same unit type within the same individual would support the hypothesis that units are subject to different changes in different phrases , more compatible with the vocal production learning of units suggested by Tyack *et al* (2019) and Janik and Knornschild (2021) as opposed to the fixed template account. Analysing change acoustic structure of units within individuals may also be a more robust way of detecting change between themes, than over a season, as this controls for variation between individuals. This could be further explored utilising DTAGs (Digital Acoustic Recording Tags) in which song may be collected over a slightly longer time-scale from the same individual (however currently DTAGS do not last longer than 48 hours) (Johnson and Tyack, 2003; Johnson *et al*, 2009; Dunlop, 2012). What this study clearly shows is that the potential for change is present because even within a 30-minute recording of a song session there are different individuals changing parameters of this unit at a fine-scale. These changes within the song session and differences between individuals could be the foundation of individuals trying to stand out (innovations) and ultimately song change over time.

While changes of the groan units within song sessions show variation between individuals and between themes these changes did not add up to a general change that could be detected across the season. This could be because those changes created by individuals are discarded in later song sessions as they conform to the dominant song when they hear the songs of other individuals. However, it is not known what happens to song innovations to make them jump these two timescales from variations introduced within a song session to part of the accepted song that is conformed to across the season. Ideally, to answer this question multiple individuals would be sampled at the same time. Furthermore, capturing the same individual in more than one location by both acoustic and photographic means at any time, never mind within the same season, is very unlikely. With current technology, it is unclear how we could track the same individual’s acoustic output over a season.

Technological development might allow such research to be undertaken, for instance if Dtags are improved to be utilised over a longer term, however Dtags currently don't last for over 48 hours (Harcourt et al., 2019). Much humpback song research to date has focused on sampling across a season in one or more locations to elucidate broadscale changes in song structure at the level of song types or theme types displayed. The research of broadscale song changes in large areas of the ocean has led to a conundrum between overall conformity at a breeding location but the need for individuality in a sexual or male dominance display (Darling *et al*., 2012, Dunlop and Noad, 2016); Lamoni *et al*., 2023). We have little idea of the changes being made by individual humpback whales in their effort of (potentially) stand out. This study goes towards operationalising a methodology to allow us to analyse fine-scale changes, alongside broadscale changes.

In our study we identified a unit type, named the 'groan', which we could track in multiple theme types and across the season. Research on whale song at such a fine-scale has been hampered by the large processing time to take fine-scale measurements of many units. We made a number of methodological efficiencies over previous measurements in earlier humpback whale song research - partly informed by them doing that work – which enabled us to create measurements for our complete dataset rather than only taking a sub-sample of the highest quality units. For context, in previous humpback song research the start and end frequencies of units are usually created by careful point measurements through placing the cursor onto what is perceived to be the beginning of the unit as implied by the signal to noise ratio of the call. The traditional method can be open to observer error and is also time intensive. The new methodology presented here had a high correlation with the traditional method but enabled measurements for the whole dataset to be derived, rather than only a subsample.

Few studies so far have investigated evolution of humpback whale songs at the level of the unit. Magnusdottir *et al.,* (2019) examined humpback whale songs in Icelandic waters over three winter seasons and found a combination of stable song unit types that occurred in all years, while other song unit types varied in presence. The methodology used by Magnusdottir *et al.,* (2019) differed from the current study in that their unit categories were classified using only statistical methods. The current study employed the commonly used method of subjective aural classification of humpback whale song units in tandem with statistical methods to arrive at a robust unit classification. Subjective aural classification utilising both the sound and spectrogram characteristics may be an important step to encapsulate connected sound types in any unit categories that may have changed dramatically due to evolution of the unit. Future studies could directly compare the methodologies used to classify unit categories. The comparison of the evolution of units classified from fully statistical methods to those classified by human subjective means would enable possible consensus to be reached across the research community, and hopefully allow comparison of unit evolution in different parts of the world. Previous research has found that humpback whales from separate oceans that do not mix usually sing different songs (Payne and Guinee, 1983; Darlin *et al*., 2014). Future research could seek to compare the song unit repertoires of populations that are not in acoustic contact at all. Recent research has sought to track the progression of phrases in acoustically isolated songs (Mercado, 2021) however, when this study is closely explored it seems the results depend on visual appraisal of particular subsets of the datasets. Furthermore, it is difficult to follow Mercado and Perazio's argument that leads them to their conclusion that song evolution is not due to cultural transmission. Further research could compare the unit repertoire of the South Pacific songs to the unit repertoire of the North Atlantic songs.

It is also possible that these two hypotheses could apply to different parts of the unit repertoire. The only way to examine this would be to really go into detail about whether some units vary more than others. Some social calls have been suggested to be quite similar to some song units and there is evidence that social calls are invariant therefore another option is that there is a combination of learned and innate calls brought forward into the song. It does seem that there are forms of song unit or particular combinations of song units that are attractive to humpbacks therefore they use these more than other possible forms or combinations of units. Research in other song producing species has found that isolated zebra finches evolve back to their wild type song through a process of cultural evolution. This shows that the appearance of something innate actually evolves via vocal learning.

Humpback whale communication systems may be useful in comparative research with other taxa, including birds and humans (Garland and McGregor, 2020). Vocal convergence via vocal production learning has been documented in a range of bird species including black capped chickadees (*Parus atricapillus*), Australian magpies (*Gymnorhina tibicen*) and Yellow-naped amazon parrots (*Amazona auropalliata*) (Nowicki, 1989; Wright; 1996 and Brown and Farabaugh, 1991). However, vocal learning in adult mammals is less widespread when considering the evidence to date. Researching cognitive learning mechanisms in large wild animals is hampered by finding practical and ethical ways of conducting research. This chapter has shown that, by utilising the natural hierarchy of the humpback whale song, passive acoustic recordings can be utilised to explore the learning capacity for song units. Efforts such as these could pave the way for future research to better understand humpback whale song production and better aid comparative efforts to birds and potentially humans. It is still unclear whether units are changing in different ways in different themes across the season, which may be due to the limited time span in which the songs were explored. Longer term datasets of song evolution may aid better understanding of how song units are evolving within separate themes.

Chapter 3 Appendices

Appendix 3.1 Protocol for grading humpback whale song quality on a four-point scale

1. Poor (P) 2. Fair (F) 3. Good (G) 4. Very Good (VG)

Poor

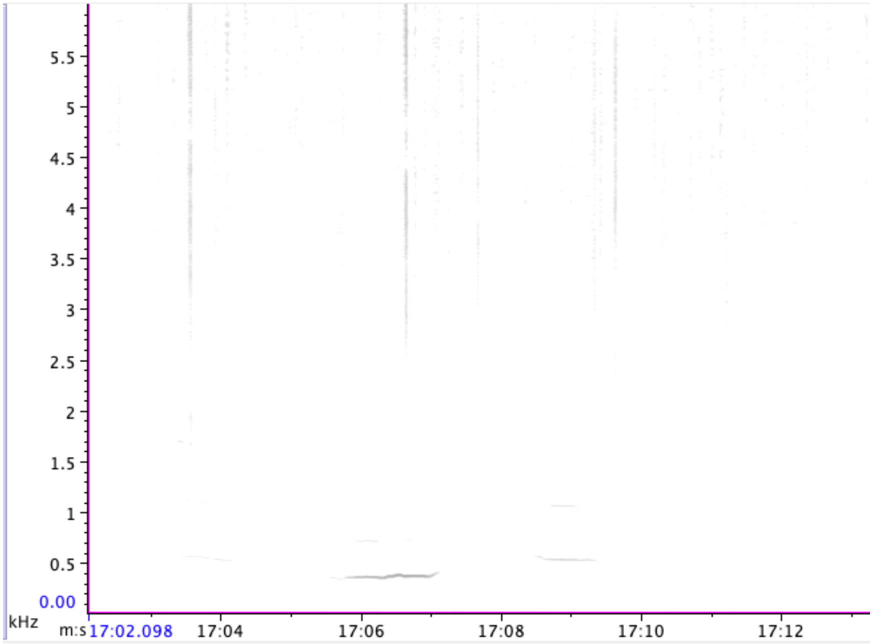


Figure A3.1: Poor Quality Humpback song: Song can be detected and units can just be discriminated – it is likely some units are not detected and the start and end of units are not clear – Poor SNR (ca. 10 dB) and some units are absent – Song is present but song type would be difficult to detect

Fair

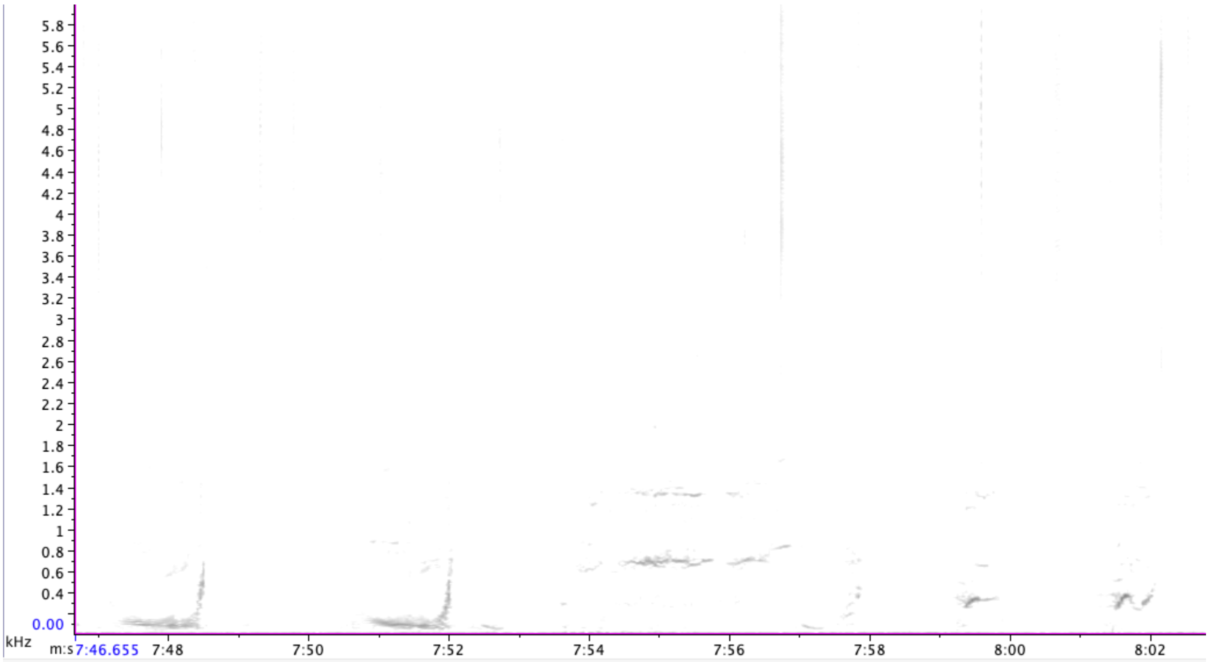


Figure A3.2: Fair – Can see units but SNR is poor (10 – 20 dB) – Song type may be detected but not transcription and measurements

Good

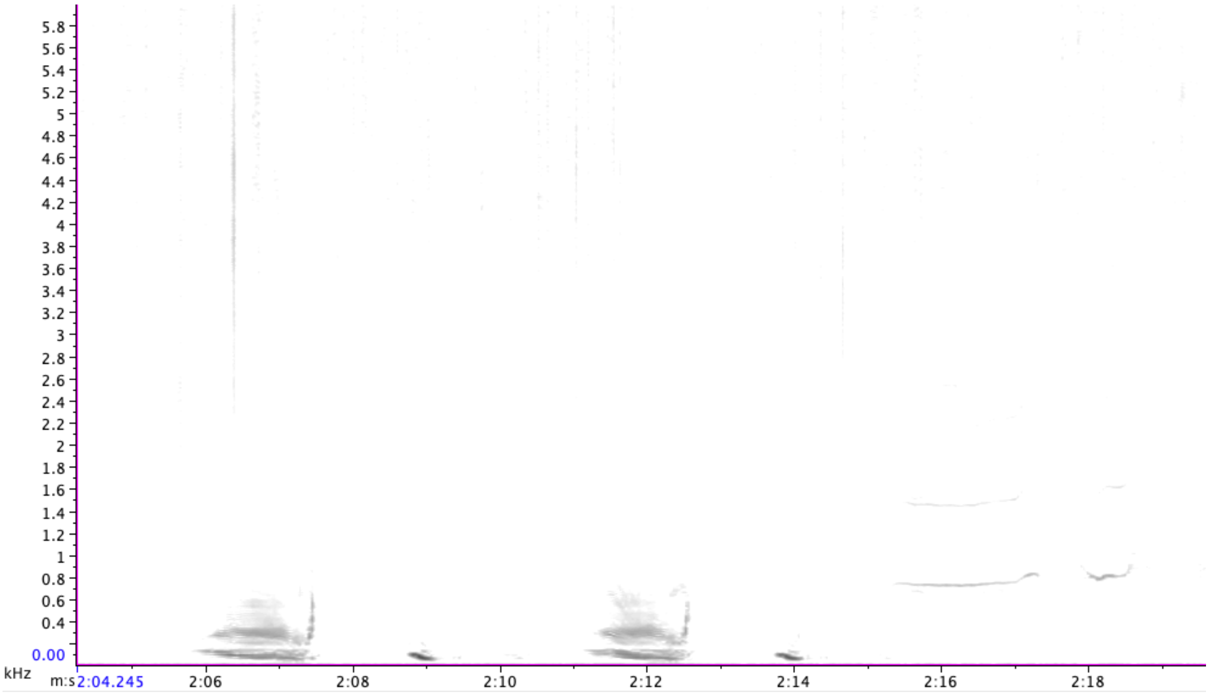


Figure A3.3: Good – Units are clear but SNR is not optimum (20 – 30 dB) – transcription is possible, but not measurements

Very Good

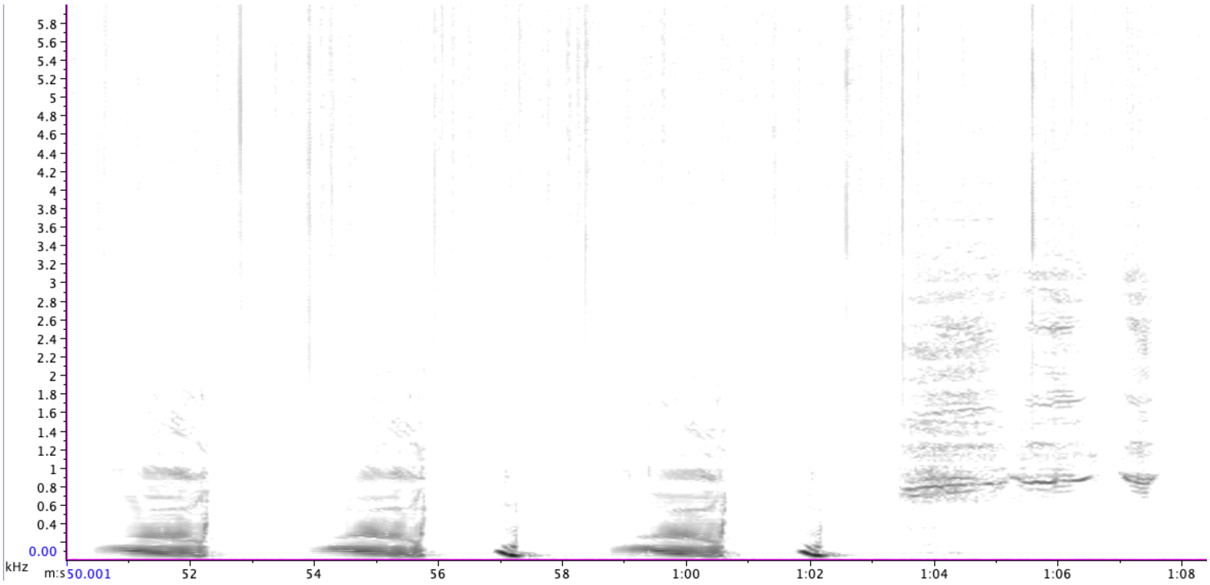


Figure A3.4: Very Good – Great SNR – All units are clear against background noise – Transcription and measurements possible ca. 40 dB

Appendix 3.2

General unit groups and their frequency ranges and further characteristics

	Unit Name			Frequency Range	Categorising within
↑ Increasing Frequency	High squeaks (hq)				
	Squeaks (Kennedy *et al.*)			Squeaks are shorter than whistles e.g. 0.6 of a second covering a large bandwidth at a high frequency	Squeaks are very short <0.5 seconds as a general rule but could be slightly longer and most energy is over 1kHz
	Whistles (ws)			>1000 Hz (most energy) >1500 Hz	If unsure of majority of energy can look at peak frequency
	Cries	Shrieks (e.g as)		500 – 1000 Hz	Cries are melodic and harmonic Shrieks are always with a contour e.g. as = ascending shriek
	Moan (m)	Siren (s)	Bellow (be)	250 – 500 Hz	A siren is really a long modulated moan (Frankel *et al.*) A moan is long if its longer than 3s Less than 1 second is a short moan So between 1 and 3 seconds is just a moan
	Groan (gr)			<250 Hz	A groan is long if its longer than 3s
	Croak	Purr	Bark	Create rule for these categories	See drawings in note book – will make online drawings to make annotated dictionary of sounds to work from

Appendix 3.3

Units and abbreviations:

Unit Short Code	Full Unit Name
a	a-unit
agr	ascending groan
ahq	ascending high squeak
ahq-mhq	ascending high squeak with modulated high squeak
amm	ascending modulated moan
as	ascending shriek
as(p)	Ascending shriek pulsated
asqb	ascending squeaky balloon
ba-sq	bark-squeak
cr	croak
cry	cry
dcry	downward cry
fw	firework
gr	groan
gr-t	groan with trumpet
gr1	groan1
gr2	groan2
hsq	high squeak
lamm	long ascending modulated moan
las	long ascending shriek
lb	long bark
lgr	long groan
lm(p)	long moan pulsated
lm(p)-as(p)	long moan pulsated with ascending shriek
lmcry	long modulated cry
ls(p)	long shriek
lsqb	long squeaky balloon
mcry	modulated cry
mgr	modulated groan
msqb	modulated squeaky balloon
msqb	modulated squeaky balloon
ncry	n-shaped cry
ngr	n-shaped groan
npurr	n-shaped purr
nws	n-shaped whistle
p	purr
sq	squeak

sqb	squeaky balloon
t	trumpet
ucry	u-shaped cry
ugr	u-shaped groan

Appendix 3.4 How to create Live Spectrograms

1. Open the sound clip you want to make a 'live' spectrogram of or if you are creating directly from a long recording – align the start of the unit at the frequency axis – so both axes will be included in your screen shot
2. Open QuickTime Player
3. Make sure you have preinstalled 'SoundFlower' (https://soundflower.en.softonic.com/mac)
   - Your system will probably reject this from installing first time round so you will have to give it permission in system preferences
4. In QuickTime – File – New Screen Recording
5. Move the cursor so you don't have a little number on the spectrogram (you will know what I mean)
6. In drop down menu – make sure 'SoundFlower (2ch)' is selected
7. This is important –In System preferences select 'Sound' and make sure your Output is also Soundflower (2ch) – you will now not be able to hear anything
8. Click the record button, this will allow you to make a screen grab – choose a grab that includes the axes- frequency up until about 5 kHz and a little room on either side of the unit temporally – so you can see clearly the start and end of the unit
9. Make sure you aren't playing music on your laptop – or it will continue playing as you make your screen grab and your whales will be singing with Taylor Swift
10. Click 'Start recording' then PLAY in Raven (be quick with pressing play in Raven or you will have a delay) – then once you see the sound bar complete – click the STOP button in the upper righthand corner of the screen
11. To save the recording click the exit button and give the recording the same name as the .wav file (add 'live' to differentiate) or if creating from a raw recording include the code name – location – year and recording number – and time location within file
    - Save in 'Live spectrograms' folder
12. To Check the recording works you must go back into System preferences and change Sound – Output back to 'Headphones'
13. Insert the .mov file to your large PowerPoint spread sheet – Give name e.g. BT FP 2013 (insert - text) then select both the text and the .mov at the same time to 'group' them so you do not lose track of what is what if you move them into a different position on the sheet

- If the heading does get lost – the .mov itself is named with the corresponding details – so this avoids mis-naming

The above process should take 4 minutes per unit start to end (excluding PPT insert)
https://www.cnet.com/how-to/record-your-computers-screen-with-audio-on-a-mac/

Appendix 3.5 Song 2 Theme examples

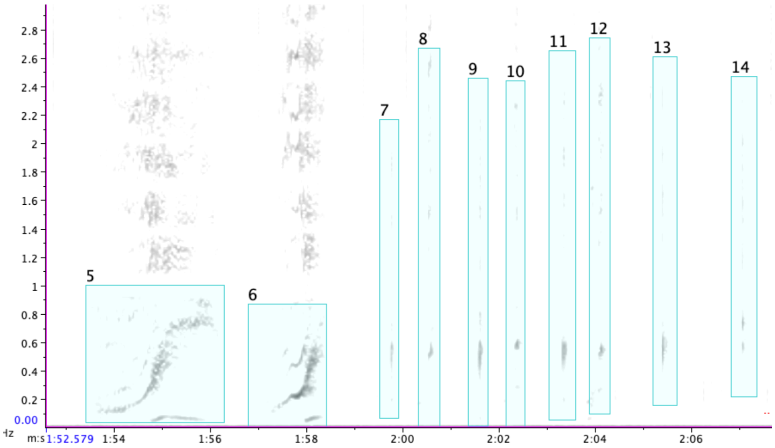


Figure A3.5.1: Song 2 Theme 4. 'a a Sq sq sq sq sq sq sq sq sq'

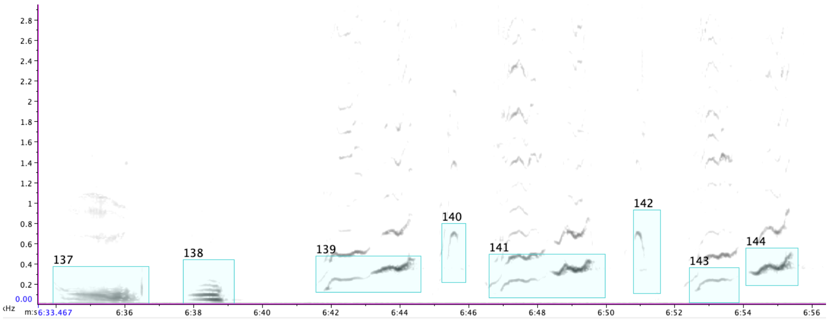


Figure A3.5.2: Song 2 Theme 5: 'gr1 gr2 amm t amm t agr ammm'

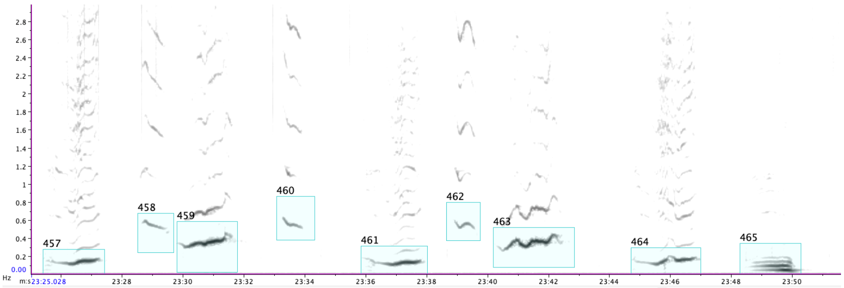


Figure A3.5.3: Song 2 Theme 6: 'agr dcry am dcry agr mcry amm mgr gr2'

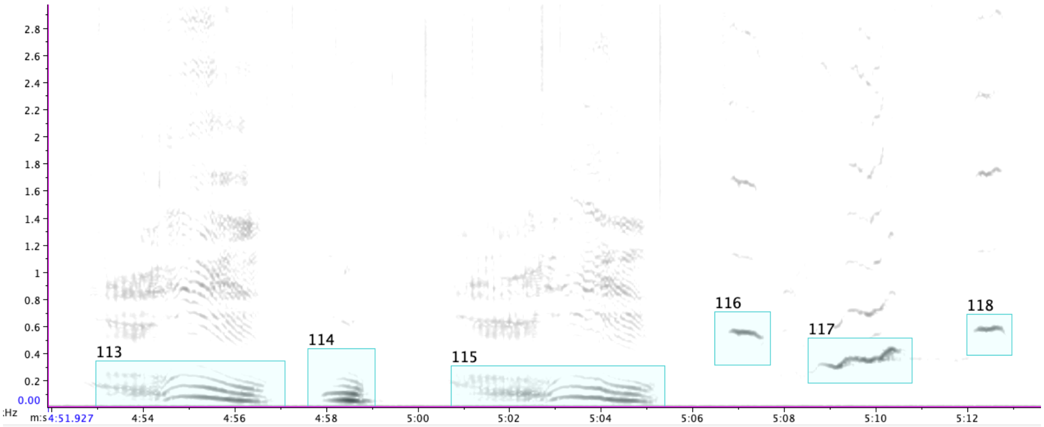


Figure A3.5.4: Song 2 Theme 7: 'npurr gr2 npurr cry amm cry'

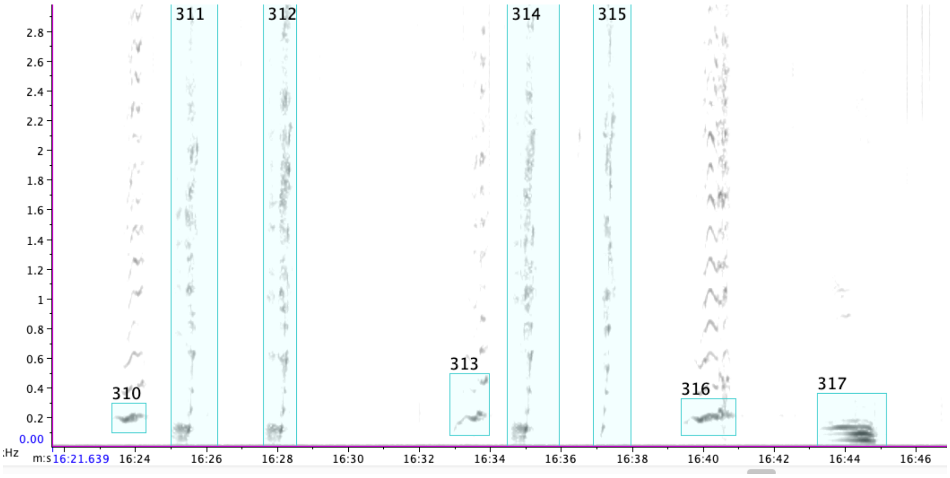


Figure A3.5.5:: Song 2 Theme 8a: 'gr ba-sq ba-sq hsq hsq gr ba-sq ba-sq gr gr2'

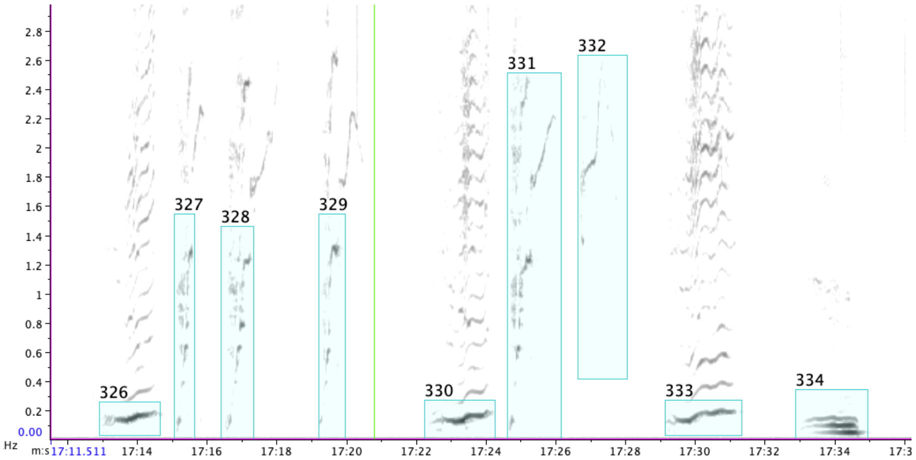


Figure A3.5.6: Song 2 Theme 8b: 'gr fw fw fw gr fw fw gr gr2'

Appendix 3.6 Theme Spectrograms

Theme 1 Spectrograms (RED)

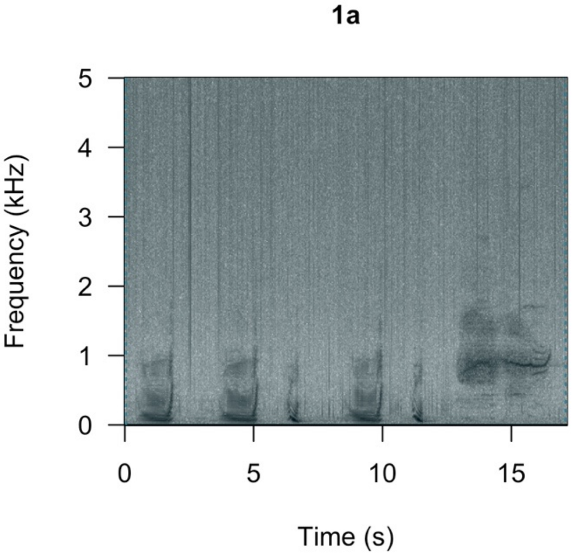


Figure A3.5: lb lb cr lb cr ls(p)

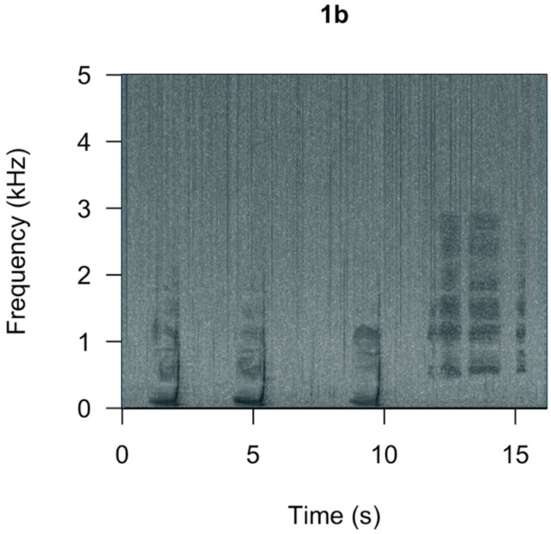


Figure A3.6: 1b: lb lb lb ls(p)

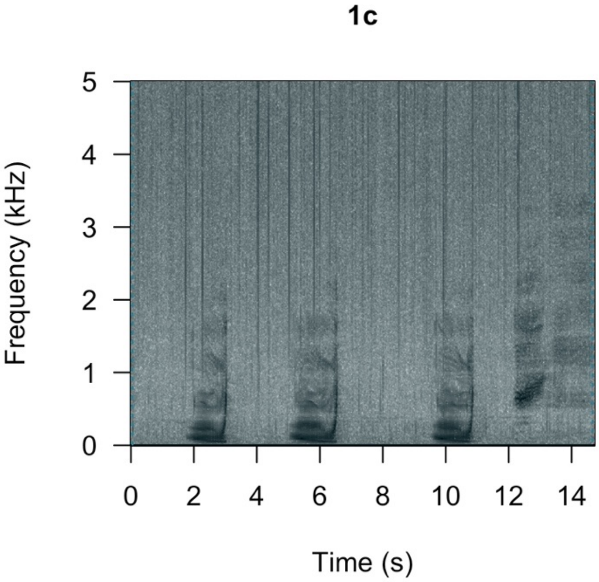


Figure A3.7: Theme 1c: lb lb lb as(p)

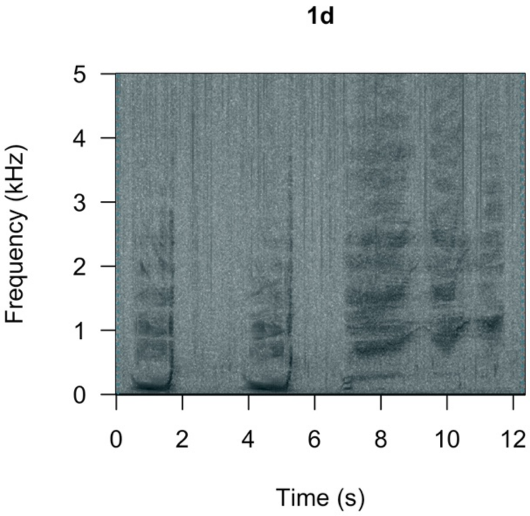


Figure A3.8: Theme 1d: lb lb las(p)

Theme 2 Spectrograms (GREEN)

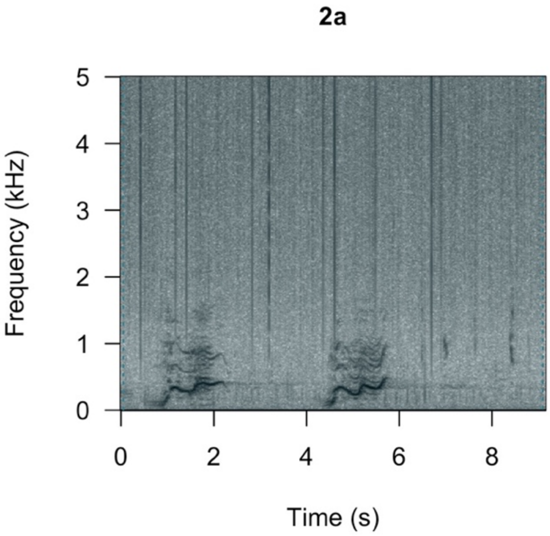


Figure A3.9: Theme 2a: amm amm sq sq sq sq

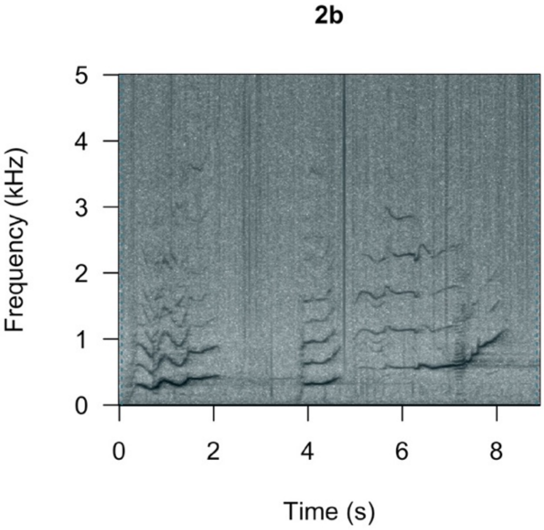


Figure A3.10: Theme 2b: amm lamm

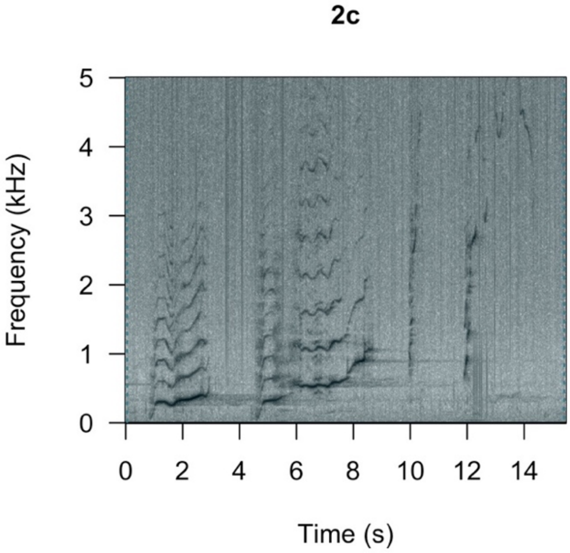


Figure A3.11: Theme 2c: amm lamm ahq ahq-mhq

Theme 3 spectrograms (BLUE)

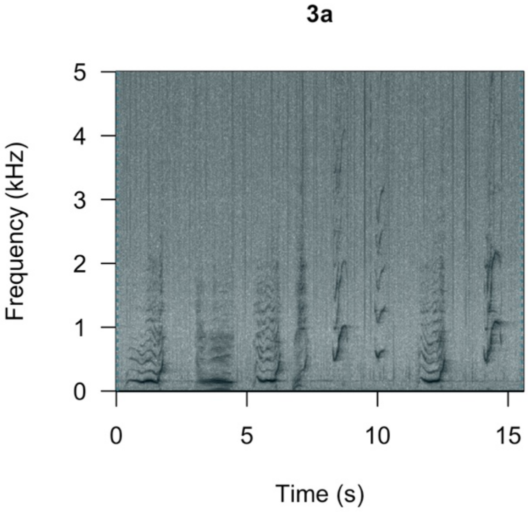
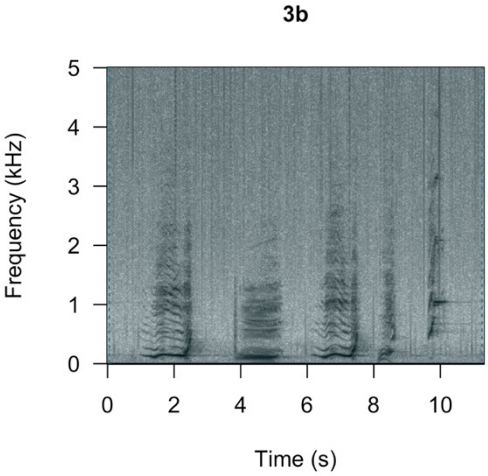


Figure A3.12: Theme 3a: ugr p ugr ngr t t ugr t



: Figure A3.13: Theme 3b: ugr p ugr ngr t t

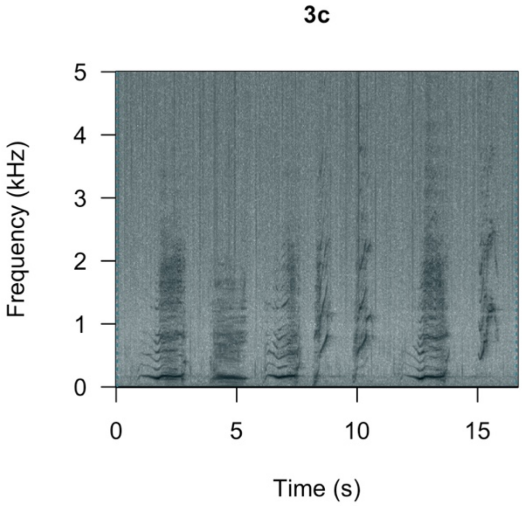


Figure A3.14: Theme 3c: ugr p ugr ngr gr-t gr-t ugr t

Appendix 3.7: Transitional Diagrams:

26/08/19 (2 song cycles)

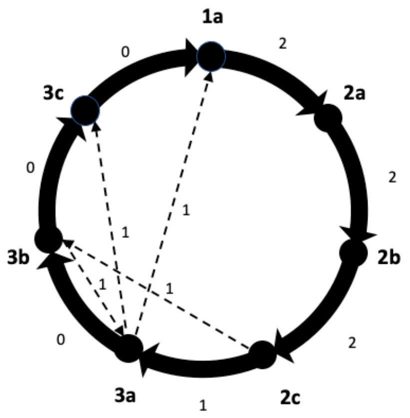


Figure A3.15: 2 complete song sessions present. The individual faithfully cycled through themes 1 and 2 with more variation between theme 2 and 3 and within b versions of theme three

31/08/19 (3 song cycles)

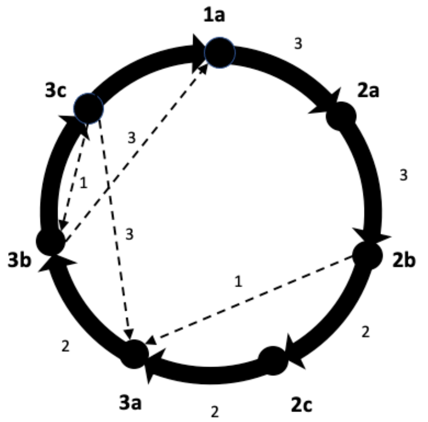


Figure A3.16: 3 complete song sessions present. The individual faithfully cycled through themes 1 and 2 with more variation between theme 2 and 3 and within b versions of theme three

2/09/19 (2 song cycles)

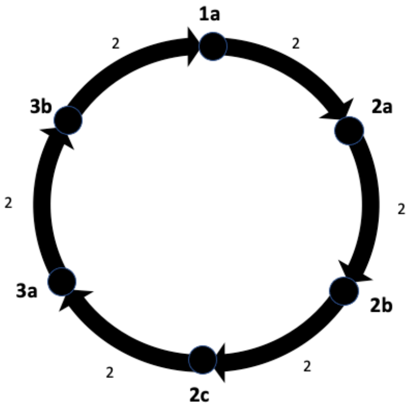


Figure A3.17: 2 complete song cycles present. The individual faithfully cycled through all themes in the same order each time.

5/09/19 (1 song cycle)

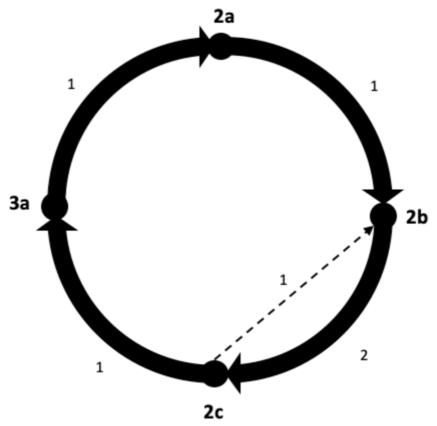


Figure A3.18: 1 complete song cycle present. The individual faithfully cycled through each theme with some switching between within theme 2 b themes before moving onto theme 3 to complete the song cycle

15/09/19 (4 song cycles)

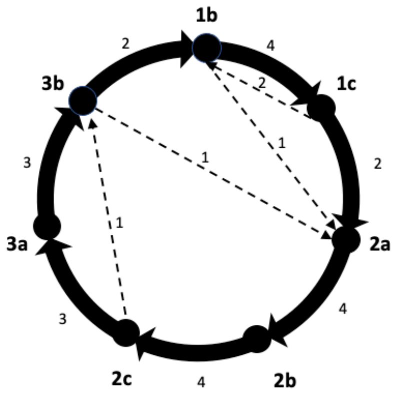


Figure A3.19: 4 complete song cycles present: The individual shows more variation in transferring between theme 1 and 2 than in earlier songs and even omits theme 1 altogether from one song cycle

Appendix 3.8: Levenshtein Distance Analysis Dendrograms

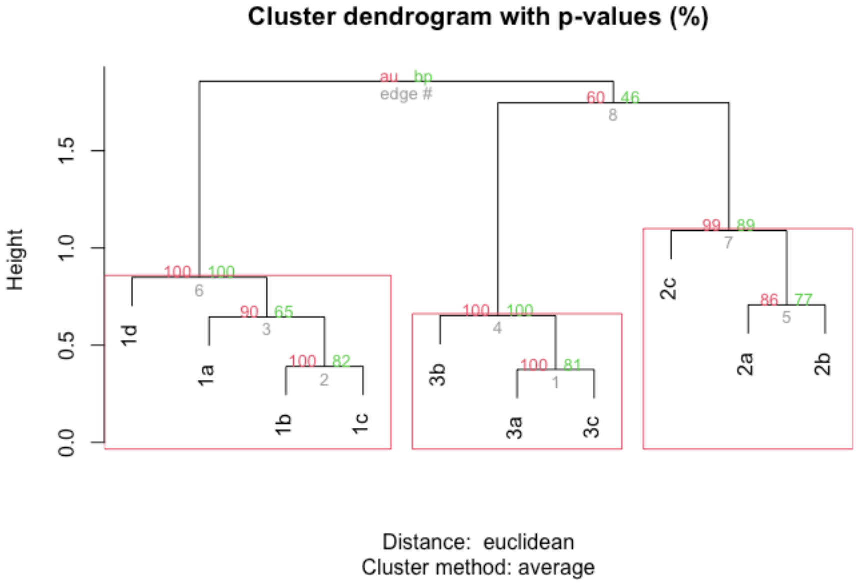


Figure A3.20: Dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Cook Islands 2019 Song 1 Type (CCC = 0.9922726). Branches with high AU values are strongly supported by the data. – UNWEIGHTED

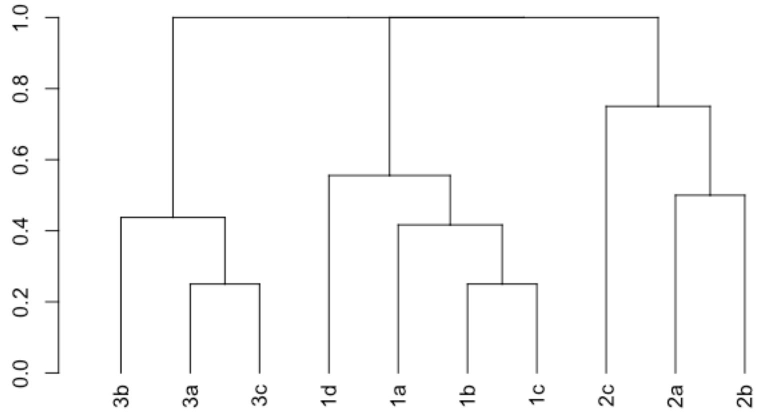


Figure A3.21: Figure 1: Dendrogram of similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Cook Islands 2019 Song 1 Type (CCC = 0.9922726) – UNWEIGHTED

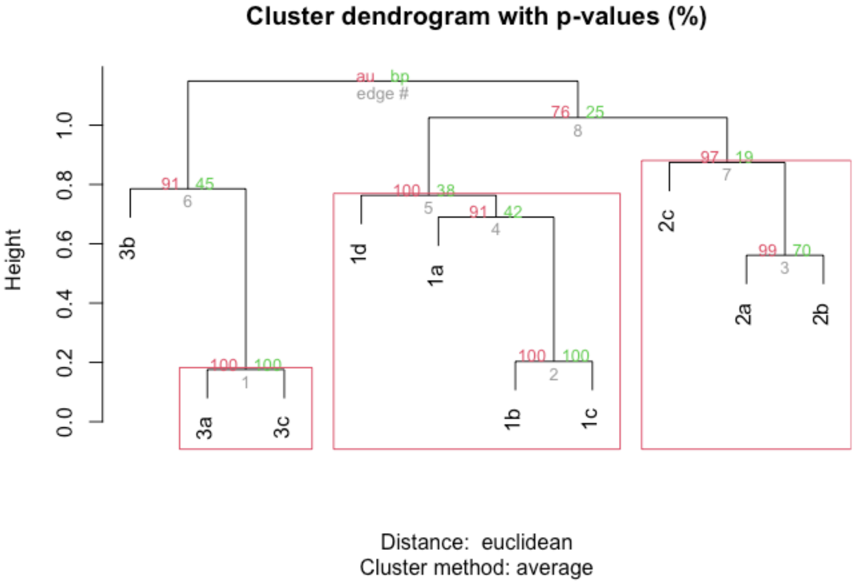


Figure A3.22. Dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Cook Islands 2019 Song 1 Type (CCC = 0.802) – WEIGHTED

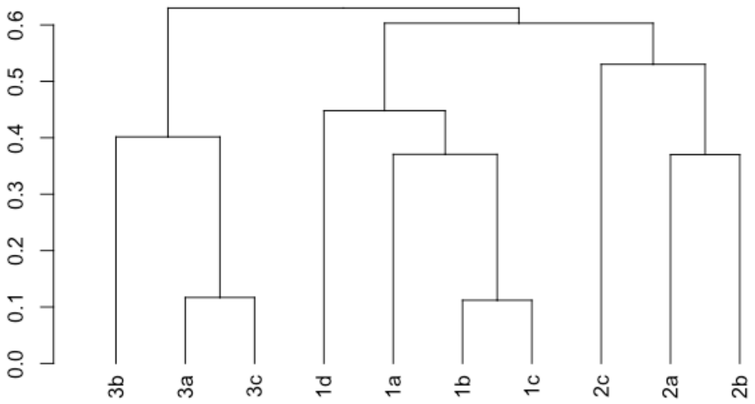


Figure A3.23: Dendrogram of similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Cook Islands 2019 Song 1 Type (CCC = 0.802) - UNWEIGHTED

Table 1: Phrases applied to each core theme type

Phrase Code	New Theme Name
1a, 1b, 1c, 1d	RED
2a, 2b, 2c	GREEN
3a, 3b, 3c	BLUE

Appendix 3.9: PCA and heatmaps of original units

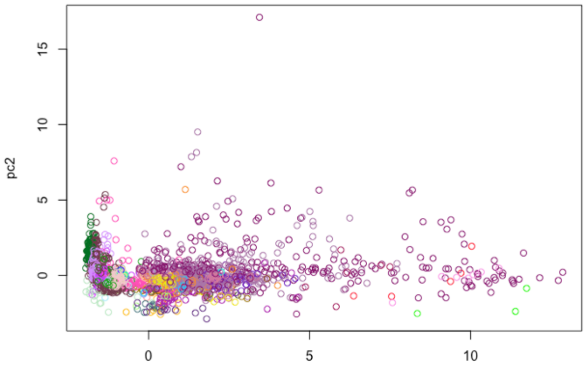


Figure A3.24: PC1 vs PC2

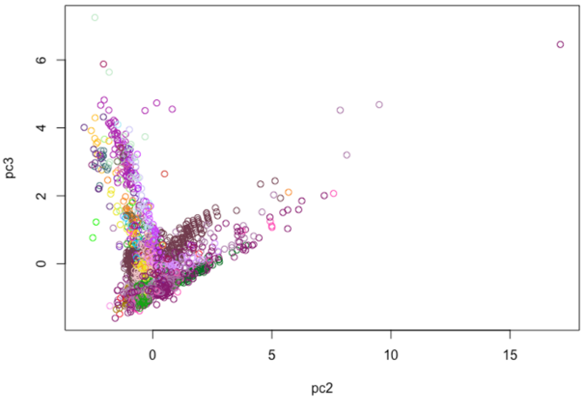


Figure A3.25: PC2 vs PC3

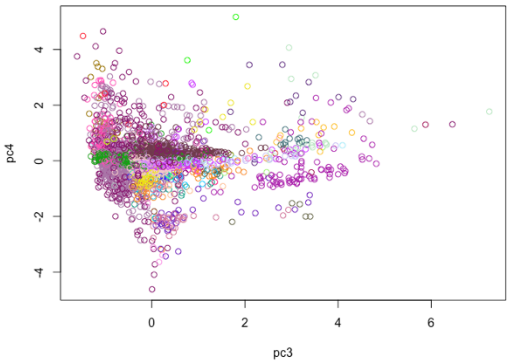


Figure A3.26: PC3 VS PC4

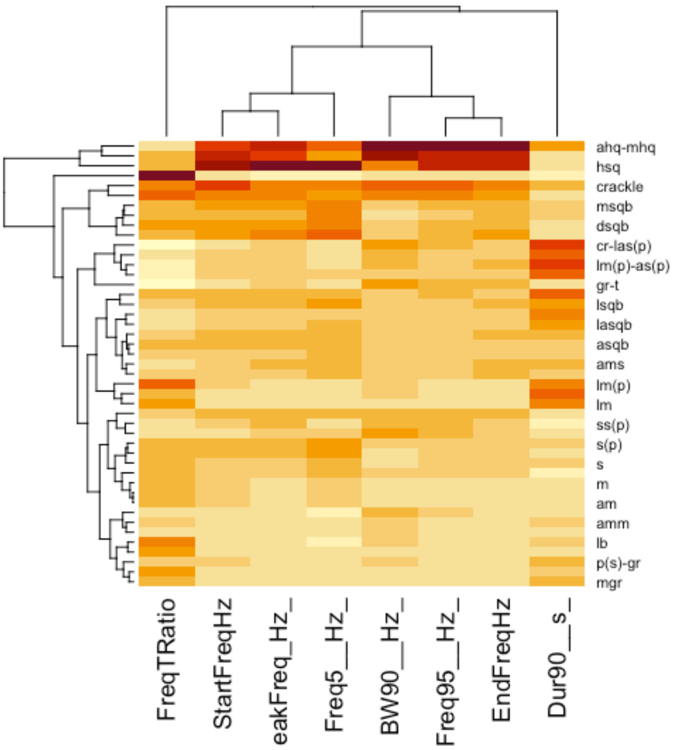


Figure A3.27: Dendrogram and heat map showing the relationship between unit types and measurement types

Appendix 3.10

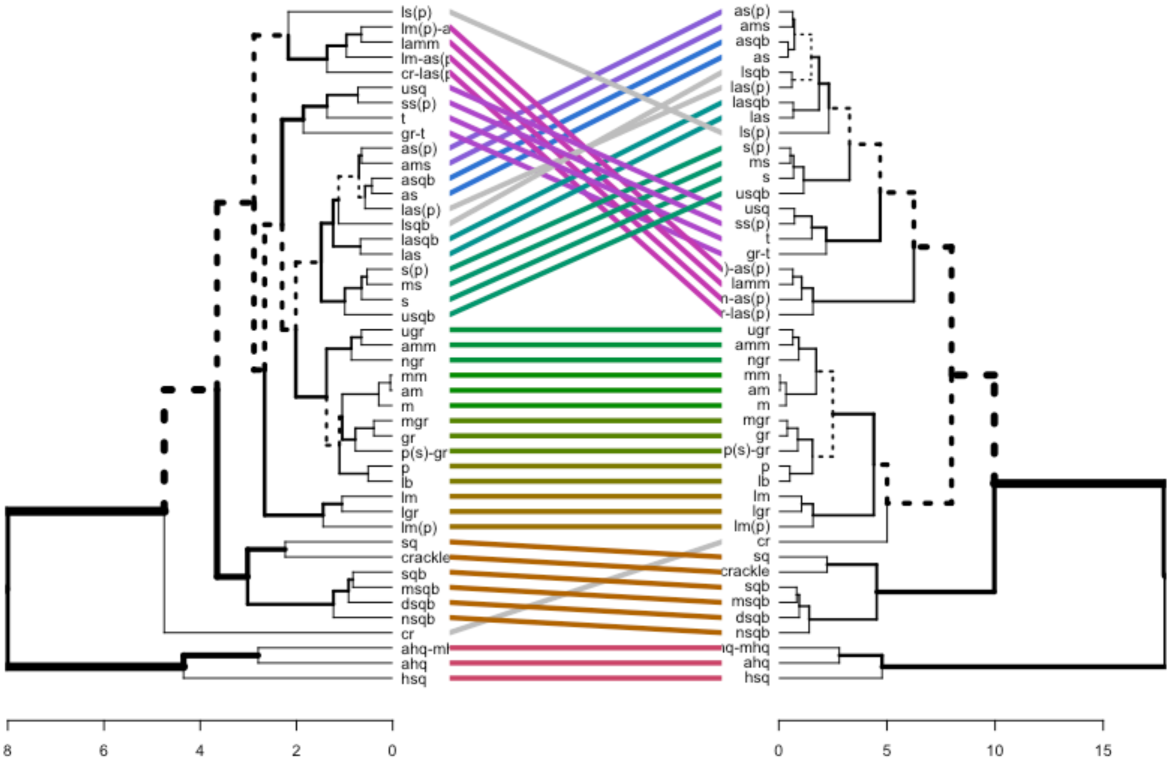


Figure A3.28: Linkage diagram of two dendrograms created by different linkage methods – WARD2 or Average-linkage.

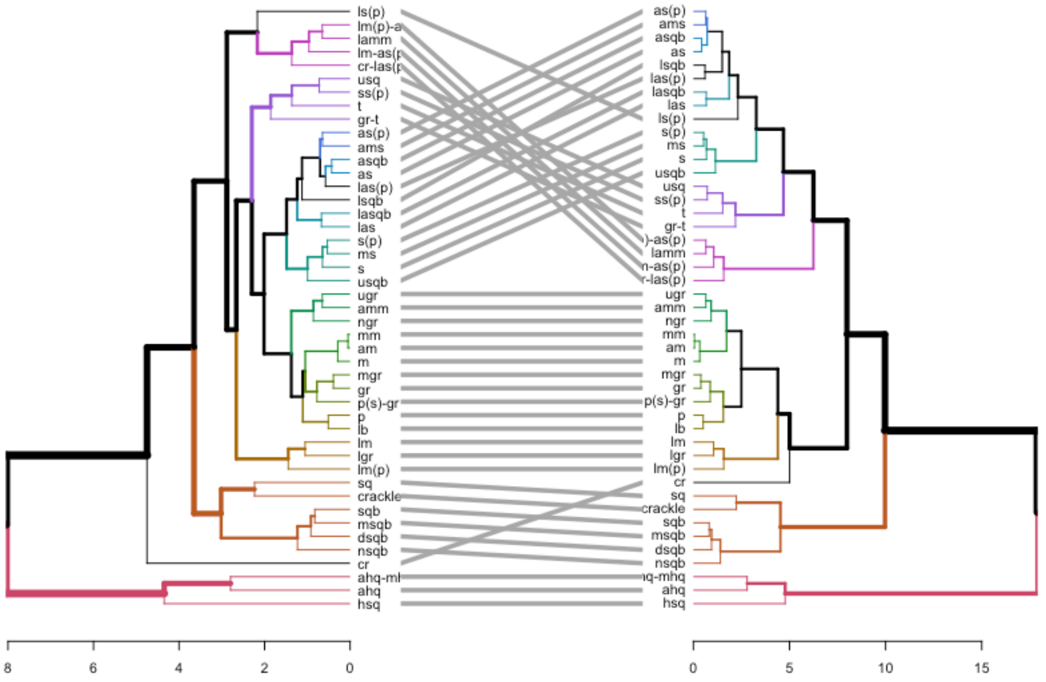


Figure A3.29: Linkage diagram of two dendrograms created by different linkage methods – WARD2 or Average-linkage. Linkage methods were compared with ward 2 showing a correlation of 0.8550327 and average linkage showing a correlation of 0.9164767. Average linkage method was therefore chosen to progress the analysis. Figure 22 (above) shows the correlation between the two linkage methods with an output of 0.1282431 (lower number is a better alignment).

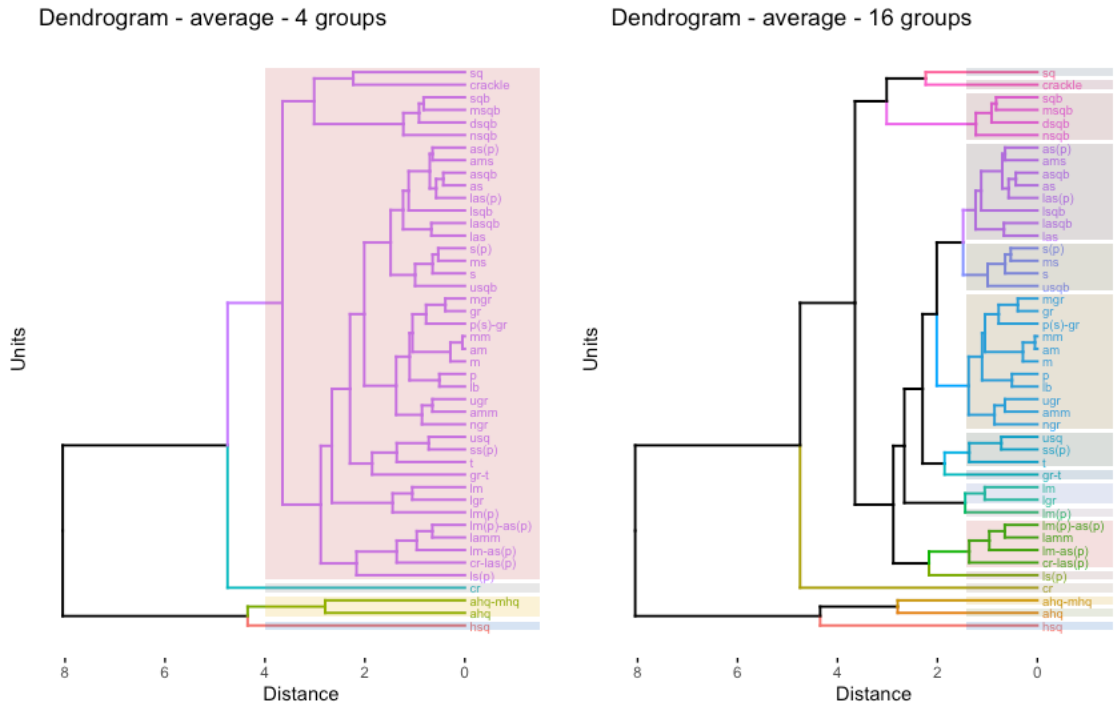


Figure A3.30: Average linkage dendrograms partitioned into 4 (left) or 16 groups (right)

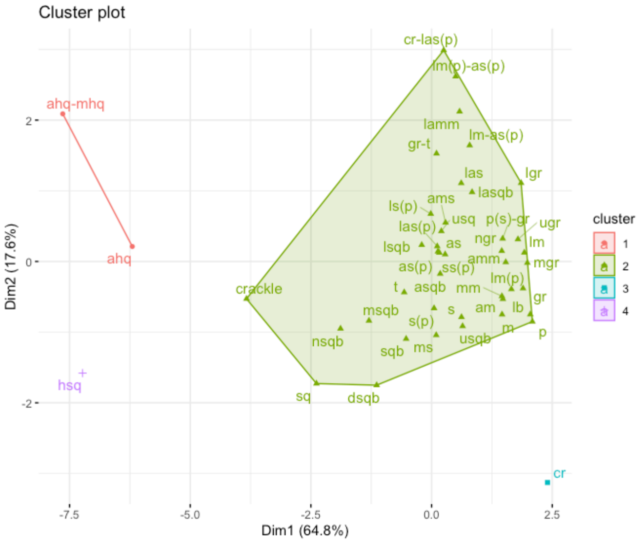


Figure A3.31: Cluster plot visualising the song units partitioned into four groups

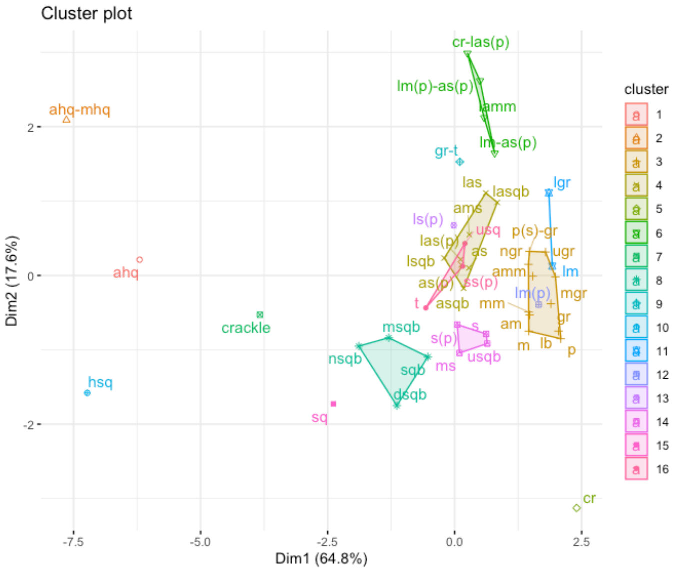


Figure A3.32: Cluster plot visualising the song units partitioned into 16 groups

Appendix 3.11: Complete list of original unit types committed to the meta-unit "Groan"

Original Unit	Full name	New Category
mgr	Modulated groan	GROAN
gr	groan	
p(s)-gr	Short purr connected to groan	
mm	Modulated moan	
am	Ascending moan	
m	moan	
p	purr	
lb	Long bark	
ugr	u-shaped groan	
amm	Ascending modulated moan	
ngr	n-shaped groan	
lm	Long moan	
lgr	Long groan	
lamm	Long ascending modulated moan	
lm(p)	Long moan (pulsated)	

Appendix 3.12:

Table 2: Data points removed from analysis. Six rows were removed from the data analysis prior to analysis detailed in Table 4. Additionally, three observations did not include a MATLAB output for Start and End Frequency and were also removed from the analysis.

Row number (Row number in excel)	Unit/Theme/SONG	Reason
2125 (2126)	gr (2d/3a) SONG 1	No MATLAB outputs
2737 (2738)	gr2 (6) SONG 2	No MATLAB outputs
3494 (3495)	lb (1c) SONG 1	0 values for low frequency – no MATLAB outputs
3364 (3365)	Lb (1c) SONG 1	Blue theme strange discrepancy
2412 (2413)	ngr (1d) SONG1	Red theme strange discrepancy
2419 (2420)	ngr (1d) SONG1	Red theme strange discrepancy

Appendix 3.13

Groan Unit type

Table 3: The mantel test outputs and number of comparisons inputted to each test

Theme	Within or Out with Recording	Number	Triangle Number	Mantel Statistic	P Value
RED	Within Recording	26230	26106	-0.01496	0.993
RED	Across Season	79070	79003	**0.03116**	0.001**
BLUE	Within Recording	191412	191271	**0.03728**	0.001**
BLUE	Across Season	738848	738720	-0.08384	1
GREEN	Within Recording	41184	41041	-0.02106	1
GREEN	Across Season	140718	140715	**0.006054**	0.018*

Red Theme

Within hour

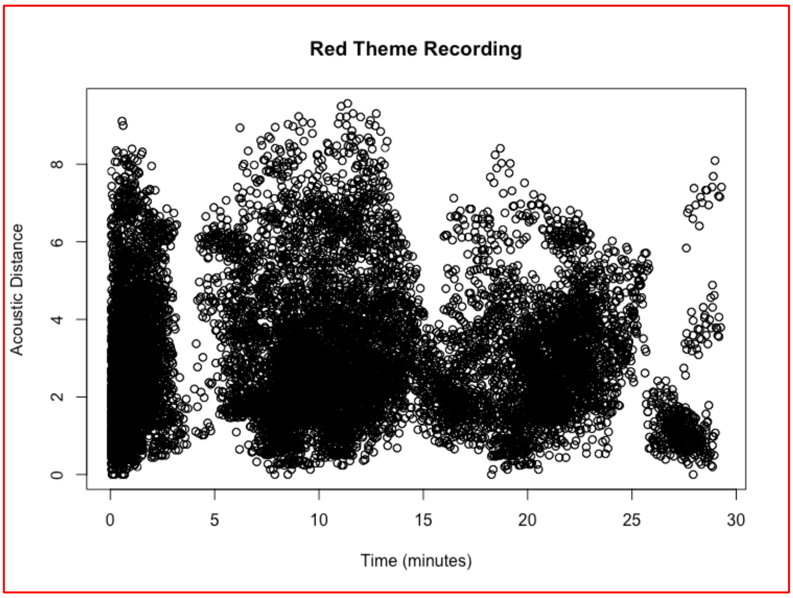


Figure A3.33: Red Theme Acoustic Distance over time – within recording. There was no relationship between acoustic distance of units and time (Mantel statistic R: -0.01496, p value = 0.993). In other words, when units became further apart in time across the recording they did not become more dissimilar in structure.

Out with hour

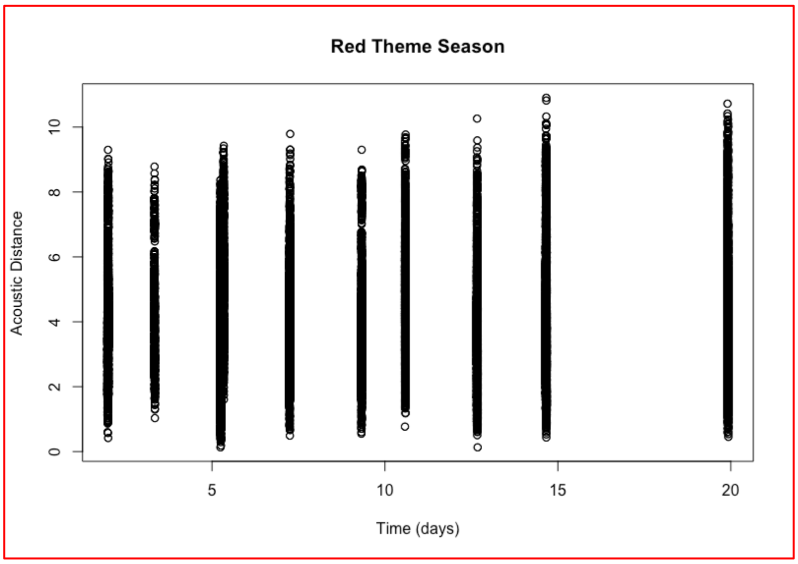


Figure A3.34: Red Theme Acoustic Distance over time – over season. Although weak there are some points occurring at higher points later in the season which suggests that at least some productions of that unit are getting a bit more different. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.03116, p value = 0.001). However, this change was negligible being close to 0. In other words when units became further apart in time across the season they did not become noticeably dissimilar in structure.

Green Theme

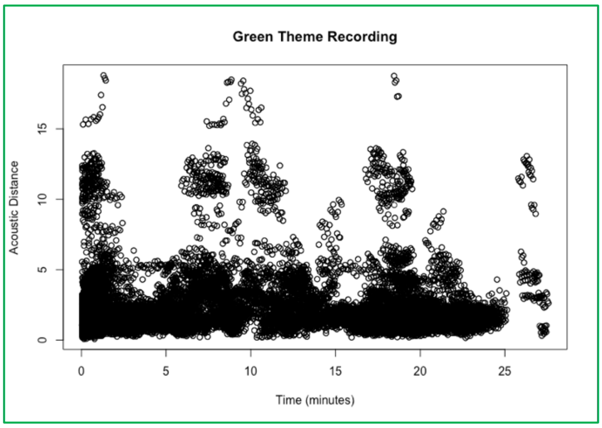


Figure A3.35: There was no relationship between acoustic distance of units and time (Mantel statistic R: -0.02106, p value = 1). In other words when units became further apart in time across the recording they did not become more dissimilar in structure.

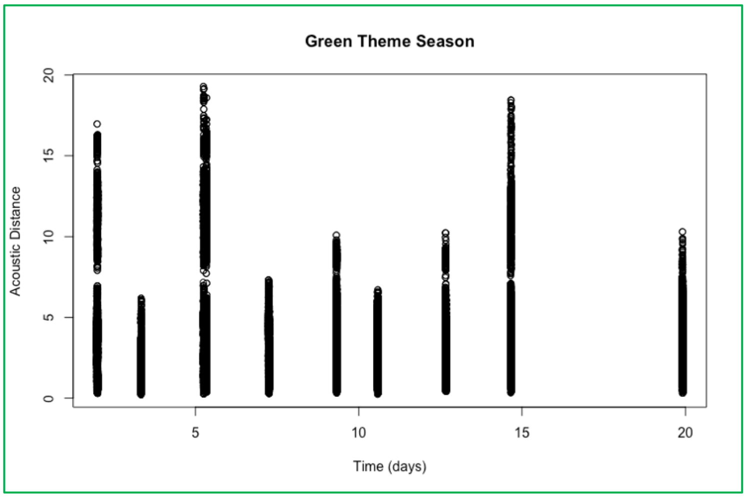


Figure A3.36: Green theme season. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.006054, p value = 0.018). However, this change was negligible being close to 0. In other words when units became further apart in time across the recording they did not become more dissimilar in structure.

Blue Theme

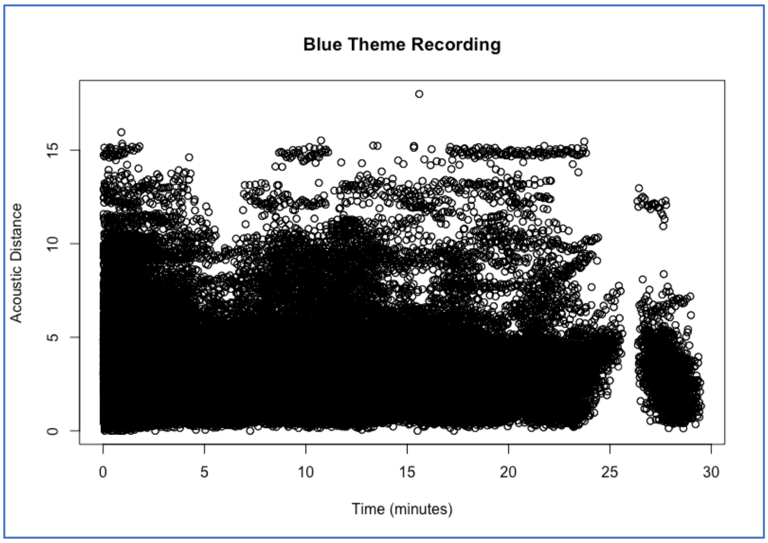


Figure A3.37: Blue within recording. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.03728, p value = 0.001). However, this change was negligible being close to 0. In other words when units became further apart in time across the recording they did not become noticeably more dissimilar in structure.

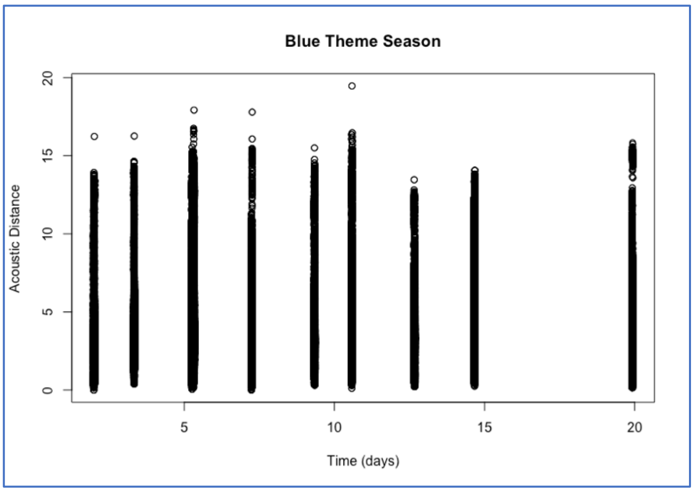


Figure A3.38: Blue theme season. There was no relationship between acoustic distance of units and time (Mantel statistic R: -0.08384p value = 1). In other words when units became further apart in time across the recording they did not become more dissimilar in structure.

Appendix 3.14: Test for Call Divergence

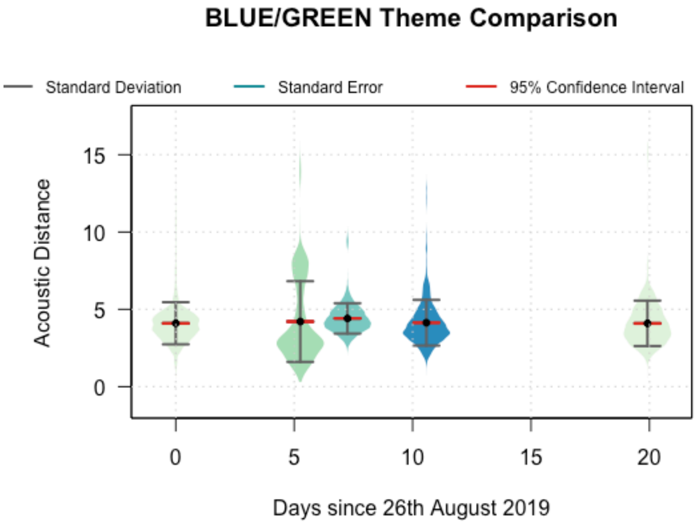


Figure A3.39: Test for Call Divergence. Blue Vs Green Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryBlueGreenComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant ($R^2 =$ 0.008522, F(1, 3) = 0.02579, p = 0.8826

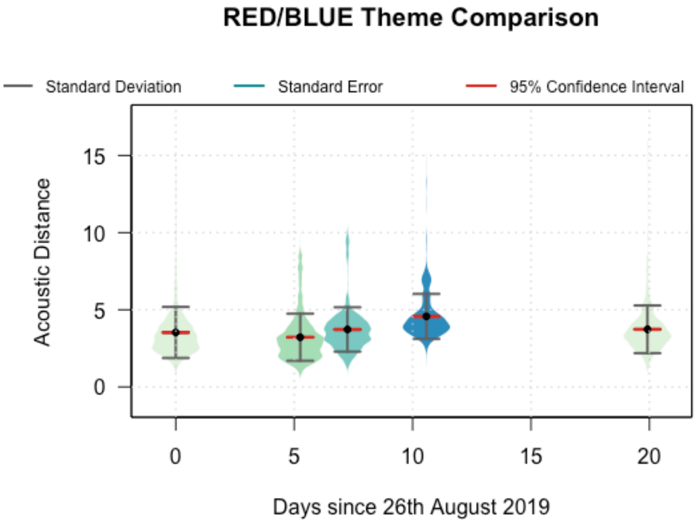


Figure A3.40: Test for Call Divergence Red Vs Blue Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryRedBlueComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant ($R^2 =$ 0.1444, F(1, 3) = 0.5062, p = 0.5281).

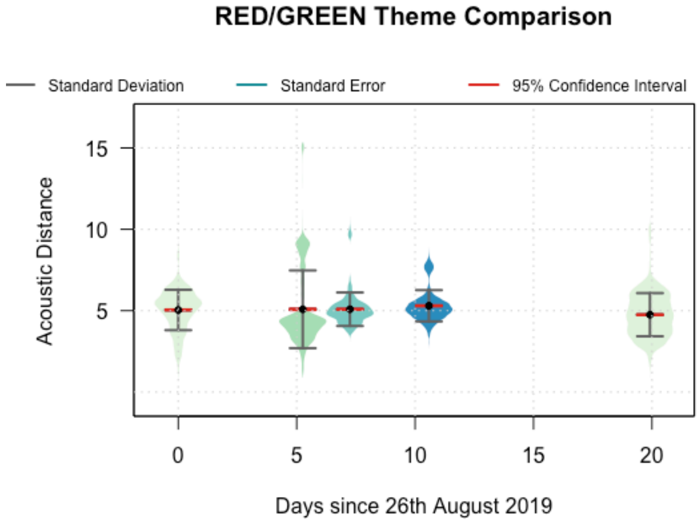


Figure A3.41: Test for Call Divergence: Red Vs Green Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryRedGreenComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant ($R^2 = 0.06956$, $F(1, 3) = 0.2243$, $p = 0.6681$).

Appendix 3.15: Test for Call Modification – Discrete Measurements

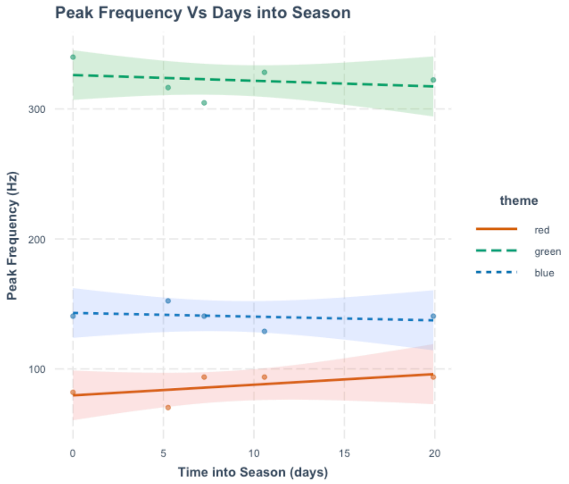


Figure A3.42: Across Season: Peak Frequency. No change in median peak frequency over the season was detected in any theme type. Each theme type groan showed a significantly different peak frequency value over the season.

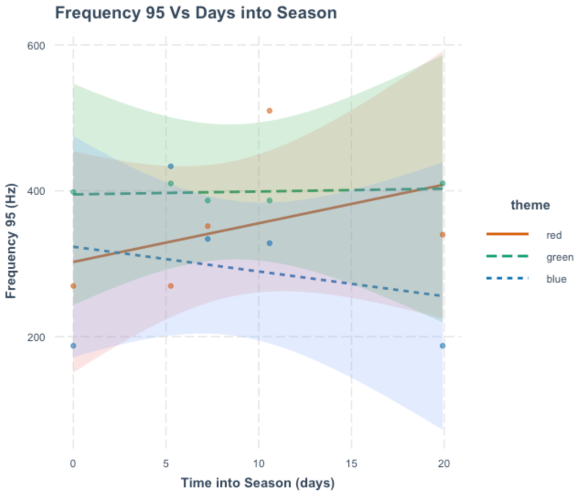


Figure A3.43: Across Season: Frequency 95. No change in median frequency 95 over the season was detected in any theme type. Frequency 95 in groans from each theme type were found not to be significantly different from each other.

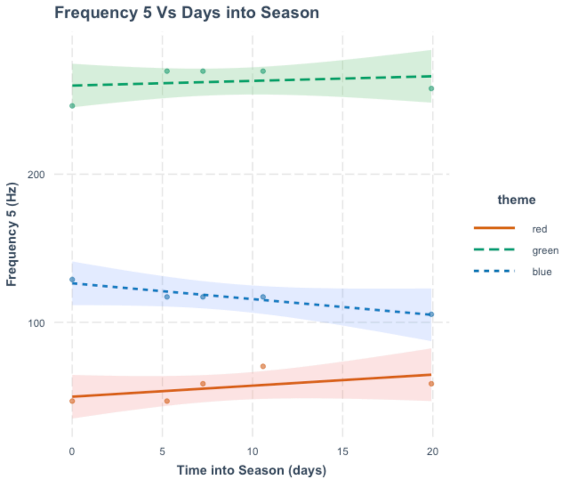


Figure A3.44: Across Season: Frequency 5: No change in median Frequency 5 over the season was detected in any theme type. Each theme type groan showed a significantly different Frequency 5 value over the season.

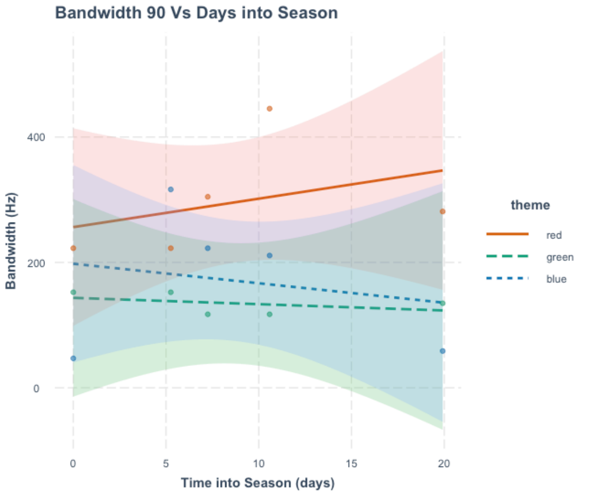


Figure A3.45: Across Season: Bandwidth 90. No change in median Bandwidth 90 over the season was detected in any theme type Bandwidth 90 in groans from each theme type were found not to be significantly different from each other.

Table 4: Model output of 4 measurement types (Peak Frequency, Frequency 95, Frequency 5 and Bandwidth)

	Peak Frequency	Frequency 95	Frequency 5	Bandwidth
(Intercept)	79.679***	302.443**	49.838***	256.286**
	[60.570, 98.789]	[150.651, 454.234]	[35.140, 64.537]	[98.724, 413.849]
	s.e. = 8.447	s.e. = 67.100	s.e. = 6.497	s.e. = 69.651
	t = 9.432	t = 4.507	t = 7.670	t = 3.680
	p = 0.000	p = 0.001	p = 0.000	p = 0.005
TimeDays	0.818	5.302	0.745	4.537
	[-0.942, 2.579]	[-8.685, 19.289]	[-0.609, 2.100]	[-9.982, 19.056]
	s.e. = 0.778	s.e. = 6.183	s.e. = 0.599	s.e. = 6.418
	t = 1.051	t = 0.858	t = 1.245	t = 0.707
	p = 0.320	p = 0.413	p = 0.245	p = 0.497
themegreen	**246.366*** **	92.617	**209.952*** **	-112.836
	[219.342, 273.391]	[-122.049, 307.282]	[189.165, 230.738]	[-335.663, 109.992]
	s.e. = 11.946	s.e. = 94.894	s.e. = 9.189	s.e. = 98.502
	t = 20.623	t = 0.976	t = 22.849	t = -1.146
	p = 0.000	p = 0.355	p = 0.000	p = 0.282
themeblue	**63.398*** **	20.861	**76.518*** **	-58.428
	[36.373, 90.423]	[-193.804, 235.527]	[55.731, 97.304]	[-281.255, 164.399]
	s.e. = 11.946	s.e. = 94.894	s.e. = 9.189	s.e. = 98.502
	t = 5.307	t = 0.220	t = 8.327	t = -0.593
	p = 0.000	p = 0.831	p = 0.000	p = 0.568
TimeDays × themegreen	-1.258	-4.909	-0.430	-5.547
	[-3.748, 1.232]	[-24.690, 14.871]	[-2.346, 1.485]	[-26.080, 14.986]
	s.e. = 1.101	s.e. = 8.744	s.e. = 0.847	s.e. = 9.077
	t = -1.143	t = -0.561	t = -0.508	t = -0.611
	p = 0.283	p = 0.588	p = 0.623	p = 0.556
TimeDays × themeblue	-1.104	-8.693	-1.811+	-7.649
	[-3.594, 1.387]	[-28.474, 11.088]	[-3.727, 0.104]	[-28.182, 12.884]
	s.e. = 1.101	s.e. = 8.744	s.e. = 0.847	s.e. = 9.077
	t = -1.002	t = -0.994	t = -2.139	t = -0.843
	p = 0.342	p = 0.346	p = 0.061	p = 0.421
Num.Obs.	15	15	15	15
R2	0.992	0.323	0.994	0.489

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

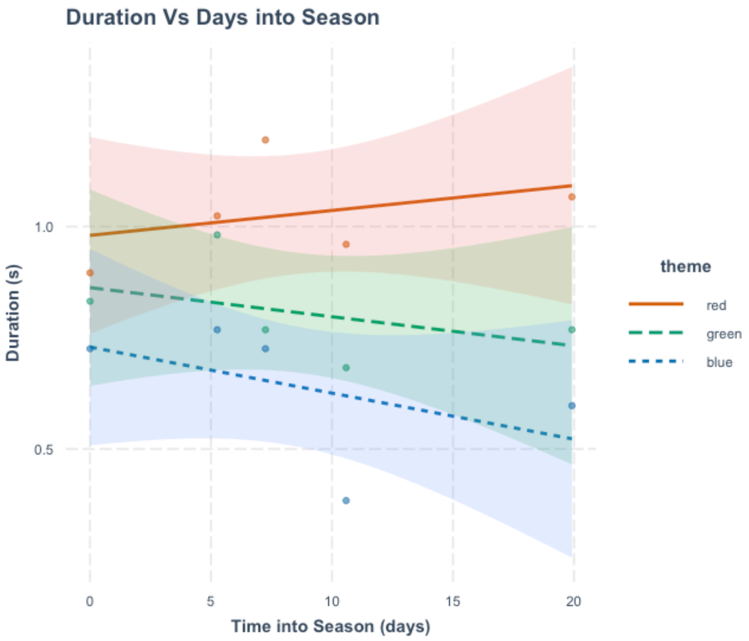


Figure A3.46: Across Season: Duration: No change in median duration over the season was detected in any theme type. Duration in groans from each theme type were found not to be significantly different from each other.

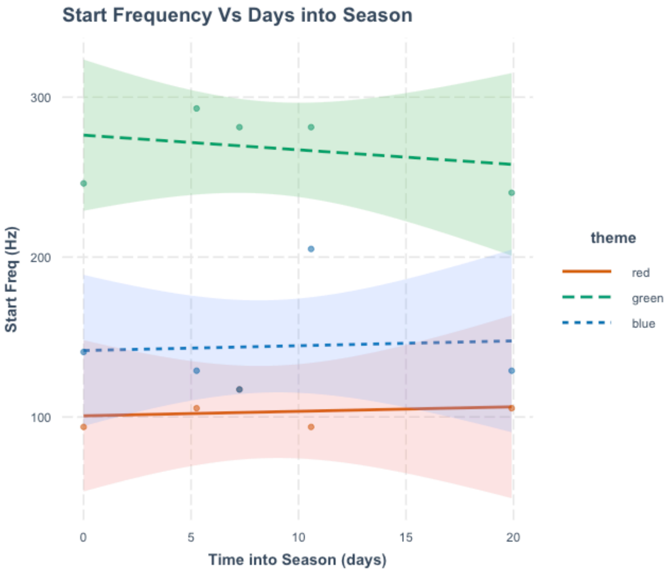


Figure A3.47: Across Season: Start Frequency. No change in median Start Frequency over the season was detected in any theme type. Start Frequency in groans from the green theme type were found to be significantly higher than the blue and red theme types

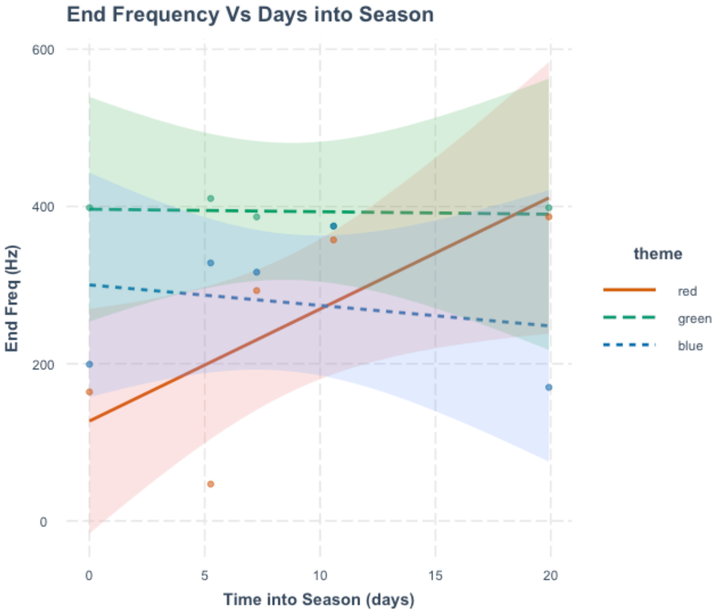


Figure A3.48: Across Season: End Frequency: End frequency was found to change over the season with significant differences between theme types in which the red theme type increased and the blue theme type showed a weak decrease while the green theme type stayed the same.

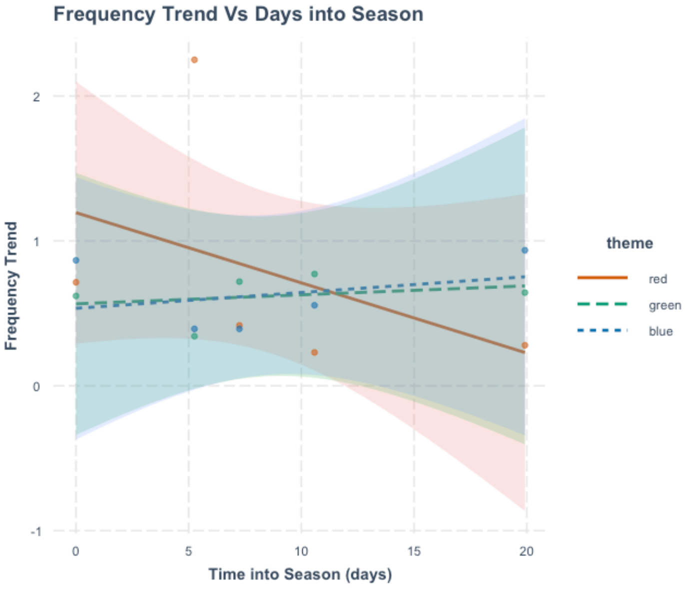


Figure A3.49: Across Season: Frequency Trend. No change in median Frequency Trend over the season was detected in any theme type. Frequency Trend in groans from each theme type were found not to be significantly different from each other.

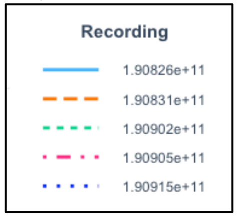
Table 5: Model output of 4 measurement types (Duration, Start Frequency, End Frequency and Frequency Ratio)

	DURATION	START FREQUENCY	END FREQUENCY	FREQUENCY RATIO
(Intercept)	0.980***	100.700***	127.030+	1.195*
	[0.759, 1.201]	[53.438, 147.963]	[-15.823, 269.883]	[0.290, 2.100]
	s.e. = 0.098	s.e. = 20.893	s.e. = 63.149	s.e. = 0.400
	t = 10.042	t = 4.820	t = 2.012	t = 2.987
	p = 0.000	p = 0.001	p = 0.075	p = 0.015
TimeDays	0.006	0.282	**14.252***	-0.048
	[-0.015, 0.026]	[-4.073, 4.637]	[1.088, 27.415]	[-0.132, 0.035]
	s.e. = 0.009	s.e. = 1.925	s.e. = 5.819	s.e. = 0.037
	t = 0.623	t = 0.146	t = 2.449	t = -1.315
	p = 0.549	p = 0.887	p = 0.037	p = 0.221
themegreen	-0.117	**175.552*****	269.462*	-0.629
	[-0.430, 0.195]	[108.713, 242.391]	[67.438, 471.487]	[-1.909, 0.651]
	s.e. = 0.138	s.e. = 29.547	s.e. = 89.306	s.e. = 0.566
	t = -0.851	t = 5.942	t = 3.017	t = -1.112
	p = 0.417	p = 0.000	p = 0.015	p = 0.295
themeblue	-0.251	40.847	173.198+	-0.660
	[-0.563, 0.061]	[-25.992, 107.686]	[-28.826, 375.223]	[-1.940, 0.620]
	s.e. = 0.138	s.e. = 29.547	s.e. = 89.306	s.e. = 0.566
	t = -1.819	t = 1.382	t = 1.939	t = -1.167
	p = 0.102	p = 0.200	p = 0.084	p = 0.273
TimeDays × themegreen	-0.012	-1.200	-14.570	0.055
	[-0.041, 0.017]	[-7.359, 4.959]	[-33.186, 4.045]	[-0.063, 0.173]
	s.e. = 0.013	s.e. = 2.723	s.e. = 8.229	s.e. = 0.052
	t = -0.955	t = -0.441	t = -1.771	t = 1.049
	p = 0.365	p = 0.670	p = 0.110	p = 0.322
TimeDays × themeblue	-0.016	0.020	**-16.867+**	0.059
	[-0.045, 0.013]	[-6.139, 6.179]	[-35.483, 1.749]	[-0.059, 0.177]
	s.e. = 0.013	s.e. = 2.723	s.e. = 8.229	s.e. = 0.052
	t = -1.255	t = 0.007	t = -2.050	t = 1.139
	p = 0.241	p = 0.994	p = 0.071	p = 0.284
Num.Obs.	15	15	15	15
R2	0.725	0.910	0.610	0.190

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Appendix 3.16 – Discrete Measurements – Song Session – Test outputs

Duration over Song Session



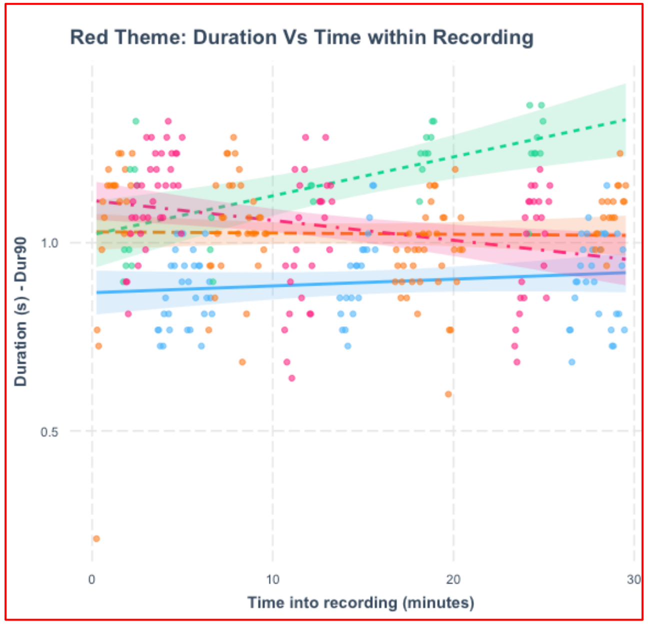


Figure A3.50: Significant difference in trend between individuals within song session. 02 increases at a faster rate while 15 decreases as compared to 26.

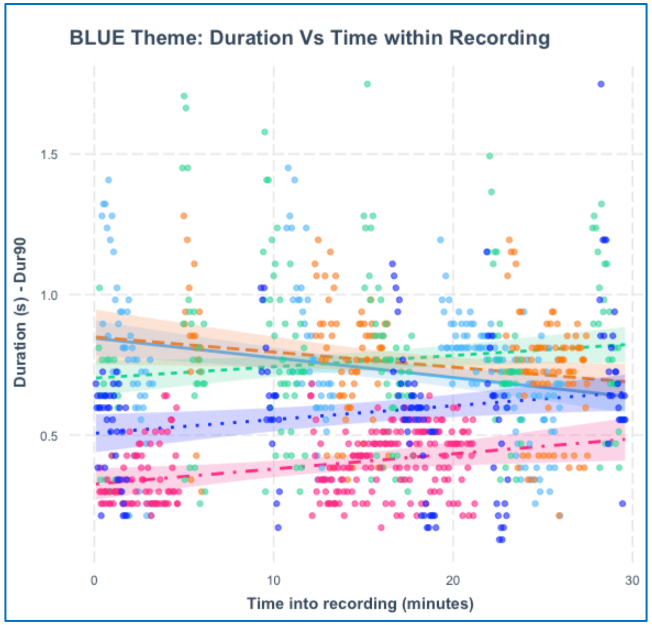


Figure A3.51: Significant difference in trend between individuals within song session. 02, 15 and 05 increase while 26 and 31 both decrease at the same rate.

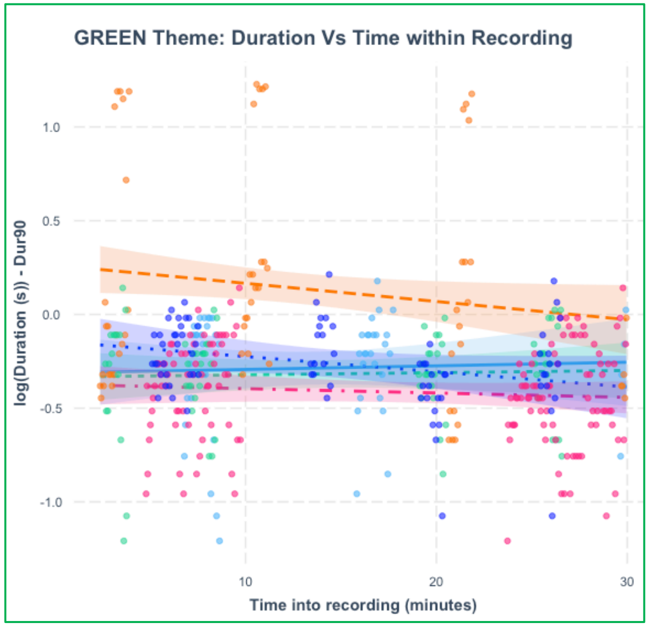


Figure A3.52: No significant difference in trend between individuals within song session. Individual 31 begins with longer groan units than individual 26.

ID	RED	BLUE	GREEN	Individual across theme change
26	NSC	-0.007***	NSC	Yes
31	-	-	NSC	Yes
02	+0.009**	+0.011***	NSC	Yes
05	NA	+0.012***	NSC	Yes
15	-0.007**	+0.012***	NSC	Yes

Table 6:

Duration – Within Recording

	RED	BLUE	GREEN
(Intercept)	0.867***	0.845***	-0.313**
	[0.808, 0.926]	[0.782, 0.909]	[-0.515, -0.111]
	s.e. = 0.030	s.e. = 0.032	s.e. = 0.103
	t = 29.082	t = 26.079	t = -3.049
	p = 0.000	p = 0.000	p = 0.002
Time5__s_	0.002	**-0.007*** **	0.002
	[-0.001, 0.005]	[-0.011, -0.003]	[-0.011, 0.015]
	s.e. = 0.002	s.e. = 0.002	s.e. = 0.007
	t = 1.138	t = -3.857	t = 0.286
	p = 0.256	p = 0.000	p = 0.775
Recording1.90831e+11	**0.162*** **	0.004	**0.576*** **
	[0.086, 0.237]	[-0.113, 0.121]	[0.329, 0.823]
	s.e. = 0.038	s.e. = 0.060	s.e. = 0.126
	t = 4.201	t = 0.070	t = 4.579
	p = 0.000	p = 0.944	p = 0.000
Recording1.90902e+11	**0.154** **	**-0.142** **	-0.021
	[0.047, 0.261]	[-0.232, -0.053]	[-0.267, 0.225]
	s.e. = 0.054	s.e. = 0.045	s.e. = 0.125
	t = 2.828	t = -3.131	t = -0.170
	p = 0.005	p = 0.002	p = 0.865
Recording1.90915e+11	**0.245*** **	**-0.339*** **	0.169
	[0.167, 0.323]	[-0.432, -0.246]	[-0.088, 0.427]
	s.e. = 0.040	s.e. = 0.047	s.e. = 0.131
	t = 6.183	t = -7.148	t = 1.295
	p = 0.000	p = 0.000	p = 0.196
Time5__s_ × Recording1.90831e+11	-0.002	0.002	-0.012
	[-0.006, 0.002]	[-0.004, 0.008]	[-0.028, 0.005]
	s.e. = 0.002	s.e. = 0.003	s.e. = 0.008
	t = -0.985	t = 0.524	t = -1.406
	p = 0.326	p = 0.600	p = 0.160
Time5__s_ × Recording1.90902e+11	**0.009** **	**0.011*** **	-0.001
	[0.002, 0.015]	[0.006, 0.016]	[-0.016, 0.015]
	s.e. = 0.003	s.e. = 0.003	s.e. = 0.008
	t = 2.700	t = 4.236	t = -0.096
	p = 0.007	p = 0.000	p = 0.924
Time5__s_ × Recording1.90915e+11	**-0.007** **	**0.012*** **	-0.010
	[-0.012, -0.002]	[0.007, 0.017]	[-0.026, 0.006]
	s.e. = 0.002	s.e. = 0.003	s.e. = 0.008
	t = -2.961	t = 4.538	t = -1.202
	p = 0.003	p = 0.000	p = 0.230
Recording1.90905e+11		-0.520***	-0.060
		[-0.604, -0.435]	[-0.291, 0.171]
		s.e. = 0.043	s.e. = 0.118

		t = -12.041	t = -0.508
		p = 0.000	p = 0.611
Time5__s_ × Recording1.90905e+11		**0.012*****	-0.004
		[0.007, 0.018]	[-0.019, 0.010]
		s.e. = 0.003	s.e. = 0.007
		t = 4.540	t = -0.583
		p = 0.000	p = 0.561
Num.Obs.	305	965	427
R2	0.298	0.336	0.245

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Peak Frequency Over Time within recording

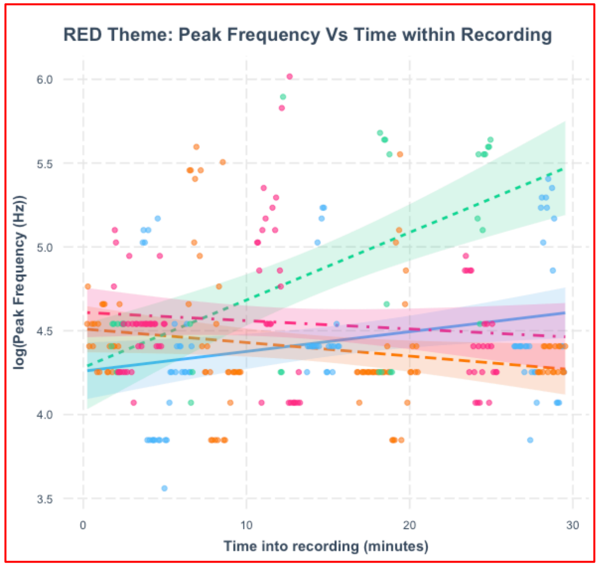


Figure A3.53: All four individuals were significantly changing the peak frequency of the groan unit over time in the red theme. Two individuals (26, 02) increased the their peak frequency while two individuals (31, 15) decreased their peak frequency. 26 and 02 started off with a similar frequency and while both increased in frequency over the duration of their song session – 02 increased at faster rate.

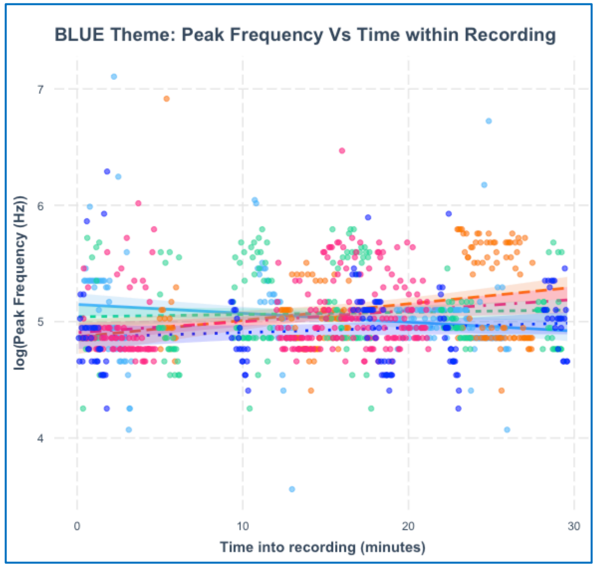


Figure A3.54: Significant difference in trend between individuals within song sessions. One individual (26) is decreasing their peak frequency – while the other 4 individuals are increasing their peak frequency.

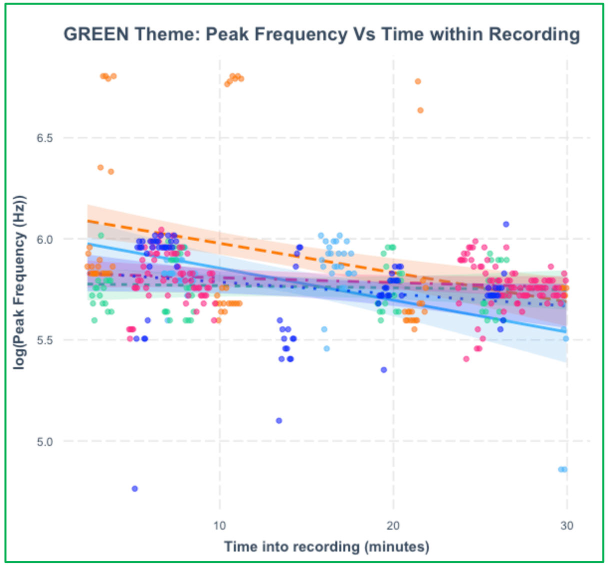


Figure A3.55: Significant difference in trend between individuals within song sessions. 26 and 31 decreasing in the same way while 02, 05 and 15 decreasing at much lower rate.

Table 7:

ID	RED	BLUE	GREEN	Individual across theme change
26	+0.012*	-0.008**	-0.016***	Yes
31	-0.020	+0.022	-0.167+	Yes
02	+0.029	+0.010*	**+0.015****	Yes
05	NA	**+0.017*****	**+0.013****	No
15	**-0.017***	**+0.012****	**+0.010+**	Yes

Table 8:

	WITHIN RECORDING - PEAK FREQUENCY		
	RED	BLUE	GREEN
(Intercept)	4.259***	5.148***	6.013***
	[4.089, 4.429]	[5.052, 5.243]	[5.881, 6.145]
	s.e. = 0.086	s.e. = 0.048	s.e. = 0.067
	t = 49.287	t = 106.306	t = 89.768
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	**0.012***	**-0.008****	**-0.016*****
	[0.003, 0.021]	[-0.013, -0.002]	[-0.024, -0.007]
	s.e. = 0.005	s.e. = 0.003	s.e. = 0.004
	t = 2.568	t = -2.804	t = -3.595
	p = 0.011	p = 0.005	p = 0.000
Recording1.90831e+11	**0.252***	**-0.279****	0.110
	[0.033, 0.472]	[-0.453, -0.104]	[-0.052, 0.271]
	s.e. = 0.112	s.e. = 0.089	s.e. = 0.082
	t = 2.260	t = -3.136	t = 1.338
	p = 0.025	p = 0.002	p = 0.182
Recording1.90902e+11	0.022	-0.106	**-0.234****
	[-0.289, 0.332]	[-0.239, 0.028]	[-0.395, -0.074]
	s.e. = 0.158	s.e. = 0.068	s.e. = 0.082
	t = 0.136	t = -1.556	t = -2.866
	p = 0.892	p = 0.120	p = 0.004
Recording1.90915e+11	**0.351****	**-0.282*****	**-0.167+**
	[0.125, 0.577]	[-0.421, -0.143]	[-0.335, 0.000]
	s.e. = 0.115	s.e. = 0.071	s.e. = 0.085
	t = 3.054	t = -3.981	t = -1.960
	p = 0.002	p = 0.000	p = 0.051
Time5__s_ × Recording1.90831e+11	**-0.020****	**0.022*****	0.001
	[-0.032, -0.008]	[0.013, 0.031]	[-0.009, 0.012]
	s.e. = 0.006	s.e. = 0.005	s.e. = 0.005
	t = -3.187	t = 4.720	t = 0.244
	p = 0.002	p = 0.000	p = 0.808
Time5__s_ × Recording1.90902e+11	**0.029****	**0.010***	**0.015****
	[0.010, 0.047]	[0.002, 0.017]	[0.005, 0.025]
	s.e. = 0.009	s.e. = 0.004	s.e. = 0.005
	t = 3.112	t = 2.459	t = 2.844
	p = 0.002	p = 0.014	p = 0.005
Time5__s_ × Recording1.90915e+11	**-0.017***	**0.012****	**0.010+**
	[-0.030, -0.003]	[0.004, 0.019]	[-0.001, 0.021]
	s.e. = 0.007	s.e. = 0.004	s.e. = 0.005
	t = -2.411	t = 2.987	t = 1.813
	p = 0.017	p = 0.003	p = 0.070
Recording1.90905e+11		**-0.242*****	**-0.182***
		[-0.368, -0.115]	[-0.333, -0.031]

		s.e. = 0.064	s.e. = 0.077
		t = -3.747	t = -2.367
		p = 0.000	p = 0.018
Time5__s_ × Recording1.90905e+11		__0.017***__	__0.013**__
		[0.009, 0.025]	[0.004, 0.023]
		s.e. = 0.004	s.e. = 0.005
		t = 4.185	t = 2.822
		p = 0.000	p = 0.005
Num.Obs.	305	965	427
R2	0.191	0.065	0.148

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Frequency 95 over Time within recording

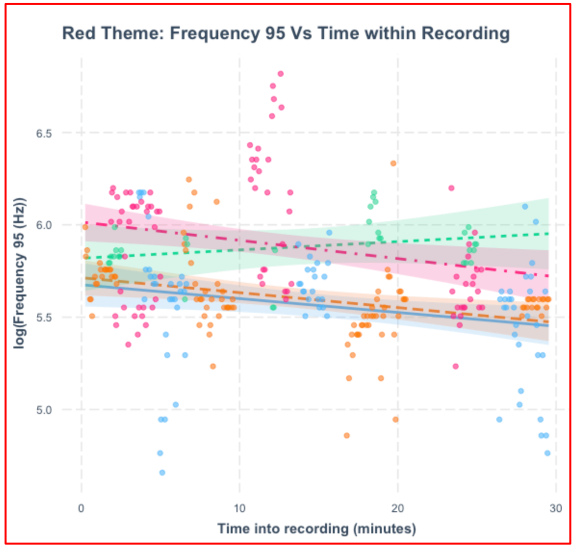


Figure A3.56: Significant difference in trend between individuals within song sessions. All individuals changing in the same way except individual 02 with slight increase in trend (open to error)

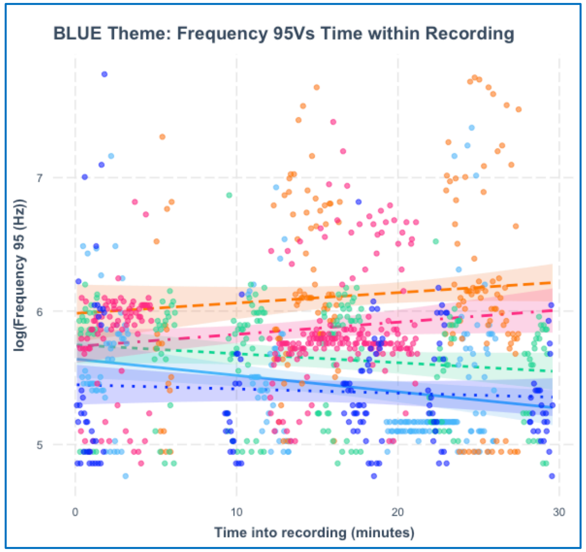


Figure A3.57: Significant difference in trend between individuals within song sessions. 31 and 5 increasing in Frequency 95. 26 and 02 decreasing at the same rate as 26

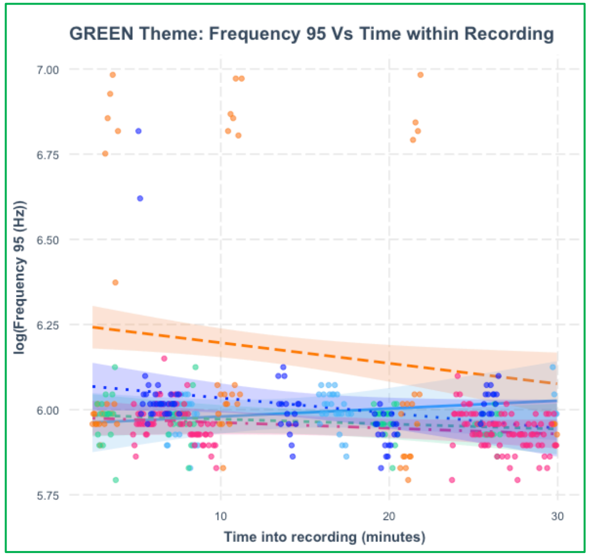


Figure A3.58: Significant difference in trend between individuals within song sessions. 31 decreasing while 26 stays the same

Table 9:

ID	RED	BLUE	GREEN	Individual across theme change
26	**-0.008***	**-0.012****	NSC	Yes
31	-	**0.020****	**-0.008***	Yes
02	**+0.012+**	-	-	Yes
05	NA	**0.021*****	-	Yes
15	-	-	-	Yes

Table 10

Within Recording – Frequency 95

	RED	BLUE	GREEN
(Intercept)	5.676***	5.641***	5.957***
	[5.558, 5.793]	[5.501, 5.781]	[5.856, 6.057]
	s.e. = 0.060	s.e. = 0.071	s.e. = 0.051
	t = 95.123	t = 79.180	t = 116.330
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	**-0.008***	**-0.012****	0.002
	[-0.014, -0.001]	[-0.020, -0.004]	[-0.004, 0.009]
	s.e. = 0.003	s.e. = 0.004	s.e. = 0.003
	t = -2.370	t = -3.075	t = 0.692
	p = 0.018	p = 0.002	p = 0.490
Recording1.90831e+11	0.038	**0.342****	**0.300*****
	[-0.114, 0.190]	[0.085, 0.599]	[0.177, 0.423]
	s.e. = 0.077	s.e. = 0.131	s.e. = 0.063
	t = 0.494	t = 2.615	t = 4.783
	p = 0.622	p = 0.009	p = 0.000
Recording1.90902e+11	0.144	0.106	0.030
	[-0.071, 0.358]	[-0.090, 0.302]	[-0.093, 0.153]
	s.e. = 0.109	s.e. = 0.100	s.e. = 0.062
	t = 1.318	t = 1.062	t = 0.482
	p = 0.189	p = 0.288	p = 0.630
Recording1.90915e+11	**0.339*****	**-0.193+**	0.122+
	[0.183, 0.495]	[-0.397, 0.012]	[-0.006, 0.250]
	s.e. = 0.079	s.e. = 0.104	s.e. = 0.065
	t = 4.277	t = -1.848	t = 1.869
	p = 0.000	p = 0.065	p = 0.062
Time5__s_ × Recording1.90831e+11	-0.001	**0.020****	**-0.008***
	[-0.009, 0.008]	[0.007, 0.033]	[-0.016, 0.000]
	s.e. = 0.004	s.e. = 0.007	s.e. = 0.004
	t = -0.136	t = 2.947	t = -2.026
	p = 0.892	p = 0.003	p = 0.043
Time5__s_ × Recording1.90902e+11	**0.012+**	0.006	-0.004
	[0.000, 0.024]	[-0.006, 0.017]	[-0.012, 0.004]
	s.e. = 0.006	s.e. = 0.006	s.e. = 0.004
	t = 1.895	t = 0.978	t = -0.950
	p = 0.059	p = 0.328	p = 0.343
Time5__s_ × Recording1.90915e+11	-0.002	0.009	-0.007
	[-0.012, 0.007]	[-0.002, 0.020]	[-0.015, 0.001]
	s.e. = 0.005	s.e. = 0.006	s.e. = 0.004
	t = -0.496	t = 1.583	t = -1.620
	p = 0.620	p = 0.114	p = 0.106
Recording1.90905e+11		0.094	0.022
		[-0.092, 0.280]	[-0.093, 0.138]
		s.e. = 0.095	s.e. = 0.059
		t = 0.989	t = 0.381
		p = 0.323	p = 0.704

Time5__s_ × Recording1.90905e+11		**0.021*****	-0.004
		[0.010, 0.033]	[-0.011, 0.003]
		s.e. = 0.006	s.e. = 0.004
		t = 3.567	t = -1.098
		p = 0.000	p = 0.273
Num.Obs.	305	965	427
R2	0.273	0.220	0.203

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Frequency 5 over time within recording

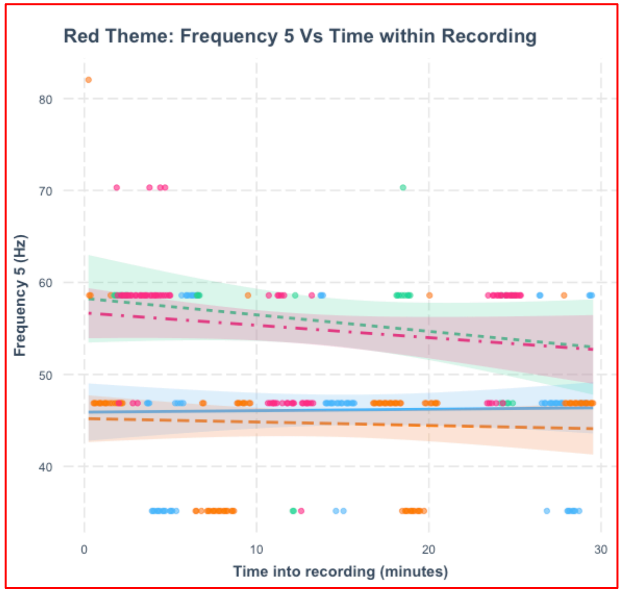


Figure A3.59: No significant difference in trend between individuals. 26 and 15 begin with a significantly higher intercept

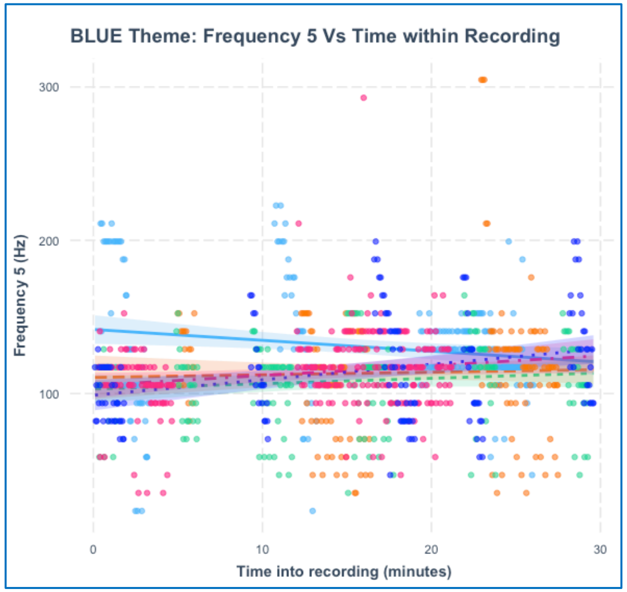


Figure A3.60: Significant difference in trend between individuals within song sessions.

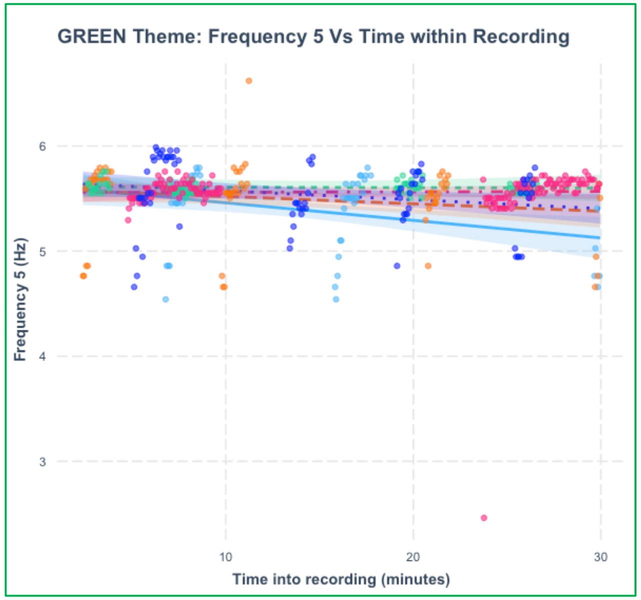


Figure A3.61: Significant difference in trend between individuals within song sessions. 26 decreases while 05 and 02 stay the same

Table 11:

ID	RED	BLUE	GREEN	Individual across theme change
26	NCS	**-0.709****	**-0.017****	Yes
31	-	**+0.880+**	-	Yes
02	-	**+1.059****	**+0.016***	Yes
05	NA	**+1.356*****	**+0.017****	Yes
15	-	**+1.715*****	-	Yes

Table 12:

	Frequency 5 – Within Recording		
	RED	BLUE	GREEN
(Intercept)	45.897***	141.834***	5.627***
	[42.749, 49.045]	[132.552, 151.116]	[5.455, 5.799]
	s.e. = 1.600	s.e. = 4.730	s.e. = 0.088
	t = 28.692	t = 29.989	t = 64.238
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	0.016	**-0.709****	**-0.017****
	[-0.151, 0.183]	[-1.229, -0.189]	[-0.028, -0.005]
	s.e. = 0.085	s.e. = 0.265	s.e. = 0.006
	t = 0.187	t = -2.675	t = -2.905
	p = 0.852	p = 0.008	p = 0.004
Recording1.90831e+11	-0.700	**-31.299*****	-0.036
	[-4.764, 3.364]	[-48.347, -14.251]	[-0.247, 0.175]
	s.e. = 2.065	s.e. = 8.687	s.e. = 0.107
	t = -0.339	t = -3.603	t = -0.338
	p = 0.735	p = 0.000	p = 0.736
Recording1.90902e+11	**12.372*****	**-38.863*****	-0.015
	[6.622, 18.121]	[-51.890, -25.836]	[-0.225, 0.195]
	s.e. = 2.921	s.e. = 6.638	s.e. = 0.107
	t = 4.235	t = -5.854	t = -0.141
	p = 0.000	p = 0.000	p = 0.888
Recording1.90915e+11	**10.791*****	**-42.905*****	0.032
	[6.608, 14.973]	[-56.487, -29.324]	[-0.188, 0.251]
	s.e. = 2.126	s.e. = 6.921	s.e. = 0.112
	t = 5.077	t = -6.200	t = 0.285
	p = 0.000	p = 0.000	p = 0.776
Time5__s_ × Recording1.90831e+11	-0.053	**0.880+**	0.010
	[-0.280, 0.174]	[-0.007, 1.766]	[-0.004, 0.024]
	s.e. = 0.115	s.e. = 0.452	s.e. = 0.007
	t = -0.458	t = 1.948	t = 1.372
	p = 0.647	p = 0.052	p = 0.171
Time5__s_ × Recording1.90902e+11	-0.195	**1.059****	**0.016***
	[-0.529, 0.139]	[0.313, 1.804]	[0.003, 0.030]
	s.e. = 0.170	s.e. = 0.380	s.e. = 0.007
	t = -1.150	t = 2.786	t = 2.402
	p = 0.251	p = 0.005	p = 0.017
Time5__s_ × Recording1.90915e+11	-0.150	**1.715*****	0.008
	[-0.403, 0.102]	[0.963, 2.467]	[-0.006, 0.022]
	s.e. = 0.128	s.e. = 0.383	s.e. = 0.007
	t = -1.171	t = 4.477	t = 1.155
	p = 0.242	p = 0.000	p = 0.249
Recording1.90905e+11		**-36.526*****	-0.070
		[-48.885, -24.167]	[-0.267, 0.128]
		s.e. = 6.298	s.e. = 0.100
		t = -5.800	t = -0.695

		p = 0.000	p = 0.487
Time5__s_ × Recording1.90905e+11		**1.356*** **	**0.017***
		[0.574, 2.137]	[0.005, 0.029]
		s.e. = 0.398	s.e. = 0.006
		t = 3.405	t = 2.738
		p = 0.001	p = 0.006
Num.Obs.	305	965	427
R2	0.307	0.078	0.079

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Bandwidth 90 over time within recording

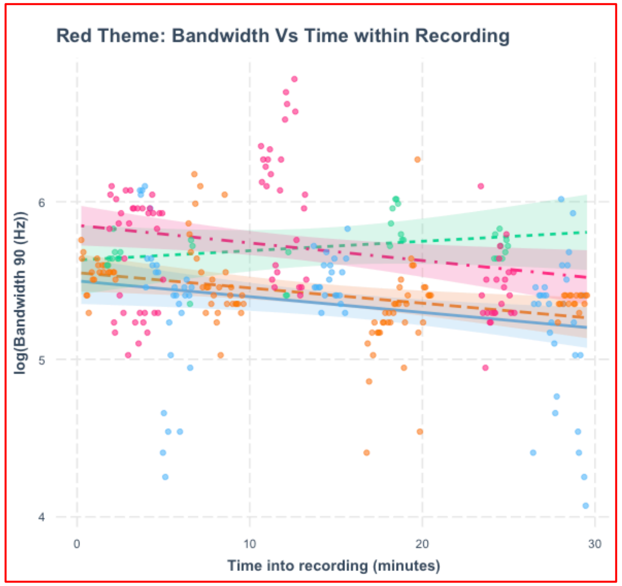


Figure A3.62: Significant difference in trend between individuals within song sessions. 02 increase while 26, 31 and 15 decrease

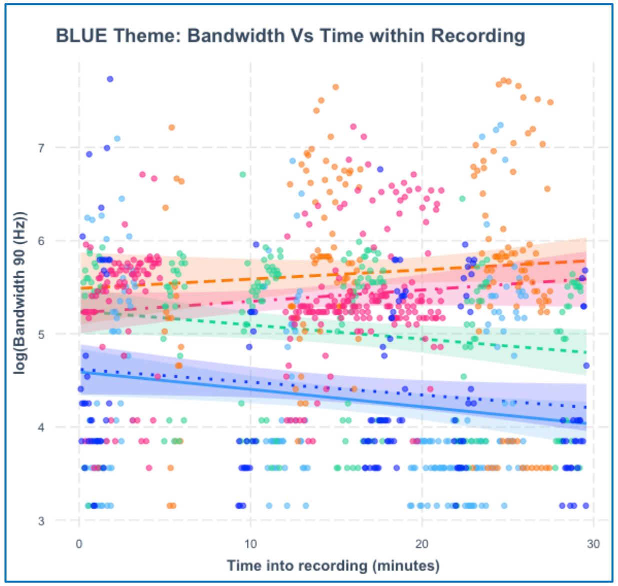


Figure A3.63: Significant difference in trend between individuals within song sessions. 05 and 31 increasing

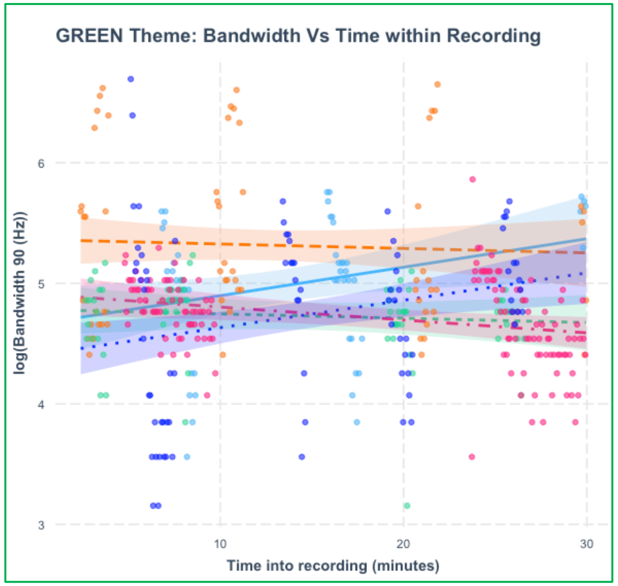


Figure A3.64: Significant difference in trend between individuals within song sessions. 31, 02 and 05 decreasing. 26 and 15 increasing in the same way

Table 13:

ID	RED	BLUE	GREEN	Individual across theme change
26	**-0.010***	**-0.019****	**0.024***	Yes
31	-	**0.029***	**-0.027***	Yes
02	**0.016***	-	**-0.027***	Yes
05		**0.031****	**-0.034****	Yes
15	-	-	-	Yes

Table 14:

	Bandwidth – Within Recording		
	RED	BLUE	GREEN
(Intercept)	5.498***	4.591***	4.662***
	[5.352, 5.643]	[4.339, 4.842]	[4.351, 4.972]
	s.e. = 0.074	s.e. = 0.128	s.e. = 0.158
	t = 74.491	t = 35.790	t = 29.532
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	**-0.010***	**-0.019****	**0.024***
	[-0.018, -0.002]	[-0.033, -0.005]	[0.003, 0.044]
	s.e. = 0.004	s.e. = 0.007	s.e. = 0.010
	t = -2.556	t = -2.600	t = 2.277
	p = 0.011	p = 0.009	p = 0.023
Recording1.90831e+11	0.052	**0.896*****	**0.702*****
	[-0.135, 0.240]	[0.434, 1.359]	[0.322, 1.082]
	s.e. = 0.095	s.e. = 0.236	s.e. = 0.193
	t = 0.547	t = 3.804	t = 3.629
	p = 0.585	p = 0.000	p = 0.000
Recording1.90902e+11	0.132	**0.654*****	0.121
	[-0.133, 0.397]	[0.300, 1.007]	[-0.258, 0.500]
	s.e. = 0.135	s.e. = 0.180	s.e. = 0.193
	t = 0.979	t = 3.631	t = 0.628
	p = 0.329	p = 0.000	p = 0.530
Recording1.90915e+11	**0.353*****	0.028	-0.256
	[0.160, 0.546]	[-0.340, 0.397]	[-0.652, 0.139]
	s.e. = 0.098	s.e. = 0.188	s.e. = 0.201
	t = 3.598	t = 0.151	t = -1.274
	p = 0.000	p = 0.880	p = 0.203
Time5__s_ × Recording1.90831e+11	0.000	**0.029***	**-0.027***
	[-0.010, 0.011]	[0.005, 0.053]	[-0.052, -0.002]
	s.e. = 0.005	s.e. = 0.012	s.e. = 0.013
	t = 0.061	t = 2.341	t = -2.147
	p = 0.952	p = 0.019	p = 0.032
Time5__s_ × Recording1.90902e+11	**0.016***	0.004	**-0.027***
	[0.001, 0.031]	[-0.017, 0.024]	[-0.051, -0.003]
	s.e. = 0.008	s.e. = 0.010	s.e. = 0.012
	t = 2.041	t = 0.357	t = -2.223
	p = 0.042	p = 0.722	p = 0.027
Time5__s_ × Recording1.90915e+11	-0.001	0.005	-0.001
	[-0.013, 0.010]	[-0.016, 0.025]	[-0.026, 0.024]
	s.e. = 0.006	s.e. = 0.010	s.e. = 0.013
	t = -0.200	t = 0.469	t = -0.070
	p = 0.842	p = 0.639	p = 0.944
Recording1.90905e+11		**0.636*****	0.248
		[0.300, 0.971]	[-0.107, 0.604]
		s.e. = 0.171	s.e. = 0.181
		t = 3.721	t = 1.373
		p = 0.000	p = 0.170

Time5__s_ × Recording1.90905e+11		**0.031****	**-0.034****
		[0.010, 0.052]	[-0.056, -0.012]
		s.e. = 0.011	s.e. = 0.011
		t = 2.862	t = -3.055
		p = 0.004	p = 0.002
Num.Obs.	305	965	427
R2	0.233	0.263	0.187

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Start Frequency over time within recording

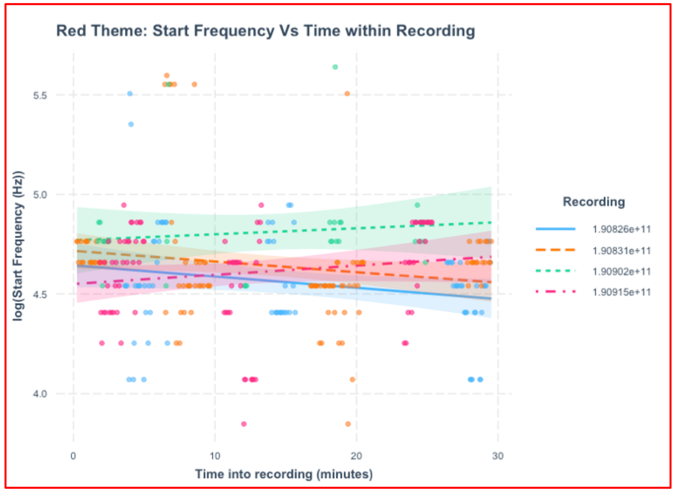


Figure A3.65: Significant difference in trend between individuals within song sessions. Individual 15 increases start frequency. All other individuals decrease or stay the same

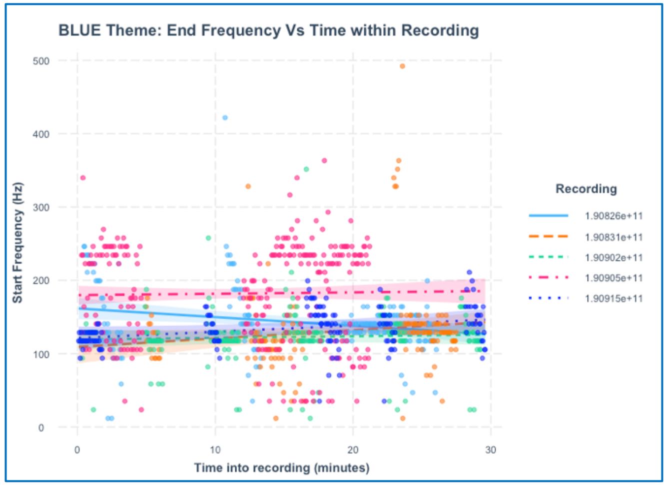


Figure A3.66– update the y axis label here - Significant difference in trend between individuals within song sessions. Individual 26 decrease while all others increase.

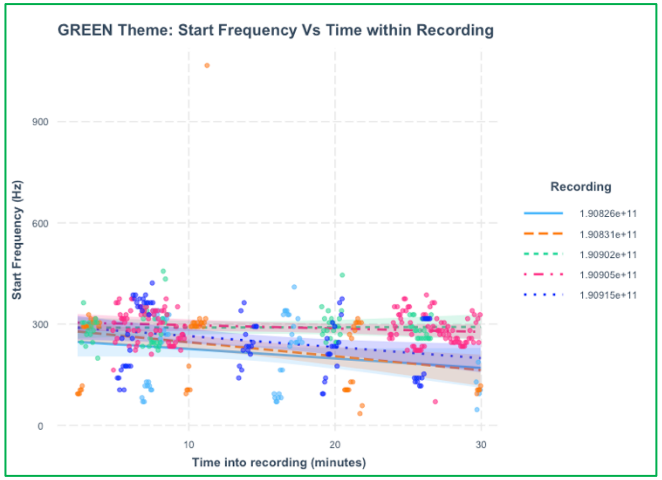


Figure A3.67: No significant difference in trend between individuals.

Table 15:

ID	RED	BLUE	GREEN	Individual across theme change
26	-0.006+	-1.174**	-2.808+	Yes
31	-	2.313**	-	Yes
02	-	1.401*	-	Yes
05		1.361*	-	Yes
15	0.010*	2.011***	-	Yes

Table 16:

Start Frequency – Within Recording

	RED	BLUE	GREEN
(Intercept)	4.644***	161.579***	254.637***
	[4.534, 4.754]	[147.108, 176.051]	[203.853, 305.420]
	s.e. = 0.056	s.e. = 7.374	s.e. = 25.835
	t = 83.139	t = 21.912	t = 9.856
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	**-0.006+**	**-1.174****	**-2.808+**
	[-0.011, 0.000]	[-1.985, -0.363]	[-6.144, 0.528]
	s.e. = 0.003	s.e. = 0.413	s.e. = 1.697
	t = -1.910	t = -2.841	t = -1.654
	p = 0.057	p = 0.005	p = 0.099
Recording1.90831e+11	0.073	**-52.406*****	33.472
	[-0.069, 0.214]	[-78.986, -25.827]	[-28.737, 95.680]
	s.e. = 0.072	s.e. = 13.544	s.e. = 31.647
	t = 1.005	t = -3.869	t = 1.058
	p = 0.315	p = 0.000	p = 0.291
Recording1.90902e+11	0.126	**-42.241*****	34.382
	[-0.075, 0.326]	[-62.552, -21.929]	[-27.574, 96.338]
	s.e. = 0.102	s.e. = 10.350	s.e. = 31.519
	t = 1.230	t = -4.081	t = 1.091
	p = 0.220	p = 0.000	p = 0.276
Recording1.90915e+11	-0.094	**-40.088*****	42.738
	[-0.240, 0.052]	[-61.263, -18.913]	[-22.004, 107.481]
	s.e. = 0.074	s.e. = 10.790	s.e. = 32.937
	t = -1.267	t = -3.715	t = 1.298
	p = 0.206	p = 0.000	p = 0.195
Time5__s_ × Recording1.90831e+11	0.000	**2.313****	-1.346
	[-0.008, 0.008]	[0.931, 3.694]	[-5.435, 2.744]
	s.e. = 0.004	s.e. = 0.704	s.e. = 2.081
	t = 0.077	t = 3.284	t = -0.647
	p = 0.939	p = 0.001	p = 0.518
Time5__s_ × Recording1.90902e+11	0.009	**1.401***	2.896
	[-0.003, 0.020]	[0.238, 2.564]	[-1.042, 6.835]
	s.e. = 0.006	s.e. = 0.592	s.e. = 2.004
	t = 1.460	t = 2.365	t = 1.446
	p = 0.145	p = 0.018	p = 0.149
Time5__s_ × Recording1.90915e+11	**0.010***	**2.011*****	-0.464
	[0.001, 0.019]	[0.839, 3.183]	[-4.601, 3.674]
	s.e. = 0.004	s.e. = 0.597	s.e. = 2.105
	t = 2.296	t = 3.366	t = -0.220
	p = 0.022	p = 0.001	p = 0.826
Recording1.90905e+11		18.219+	52.178+
		[-1.050, 37.489]	[-6.030, 110.387]

		s.e. = 9.819	s.e. = 29.612
		t = 1.855	t = 1.762
		p = 0.064	p = 0.079
Time5__s_ × Recording1.90905e+11		**1.361***	1.825
		[0.143, 2.579]	[-1.789, 5.438]
		s.e. = 0.621	s.e. = 1.838
		t = 2.192	t = 0.993
		p = 0.029	p = 0.321
Num.Obs.	305	965	427
R2	0.101	0.175	0.147

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

End frequency over time within recording

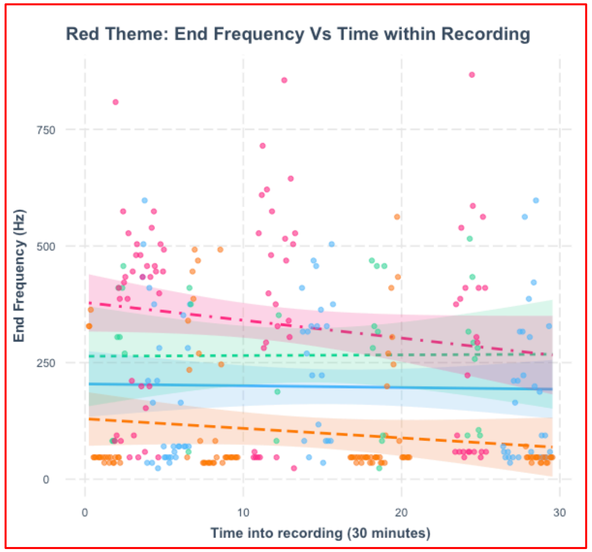


Figure A3.68: No significant difference in trend between individuals.

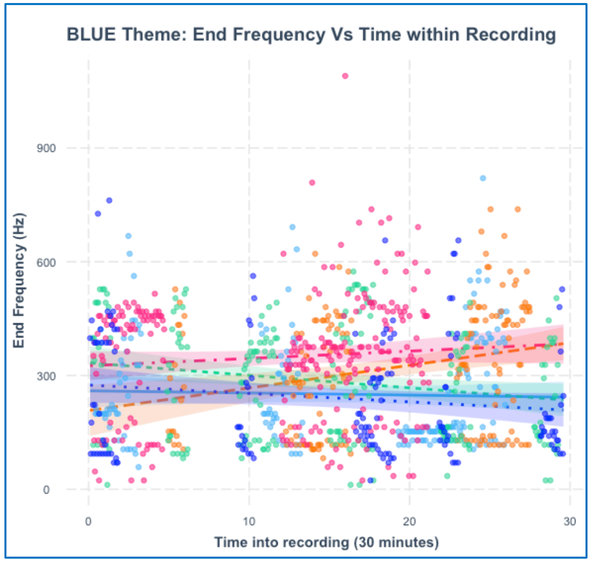


Figure A3.69: Significant difference in trend between individuals within song sessions. Individuals 31 and 05 increase End Frequency while individuals 02, 26 and 15 decrease.

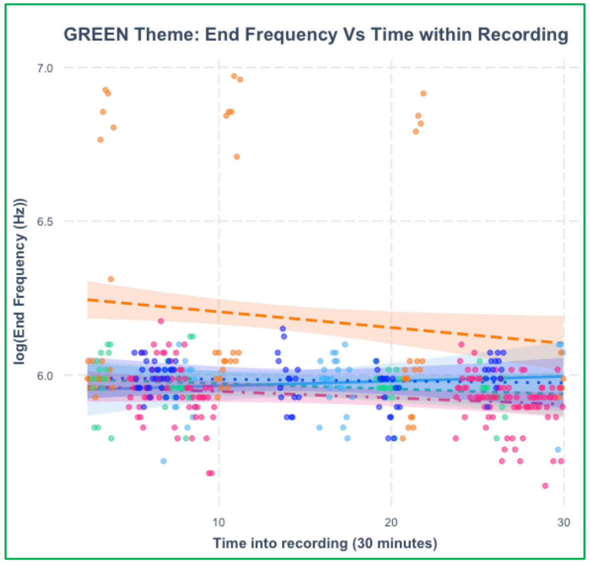


Figure A3.70: Significant difference in trend between individuals within song sessions. Slight larger rate of decrease for individual 31.

Table 17:

ID	RED	BLUE	GREEN	Individual across theme change
26	NSC	NSC	NSC	No
31	-	**6.530****	**-0.007+**	Yes
02	-	-	-	No
05	NA	-	-	No
15	-	-	-	No

Table 18:

End Frequency – Within Recording

	RED	BLUE	GREEN
(Intercept)	204.179***	259.710***	5.949***
	[133.277, 275.081]	[215.907, 303.512]	[5.851, 6.047]
	s.e. = 36.028	s.e. = 22.320	s.e. = 0.050
	t = 5.667	t = 11.636	t = 119.360
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	-0.381	-0.566	0.002
	[-4.143, 3.381]	[-3.021, 1.889]	[-0.005, 0.008]
	s.e. = 1.912	s.e. = 1.251	s.e. = 0.003
	t = -0.199	t = -0.453	t = 0.471
	p = 0.842	p = 0.651	p = 0.638
Recording1.90831e+11	-74.730	-52.102	**0.308*** **
	[-166.260, 16.800]	[-132.555, 28.351]	[0.188, 0.428]
	s.e. = 46.509	s.e. = 40.996	s.e. = 0.061
	t = -1.607	t = -1.271	t = 5.045
	p = 0.109	p = 0.204	p = 0.000
Recording1.90902e+11	59.416	**73.819***	0.041
	[-70.075, 188.906]	[12.340, 135.299]	[-0.079, 0.160]
	s.e. = 65.798	s.e. = 31.328	s.e. = 0.061
	t = 0.903	t = 2.356	t = 0.666
	p = 0.367	p = 0.019	p = 0.506
Recording1.90915e+11	**174.765*** **	15.170	0.043
	[80.554, 268.976]	[-48.924, 79.265]	[-0.082, 0.168]
	s.e. = 47.872	s.e. = 32.660	s.e. = 0.064
	t = 3.651	t = 0.464	t = 0.675
	p = 0.000	p = 0.642	p = 0.500
Time5__s_ × Recording1.90831e+11	-1.669	**6.530****	**-0.007+**
	[-6.788, 3.450]	[2.347, 10.713]	[-0.015, 0.001]
	s.e. = 2.601	s.e. = 2.131	s.e. = 0.004
	t = -0.642	t = 3.064	t = -1.666
	p = 0.522	p = 0.002	p = 0.097
Time5__s_ × Recording1.90902e+11	0.526	-2.738	-0.003
	[-6.998, 8.050]	[-6.257, 0.782]	[-0.011, 0.004]
	s.e. = 3.823	s.e. = 1.793	s.e. = 0.004
	t = 0.138	t = -1.527	t = -0.848
	p = 0.891	p = 0.127	p = 0.397
Time5__s_ × Recording1.90915e+11	-3.441	-1.649	-0.002
	[-9.128, 2.247]	[-5.197, 1.899]	[-0.010, 0.006]
	s.e. = 2.890	s.e. = 1.808	s.e. = 0.004
	t = -1.191	t = -0.912	t = -0.525
	p = 0.235	p = 0.362	p = 0.600
Recording1.90905e+11		**65.930***	0.018

		[7.603, 124.256]	[-0.094, 0.130]
		s.e. = 29.721	s.e. = 0.057
		t = 2.218	t = 0.317
		p = 0.027	p = 0.751
Time5__s_ × Recording1.90905e+11		2.503	-0.004
		[-1.185, 6.190]	[-0.011, 0.003]
		s.e. = 1.879	s.e. = 0.004
		t = 1.332	t = -1.022
		p = 0.183	p = 0.307
Num.Obs.	305	965	427
R2	0.246	0.088	0.241

+ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Frequency Ratio over time within recording

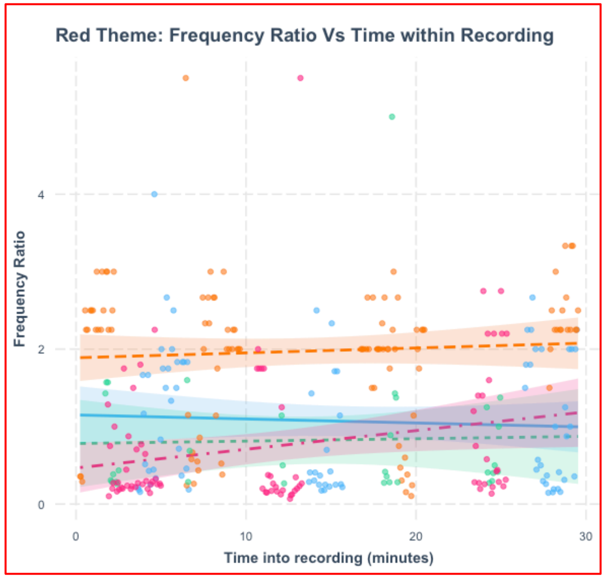


Figure A3.71: Individual 15 possible increase as compared to individual 26 – open to error.

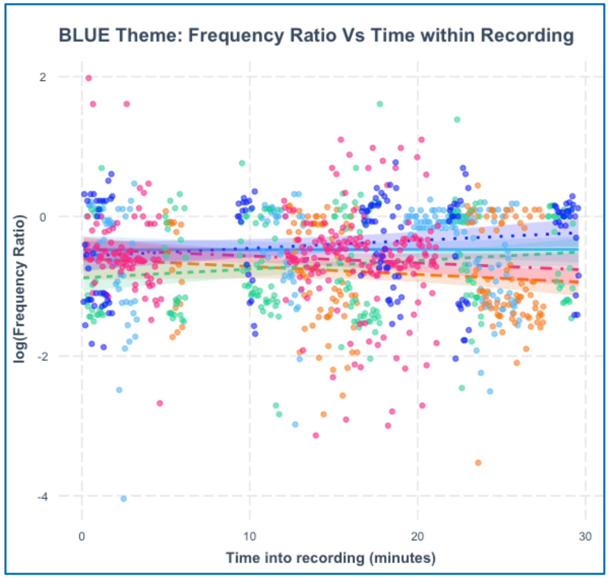


Figure A3.72: No significant difference in trend between individuals.

Figure A3.73: Individual 02 possible increase as compared to individual 26 – open to error

Table 19:

ID	RED	BLUE	GREEN	Individual across theme change
26	NSC	NSC	NSC	No
31	-	**6.530****	**-0.007+**	Yes
02	-	-	-	No
05	NA	-	-	No
15	-	-	-	No

Table 20:

Frequency Trend – Within Recording

	RED	BLUE	GREEN
(Intercept)	1.151***	-0.479***	0.657***
	[0.779, 1.522]	[-0.678, -0.280]	[0.541, 0.773]
	s.e. = 0.189	s.e. = 0.101	s.e. = 0.059
	t = 6.088	t = -4.734	t = 11.119
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	-0.005	0.000	**-0.007+**
	[-0.025, 0.015]	[-0.011, 0.011]	[-0.015, 0.000]
	s.e. = 0.010	s.e. = 0.006	s.e. = 0.004
	t = -0.516	t = 0.036	t = -1.921
	p = 0.606	p = 0.971	p = 0.055
Recording1.90831e+11	**0.738****	-0.126	-0.103
	[0.258, 1.218]	[-0.490, 0.239]	[-0.245, 0.039]
	s.e. = 0.244	s.e. = 0.186	s.e. = 0.072
	t = 3.025	t = -0.675	t = -1.422
	p = 0.003	p = 0.500	p = 0.156
Recording1.90902e+11	-0.368	**-0.401****	0.068
	[-1.048, 0.311]	[-0.680, -0.122]	[-0.074, 0.210]
	s.e. = 0.345	s.e. = 0.142	s.e. = 0.072
	t = -1.067	t = -2.823	t = 0.945
	p = 0.287	p = 0.005	p = 0.345
Recording1.90915e+11	**-0.685****	-0.091	0.086
	[-1.179, -0.191]	[-0.382, 0.199]	[-0.062, 0.234]
	s.e. = 0.251	s.e. = 0.148	s.e. = 0.075
	t = -2.727	t = -0.617	t = 1.141
	p = 0.007	p = 0.537	p = 0.254
Time5__s_ × Recording1.90831e+11	0.012	-0.012	0.001
	[-0.015, 0.038]	[-0.030, 0.007]	[-0.008, 0.011]
	s.e. = 0.014	s.e. = 0.010	s.e. = 0.005
	t = 0.843	t = -1.192	t = 0.315
	p = 0.400	p = 0.234	p = 0.753
Time5__s_ × Recording1.90902e+11	0.008	0.012	**0.009+**
	[-0.031, 0.048]	[-0.004, 0.028]	[0.000, 0.018]
	s.e. = 0.020	s.e. = 0.008	s.e. = 0.005
	t = 0.412	t = 1.506	t = 1.952
	p = 0.681	p = 0.132	p = 0.052
Time5__s_ × Recording1.90915e+11	**0.029+**	0.011	0.000
	[0.000, 0.059]	[-0.005, 0.027]	[-0.010, 0.009]
	s.e. = 0.015	s.e. = 0.008	s.e. = 0.005
	t = 1.935	t = 1.361	t = -0.048
	p = 0.054	p = 0.174	p = 0.962
Recording1.90905e+11		0.011	0.130+
		[-0.254, 0.275]	[-0.003, 0.263]
		s.e. = 0.135	s.e. = 0.068
		t = 0.078	t = 1.925

		p = 0.938	p = 0.055
Time5__s_ × Recording1.90905e+11		-0.010	0.006
		[-0.027, 0.007]	[-0.002, 0.015]
		s.e. = 0.009	s.e. = 0.004
		t = -1.185	t = 1.539
		p = 0.236	p = 0.125
Num.Obs.	305	965	427
R2	0.276	0.050	0.270

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

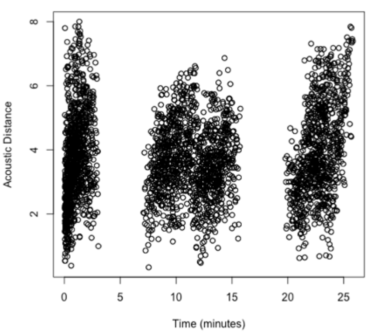
Appendix 3.17 – Euclidean Distance – Individual and Theme split

Table 21:

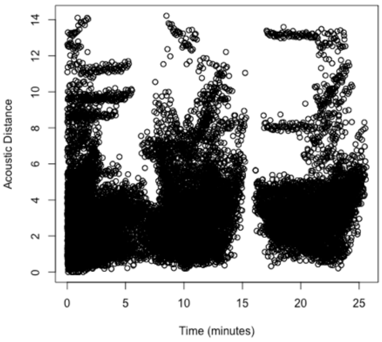
	Mantel	Sig	Mantel	Sig	Mantel	Sig
	Red		Blue		Green	
2608	**0.1107**	0.001**	**0.1654**	0.001**	**0.2805**	0.001**
3108	-0.02776	0.999	**0.02884**	0.001**	-0.02284	0.928
0209	**0.06242**	0.016*	-0.0323	1	0.009096	0.24
0509	**0.5903**	0.001**	**0.03102**	0.001**	**0.04153**	0.001**
1509	-0.005071	0.662	**0.05633**	0.001**	**0.1171**	0.001**

Appendix 3.18 Individual Mantel Tests

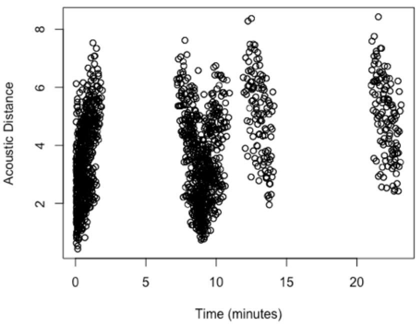
Red Theme Recording 260819



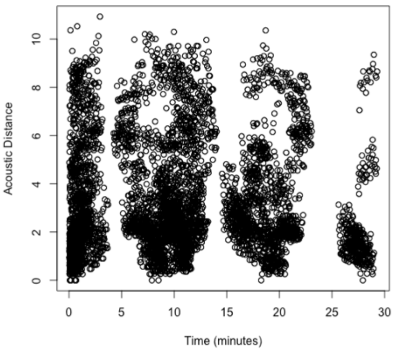
Blue Theme Recording 260819



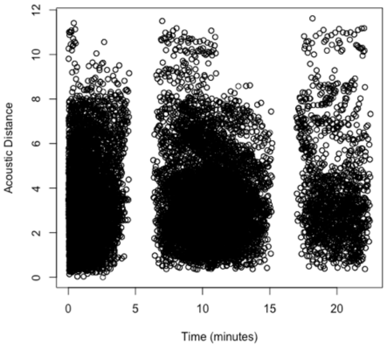
Green Theme Recording 260819



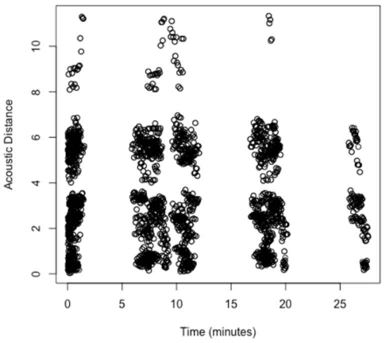
Red Theme Recording 310819



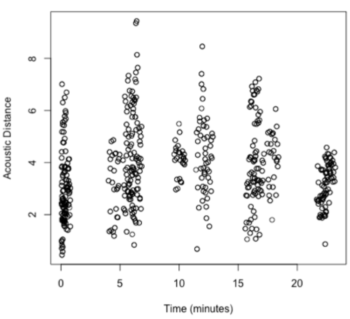
Blue Theme Recording 310819



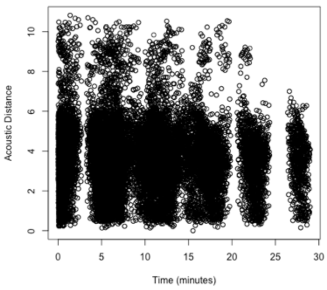
Green Theme Recording 310819



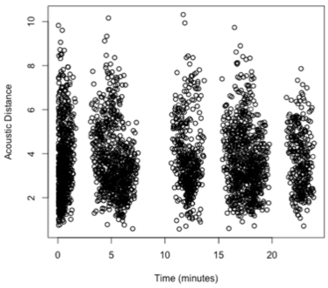
Red Theme Recording 020919



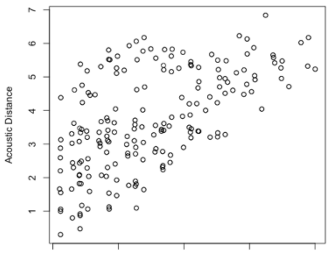
Blue Theme Recording 020919



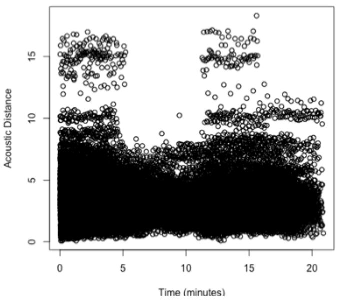
Green Theme Recording 020919



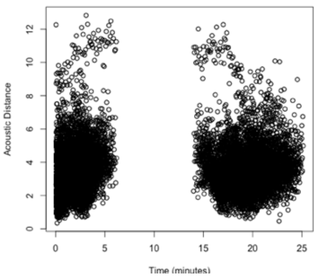
Red Theme Recording 050919



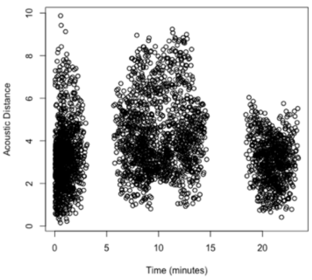
Blue Theme Recording 050919



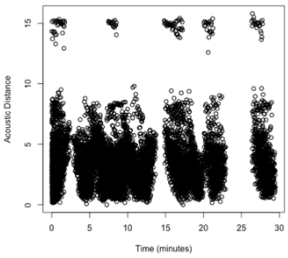
Green Theme Recording 050919



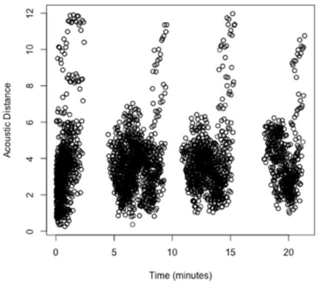
Red Theme Recording 150919



Blue Theme Recording 150919



Green Theme Recording 150919



Appendix 3.19 Original fine-scale unit summaries

Unit	N	Freq95		Peak Frequency		Freq5		BW90		Duration90		Start Frequency		End Frequency		Frequency Ratio	
		Mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
ahq	5	4579.69	644.02	2357.81	963.77	832.03	115.12	3747.66	599.69	0.55	0.25	2821.88	1940.42	3719.53	688.25	0.81	0.67
ahq-mhq	3	5656.25	785.45	2679.69	82.31	1238.28	632.63	4417.97	1064.02	2.06	0.21	2335.94	1551.41	4894.53	818.83	0.49	0.36
am	14	388.39	28.28	354.91	43.47	308.04	73.75	80.36	73.52	0.62	0.24	318.92	83.90	375.84	30.99	0.84	0.20
amm	375	394.56	40.41	322.22	47.84	252.94	50.02	141.63	69.87	0.77	0.19	254.88	78.98	389.56	30.76	0.66	0.21
ams	2	955.08	41.43	779.30	240.31	550.78	16.57	404.30	24.86	1.47	0.09	539.06	16.57	955.08	41.43	0.56	0.01
as	16	902.34	147.98	733.89	154.51	635.74	99.11	266.60	110.72	1.22	0.45	615.23	104.73	943.36	140.10	0.66	0.11
as(p)	48	1132.32	514.82	664.79	80.49	585.45	46.87	546.87	530.44	0.95	0.55	601.56	56.19	1004.15	197.74	0.62	0.13
asqb	52	959.59	249.92	774.34	265.63	660.53	249.36	299.05	184.01	1.25	0.62	685.55	253.04	937.73	234.22	0.80	0.69
cr	173	90.90	18.57	61.17	15.88	42.74	11.43	48.16	14.15	0.24	0.05	83.59	21.48	39.97	10.26	2.12	0.41
cr-las(p)	11	1706.68	542.09	639.20	445.23	264.20	231.27	1442.47	627.09	3.26	0.61	108.66	57.19	870.38	355.84	0.20	0.23
crackle	7	3125.56	716.15	1789.62	585.03	1049.67	145.25	2075.89	695.25	1.68	1.73	2514.51	973.81	2152.90	652.99	1.17	0.40
dsqb	1	1324.22		1277.34		1183.59		140.62		0.47		1335.94		1183.59		1.13	
gr	125	303.94	314.70	199.78	53.80	172.97	43.20	130.97	306.95	1.21	0.57	195.94	59.77	201.09	68.82	1.01	0.21
gr-t	34	1535.85	648.65	695.54	351.38	176.47	198.26	1359.38	637.64	0.47	0.12	73.07	127.07	1209.10	483.15	0.07	0.12
hsq	7	4155.13	291.47	3239.40	267.82	2139.51	552.85	2015.63	715.45	0.30	0.10	3318.08	1279.21	3585.94	330.97	0.95	0.36
lamm	16	942.63	119.81	771.97	207.65	344.97	108.59	597.66	137.06	2.97	0.67	323.73	217.39	926.51	120.46	0.35	0.21
las	5	792.19	78.00	698.44	133.51	487.50	136.81	304.69	92.27	2.33	0.90	475.78	146.98	862.50	209.07	0.56	0.16
las(p)	1	960.94		796.88		714.84		246.09		1.71		714.84		984.38		0.73	
lasqb	1	691.41		632.81		539.06		152.34		1.88		316.41		703.12		0.45	
lb	357	326.42	128.66	102.25	58.33	50.62	9.69	275.80	126.62	1.00	0.16	105.27	32.64	216.16	194.10	1.20	1.00
lgr	23	545.69	698.95	189.54	151.80	120.75	47.20	424.93	707.81	3.03	1.12	144.70	39.91	180.88	86.03	0.91	0.30
lm	19	259.66	43.19	228.82	21.17	212.79	21.49	46.88	43.15	2.30	0.55	236.23	20.40	221.42	26.17	1.07	0.08
lm-as(p)	1	890.62		644.53		222.66		667.97		2.90		445.31		750.00		0.59	

lm(p)	2	527.34	16.57	251.95	8.29	240.23	8.29	287.11	8.29	2.58	0.33	363.28	165.73	251.95	8.29	1.45	0.71
lm(p)-as(p)	9	1072.92	272.58	773.44	230.09	303.39	130.68	769.53	195.57	3.54	0.40	320.31	164.38	983.07	127.63	0.33	0.15
ls(p)	82	1189.74	558.64	848.61	268.68	719.56	66.77	470.18	548.33	3.00	0.53	807.59	263.11	881.48	237.27	0.93	0.27
lsqb	12	1058.59	343.89	942.38	420.11	860.35	415.00	198.24	92.06	2.06	0.59	857.42	442.02	1051.76	269.79	0.77	0.20
m	15	381.25	26.89	353.91	36.04	333.59	31.59	47.66	16.25	0.60	0.26	352.34	40.95	378.91	31.22	0.93	0.12
mgr	15	258.59	159.05	176.56	36.65	140.62	24.26	117.97	175.70	1.48	0.79	157.03	50.66	203.12	140.95	0.92	0.34
mm	11	397.37	18.50	360.09	29.69	311.08	53.28	86.29	46.37	0.64	0.20	322.80	60.07	388.85	31.80	0.83	0.14
ms	1	867.19		796.88		773.44		93.75		0.51		832.03		902.34		0.92	
msqb	52	1500.45	212.88	1328.05	239.20	1128.83	320.49	371.62	327.24	1.07	0.65	1245.79	310.33	1347.88	175.34	0.93	0.21
ngr	135	761.28	520.95	232.20	150.87	80.64	39.42	680.64	517.64	0.34	0.09	98.44	62.16	369.88	219.33	0.60	1.05
nsqb	2	1658.20	207.16	1558.59	182.30	1347.66	198.87	310.55	8.29	0.68	0.00	1335.94	447.47	1658.20	74.58	0.80	0.23
p	220	225.96	181.87	131.30	27.15	99.45	21.17	126.51	187.03	0.67	0.18	125.50	38.56	120.97	34.41	1.10	0.38
p(s)-gr	3	464.84	6.77	406.25	6.77	214.84	6.77	250.00	6.77	1.66	0.37	308.59	108.25	390.62	17.90	0.80	0.31
s	9	682.29	107.05	657.55	105.54	630.21	92.42	52.08	26.28	0.90	0.39	645.83	97.77	677.08	112.37	0.96	0.04
s(p)	13	1025.84	276.35	819.41	64.27	752.70	82.33	273.14	238.70	0.95	0.50	766.23	115.57	841.95	88.45	0.91	0.12
sq	273	2399.90	1221.80	1587.10	1220.86	810.74	546.61	1589.16	959.65	0.29	0.29	1715.14	1289.81	1586.97	1233.58	1.37	1.33
sqb	42	1101.56	356.12	1067.24	360.44	1016.18	342.38	85.38	94.33	0.86	0.46	1035.44	346.97	1057.76	341.64	0.98	0.11
ss(p)	2	1341.80	124.30	832.03	232.02	292.97	33.15	1048.83	91.15	0.21	0.06	363.28	381.17	826.17	306.60	0.56	0.67
t	581	1543.57	633.69	884.43	344.81	597.31	176.75	946.25	608.69	0.37	0.25	835.60	643.12	1202.78	454.28	0.78	0.78
ugr	532	333.76	110.90	156.22	57.96	121.04	17.05	212.72	114.96	0.61	0.26	157.63	50.39	367.60	120.43	0.50	0.26
usq	2	1587.89	190.59	574.22	82.86	439.45	91.15	1148.44	99.44	0.32	0.03	269.53	0.00	632.81	149.16	0.44	0.10
usqb	1	703.12		585.94		539.06		164.06		0.13		597.66		726.56		0.82	

Appendix 3.20 Alternative Hypotheses – Complete Results

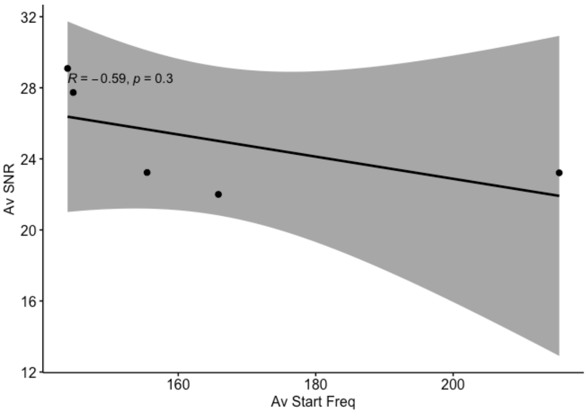


Figure A3.74: Average Start Frequency and average SNR per recording. R = -0.59, p = 0.30. No significant relationship between Start frequency and SNR.

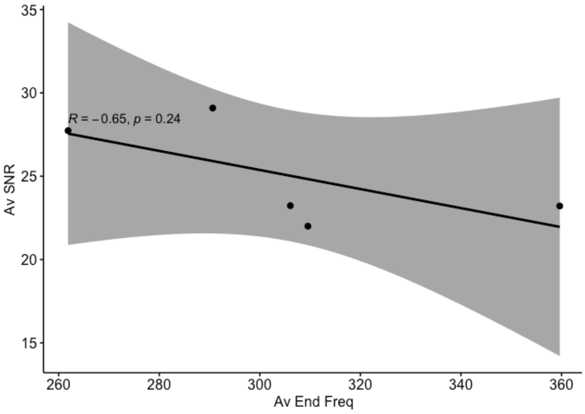


Figure A3.75: Average End Frequency and average SNR per recording. R = -0.65, p = 0.24. No Significant relationship between End Frequency and SNR.

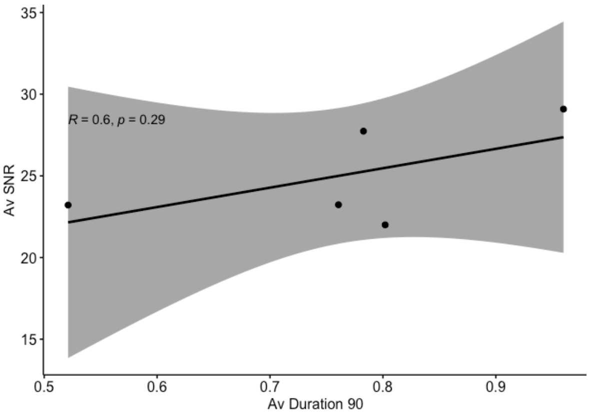


Figure A3.76: Average 'Duration 90' and average SNR per recording. R = 0.60, p = 0.29. No Significant relationship between robust measurement 'Duration 90' and SNR.

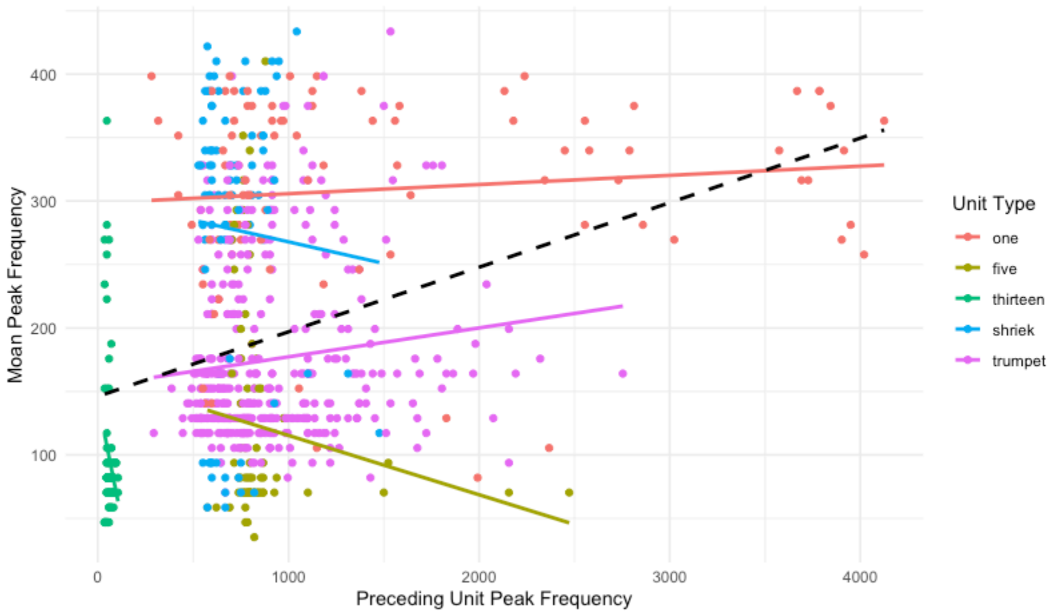


Figure A3.77: Coarticulation analysis of 'groan' units using linear regression, exploring the relationship between peak frequencies of 'groan' units and various preceding unit types. The intercept suggests an expected peak frequency of approximately 298.6 Hz when the preceding unit's peak frequency is zero. Significant effects are observed for specific preceding unit types ('five' and 'thirteen' with lower peak frequencies, and 'trumpet' with a higher peak frequency), while 'shriek' shows no statistically significant effects. Interaction terms hint at potential interactions, and the model demonstrates a moderately strong relationship (R-squared = 0.4306). These findings shed light on the influential role of preceding unit types and their interactions in shaping the peak frequency of 'groan' units.

Table 22:

Term	Estimate	Std.error	Statistic	P.value
(Intercept)	298.569728	12.7264564	23.4605549	2.49E-92
preceding_peak_frequency	0.0072366	0.0069438	1.04216685	0.29766016
preceding_unit_typefive	-136.51721	30.9243162	-4.4145588	1.16E-05
preceding_unit_typethirteen	-156.1882	32.8477138	-4.7549184	2.37E-06
preceding_unit_typeshriek	3.30095216	37.7518845	0.08743808	0.93034595
preceding_unit_typetrumpet	-144.11002	16.1388354	-8.9293938	3.08E-18
preceding_peak_frequency:PUtypefive	-0.0539773	0.03222477	-1.6750238	0.09433403
preceding_peak_frequency:PUtypethirteen	-0.7565702	0.47435958	-1.5949297	0.11113669
preceding_peak_frequency:PUtypeshriek	-0.0412423	0.04953526	-0.8325844	0.40533631
preceding_peak_frequency:PUtypetrumpet	0.01554911	0.01242859	1.25107609	0.21128523

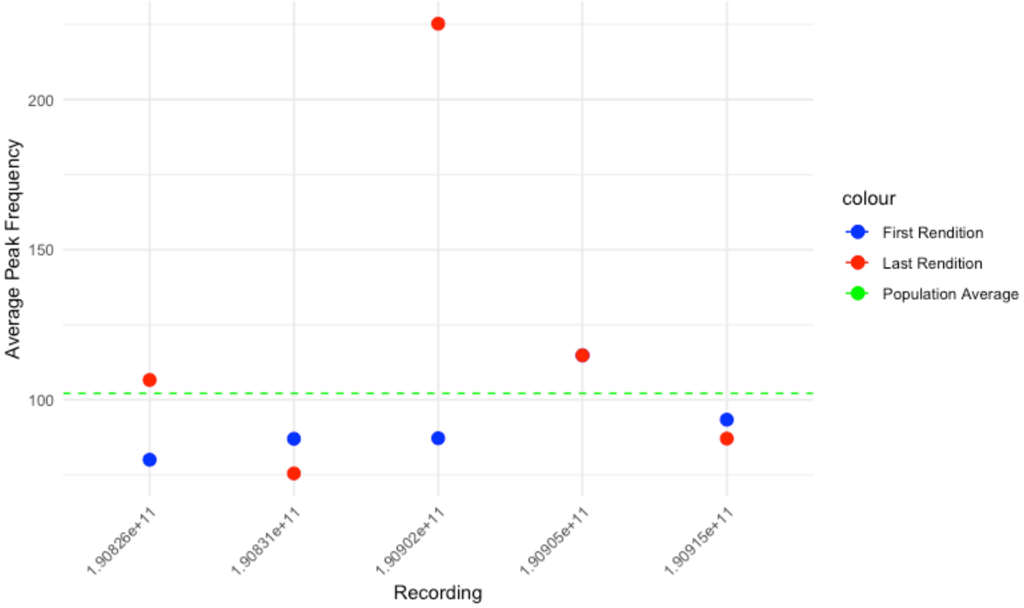


Figure A3.78: Exhaustion effects explored through a paired t-test on differences between "First Rendition" and "Last Rendition" values compared to the "Overall Population Average." The t-statistic (-0.98, 4 degrees of freedom) showed a mean difference of approximately -21.66, suggesting 'FirstRenditionDiff' was generally lower than 'LastRenditionDiff.' Despite this, the non-significant p-value (0.384) and a 95 percent confidence interval (-83.21, 39.89) containing the null hypothesis value of 0 indicate no significant difference in means. Consequently, we do not reject the null hypothesis, signifying that the true difference between the variables is not significantly different from zero.

4 Chapter 4: Fine-Scale Analysis of Humpback Whale Song Evolution and Population Connectivity in the North Atlantic

Abstract:

Humpback whales are widely distributed across the world's oceans, having recovered overall well from whaling, although some populations, such as the one that breeds among the Cape Verde archipelago, have not rebounded as successfully as others. Humpback whales undertake one of the world's longest mammalian migrations, covering approximately 9,000 km, moving from high-latitude feeding areas in summer to low-latitude breeding areas in winter across the northern and southern hemisphere oceans. Climate change has accentuated the importance of understanding the migration patterns of these baleen whales to assess potential impacts on their habitat utilisation. This thesis chapter focusses on population connectivity and song evolution of humpback whales in the North Atlantic, in particular the breeding locations of the Eastern Caribbean and feeding grounds off the west coast of Scotland. Through the analysis of acoustic data collected from both locations, I provide insights into the matching of humpback whale songs between their breeding and feeding locations. I analysed songs recorded off Scotland and in the Eastern Caribbean to understand if these two locations were connected by migration, and also studied fine-scale unit change in both locations. I found that the same song was being sung in both places, and that fine-scale unit change suggested complex vocal production learning in humpback whales.

4.1 Introduction

Humpback whales are widely distributed across all the world's oceans (Jackson *et al*., 2014). However, they were severely exploited by whaling during the 19th and 20th centuries, which resulted in a decline in their populations. In the later 20th century, conservation efforts have helped these populations to recover significantly, resulting in their removal from the Threatened list to Least Concern on the ICUN Red List (Stevick *et al*., 2003; IUCN, 2008; Cook *et al*., 2018). Despite this progress, some humpback whale populations have recovered less well than others. For instance, the Cape Verde population is still of concern despite the overall increase in the North Atlantic humpback whale population (Wenzel *et* *al*., 2020). With global climate change, understanding the migration patterns of baleen whales is critical to assess the potential impact of such changes on their dependence on multiple environments (Ramp *et al*., 2015). The humpback whale's migration is the longest of any mammal in the world (ca. 9,000 km), moving from high-latitude cold feeding areas in summer to low-latitude tropical breeding areas in winter across both the northern and southern hemisphere oceans (Dawbin, 1966; Mann *et al*., 2000; Smith & Dunlop, 2008). Due to diverging genetic trajectories after being isolated from each other for thousands of years, the humpback whale is classified into three subspecies based on the ocean and hemisphere they inhabit: the North Atlantic humpback whale (*M. n. novaeangliae*), the Southern (Hemisphere) humpback whale (*M. n. australis*), and the North Pacific humpback whale (*M. n. kuzira*) (Jackson *et al*., 2014). Additionally, a separate sub-population known as the Arabian Sea population, which appears not to migrate, is recognised (Pomilla *et al*., 2014).

Humpback whales in the North Atlantic breed in low-latitude areas on the western and eastern Atlantic, migrating there along the Antillean Island Chain and around the Cape Verdes, respectively. Western breeding individuals have been found to migrate to feeding grounds across the north Atlantic, including western feeding grounds in north-eastern United States, eastern Canada, and Western Greenland, and eastern feeding grounds in northern Norway and Iceland. These migration routes have been mapped through satellite telemetry tags and mark-recapture efforts of whale tail markings. However, population connectivity can also be determined through humpback whale singing patterns, as evidenced by the South Pacific whale song research (Garland *et al*., 2015).

There has been limited research on the connections between humpback whale populations that breed in the north-western Atlantic and feed in the north-eastern Atlantic. Stevick (2018) described the migration route of humpback whales from feeding grounds in Norway to breeding grounds in the West Indies. More recently, Kettemer *et al*. (2022) documented the roundtrip migration of a pregnant female humpback whale between the Barents Sea and the West Indies. Furthermore, research conducted in collaboration with citizen scientists has yielded photographic evidence of the same individual whale traveling from the West Indies to Norway, via Scotland (Pix, 2020).

Male Humpback whales predominantly sing on winter breeding grounds however recent research has detected singing on their feeding ground locations (Kowarski *et al*., 2019; Magnúsdóttir *et al*., 2014; Tyarks *et al*., 2021; Vu *et al*., 2012). It is thought that singing on feeding grounds occurs prior to migration to winter breeding locations and that song fragments rather than full songs are produced during that time (Magnúsdóttir *et al*., 2014). Additionally, some individuals may opt not to migrate and stay in their feeding locations year-round (Brown *et al*., 1995).

Population connectivity between feeding locations has been investigated. While high site fidelity was detected some (5% of re-sightings) long distance (>550 km) movement was detected in the Eastern feeding locations (Stevick *et al*., 2006). Furthermore, individuals from different feeding grounds migrate to breeding locations in the Caribbean at different times, with individuals from the Eastern feeding locations arriving later than those from the Western feeding grounds (Stevick *et al*., 2003). Additionally, individuals from the Eastern feeding locations were less likely to migrate to the Caribbean breeding locations than individuals feeding farther to the west (Stevick *et al*., 2003).

Humpback whales have also been found to sing on migration in both the North Atlantic and South Pacific (Kowarski *et al*., 2022; Owen *et al*., 2019). For example, in the South Pacific Ocean, individuals from multiple breeding aggregations have been found to be singing as they pass through the Kermedec Islands (near New Zealand) on their way to breeding locations (Owen *et al*., 2019). In the North Atlantic humpback whale songs have been detected in the Autumn on north-eastern feeding locations before their return migration to breeding locations (Kowarski *et al*., 2022). There is not much research into whether individuals continue to sing when they return to feeding grounds from breeding locations and whether they sing en route. In the North Atlantic humpback whale songs have been detected in spring and mid-winter on the southernmost feeding locations in the North Atlantic (Risch *et al*., 2012; Van Geel *et al*., 2022).

One of the potential migratory pathway for humpback whales is through Scottish and Irish shelf waters off the west coast of Scotland. Humpback whales have also been spotted on the east coast of Scotland in recent years (WDC, 2018; O'Neil *et al*., 2019). Some research shows that humpbacks have been found singing off of the length of the British Isles between October and March (Charif *et al.*, 2006). Charif *et al.,* (2006) detected humpback song as far north as the Shetland and Faroe Islands to waters west of the English Channel. These authors speculate that this is evidence of singing on migratory corridors between summer feeding locations near Norway and Iceland, and breeding locations primarily in the Caribbean (Charif *et al*, 2006). Risch *et al*., (2019) reported preliminary findings from 12 static recorders placed in Scottish and Northern Irish waters in 2018. Their detection of humpback whale song during the months of March and April at three of the sites in Scotland in 2018 demonstrated the feasibility of using PAM to determine both spatial and temporal distribution of humpback whales in Scottish waters. Furthermore, a small sample of their recordings were of high enough song quality (of 'Fair' quality on four-point song quality rating SNR ca. 20 dB) to determine song structure, which could therefore enable song matching between and within feeding grounds and breeding grounds within the North Atlantic population. This shows that waters off the west coast of Scotland may be an important migratory pathway for humpback whales. Relatively little is known about migratory behaviour in humpback whales (Modest *et al*., 2021). It is important to determine the function of these locations for humpback whales to better protect these recovering populations.

Recent research has identified the presence of humpback whale song in offshore waters off Scotland's Atlantic Frontier from early January to March and April at four sites in 2021, as reported by Van Geel *et al*. (2022). Prior to this study, baseline information on cetacean occurrence and distribution in the region was severely lacking. The study by Van Geel *et al*. (2022) highlights the effectiveness of passive acoustic monitoring in filling this crucial data gap in Scottish waters and emphasises the need for further research. Although Van Geel *et al*.'s study focused on occurrence and distribution, there has been no analysis of song evolution in Scottish waters to date, nor has there been an investigation of how the relationship between humpback whale song in Scottish waters and breeding locations, such as those in the Eastern Caribbean, may be connected. Therefore, the goal of this chapter is to examine the connectivity between humpback populations based on their songs in both the Eastern Caribbean and Scottish and Irish waters.

Additionally, this chapter aims to track the fine-scale evolution of song and unit types within one song across multiple seasons and sites, expanding upon the findings in the previous chapter. In Chapter 3, I found that humpback whale song units were generally stable over the time-scale of one breeding season but that there was variation in unit evolution within song sessions and between individuals. It is important to understand whether this is a species-wide pattern through analysing song recordings from a distinct population and over a longer time-scale. Here I track the evolution of a unit type within one song type and across three different themes to illuminate how humpback whale song units may be stored in the brain through examination of another humpback whale population. Furthermore, I track the evolution of a humpback whale song unit over multiple years and locations to examine whether a longer time-frame may lead to further change in song units.

4.2 Methodology

4.2.1 Data Collection

Data was collected from three different sites through collaboration with three different research groups.

COMPASS 2020

Acoustic data in Scotland 2020 were collected by the COMPASS project (The COMPASS project is a Marine Scotland project funded under EU INTERREG VA). The COMPASS project focused their efforts on inshore waters of the Scottish West Coast and Northern Ireland. Acoustic recorders (SoundTrap, Ocean Instruments) were deployed at 12 different locations (see Figure 4.1) at a sample rate of 96 kHz and set to a duty cycle of 20/40 minutes on/off. At each site recorders were deployed in depths from 50 to 110 m of water and were deployed three to five metres above the sea floor. Initial studies by Risch *et al*. (2019) discovered peaks in humpback whale song at Tolsta and Stanton banks during March and April. For this reason, recordings in March and April 2020 were further investigated for humpback whale song. Raw acoustic files were scanned in PAMGUARD utilising a bespoke moan detector. My fine-scale study of humpback whale song evolution required song recordings with high SNR to enable full song description and measurements for individual units. For this reason, only recordings labelled as quality rating 'Good' (i.e. SNR above ca. 30 dB – see Appendix 3.1 for examples of song recordings on four-point quality scale) and upwards were investigated for further analysis across both sites and years.

SAMOSAS 2021

Acoustic data in Scotland 2021 was collected by the SAMOSAS project between September 2020 and August 2021. Humpback whale song detections were focused on the outermost three of a total of 10 moorings, all of which were deployed on the continental shelf to the west of the Outer Hebrides, Scotland (see Figures 4.2; 4.3 and 4.4). At each recording site passive acoustic recorders (Sylence-LP-440; RTSYS, France) were deployed at depths between 61 and 174 m and approximately 5 m above the seabed. Acoustic recorders collected data as a sample rate of 64 kHz and on a duty cycle of 25/35 minutes on/off.
The outermost three moorings (EL1, N1 and S1) were further analysed for humpback whale song as preliminary auditing by Denise Risch had revealed high quality song recordings at these sites. An hourly audit of recordings was provided by Denise Risch. All recordings flagged as containing 'good' or better humpback song was further investigated for suitability to fine-scale song analysis.

Eastern Caribbean 2020

The survey effort focused on the Eastern coast of the Lesser Antilles (the northernmost site off St Kits and Nevis and the southernmost site off Grenada) during February to April in 2020. Acoustic recordings in the Eastern Caribbean were made during offshore boat-based surveys in which a two-element hydrophone array (BENTHOS AQ4) was towed behind the vessel on a 100-metre cable to record sound continuously. The frequency range of the hydrophone array continuously monitored between 10 Hz and 15 kHz. An audio interface UMC202 was connected to a computer running PamGuard version 2.01.03 which allowed acoustic presence of species to be monitored by onboard surveyors every 30 minutes. Monitoring captured data on recorded species, level of anthropogenic noise and status of engine (on or off). Special effort was made in 2020 to record long samples of humpback whale song with the vessel's engine off to improve SNR. I was provided with all recordings and an audit file which noted humpback presence and song quality. I further investigated any positive humpback whale song recordings for suitability to fine-scale analysis in Raven noting SNR quality and presence of multiple humpback individuals or other species.

For each site, from the recordings that met fine-scale analysis SNR requirements, I then chose one recording (maximum 35 minutes long) per day with a minimum of 72 hours between each recording to maximise the likelihood of capturing different individuals as individuals are likely to move location in this timeframe (see Figure 4.5 and 4.6).

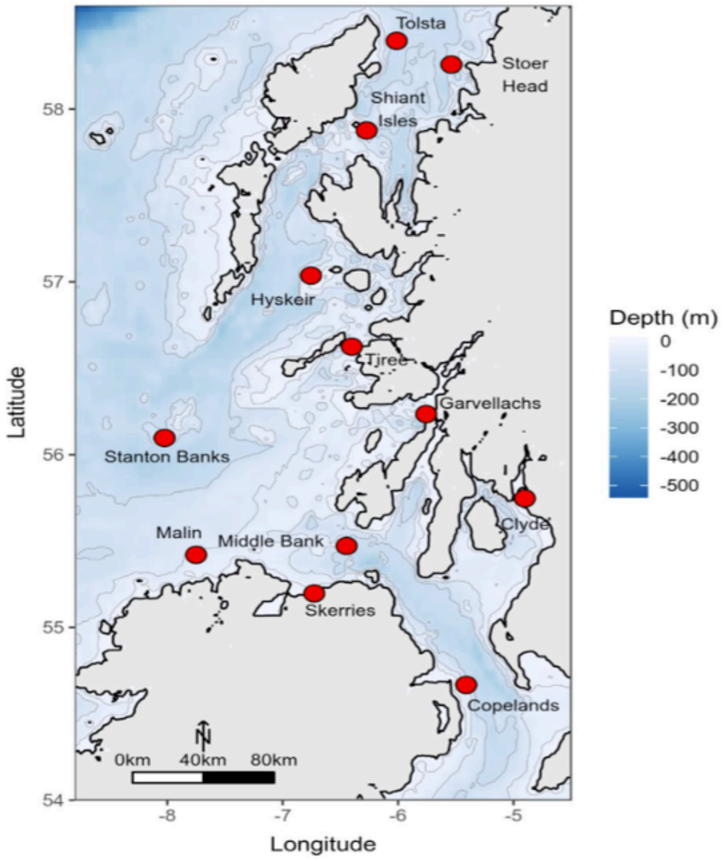


Figure 4.1: COMPASS: Map of the study area on the west coast of Scotland and locations of PAM moorings. The Tolsta site is the northern most site on the map. Taken from Risch et al., 2019.

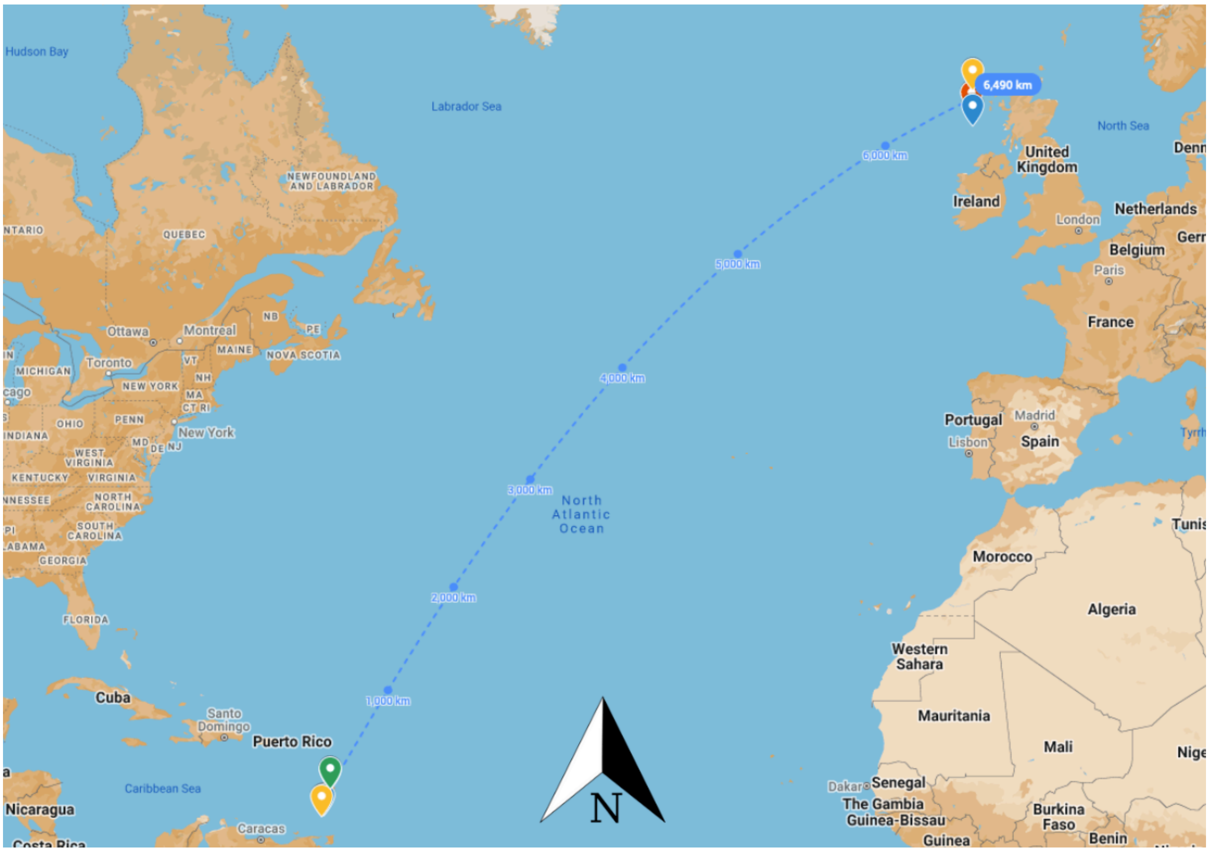


Figure 4.2: Study locations: North Atlantic Ocean: Eastern Caribbean and Scotland - study locations separated by 6,500 km

Figure 4.3: Study locations in North Atlantic eastern feeding grounds context. The three markers represent the sites of the three outermost SAMOSAS recordings in 2021 EL1 (yellow), N1 (red) and S1 (blue).

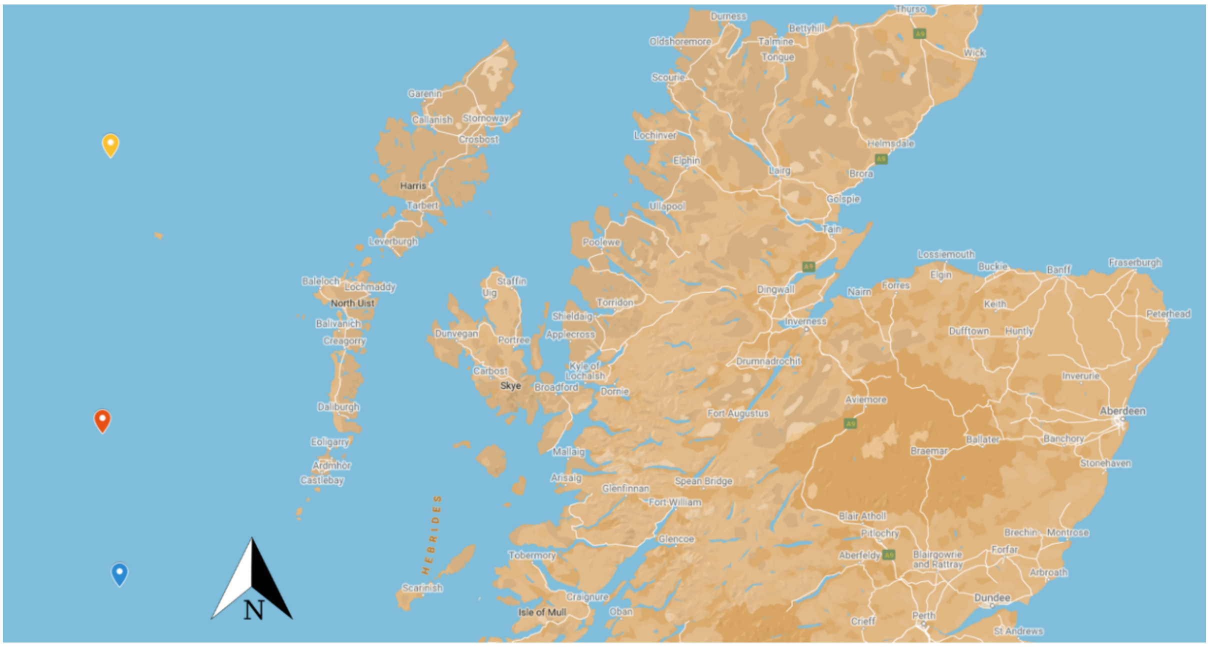


Figure 4.4: Close up of Scotland Recording locations on the Scottish North Atlantic Frontier. The three markers represent the sites of the three outermost SAMOSAS recordings in 2021 EL1 (yellow), N1 (red) and S1 (blue).

Figure 4.5: Caribbean Sea map - Lesser Antilles in Eastern Caribbean

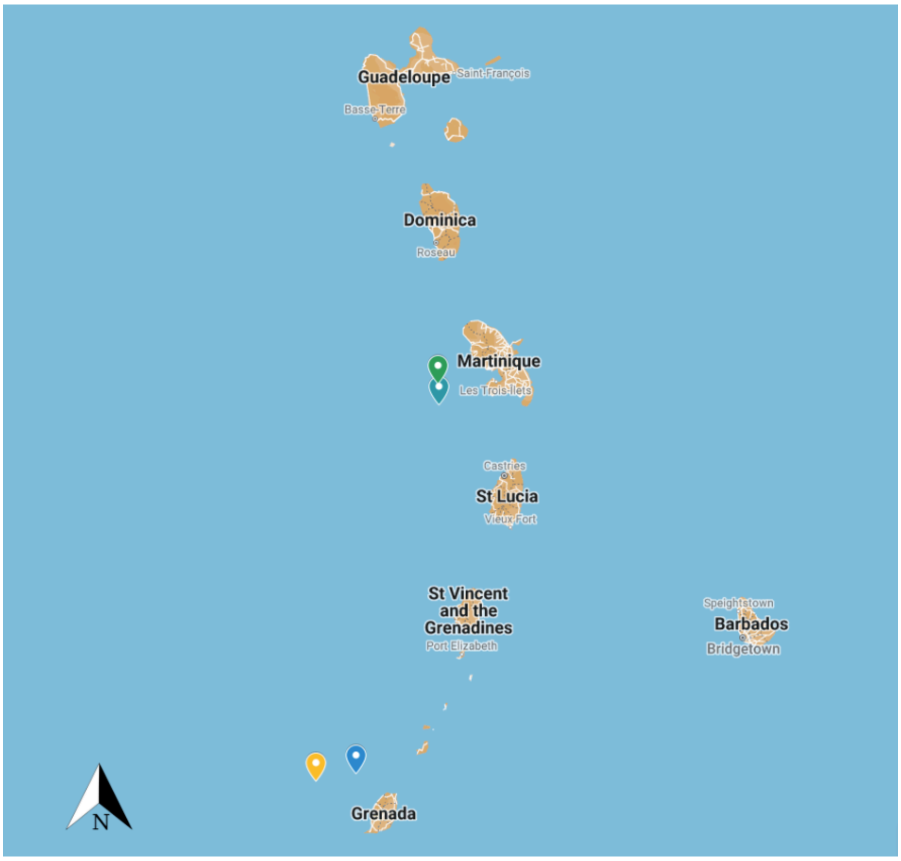


Figure 4.6: Recording locations of Eastern Caribbean recordings. The markers represent each of the locations of the recordings chosen for further analysis. The yellow and blue markers represent the recordings made off West Grenada (south atilles) and the green and light blue markers represent the recordings made off West Martinque

4.2.2 Song and Theme level analysis:

Spectrograms were viewed in Raven (Version 1.6) and a preset spectrogram view was applied (FFT: 2048, Brightness: 65, Contrast: 63, 512-point hop size) displaying approximately 10 seconds of song from 0 - 5 kHz on a 23-inch screen. Song recordings were transcribed first at the unit level by a human classifier utilising descriptive unit names and a short hand code (See Appendix 4.1 for a complete list of unit names and codes). As per the full protocol described in section 3.2.2 a unit catalogue was created to enable rapid comparison of dozens of units (Please see this online link) (https://figshare.com/s/f0820b881f013bc3bf75).

Phrases were delineated by firstly identifying the longest gap in a series of units and then observing whether the delineated sequence of units between these longer gaps was repeated in such a way that 'hanging units' at the end of a theme were minimised (Cholewiak *et al*., 2013). Clear patterns of units were identified from the song spectrogram and each pattern was allocated to a phrase type as per the full phrase protocol described in section 3.2.2.

Small changes to a phrase sequence, for example the substitution of one unit for another unit, created similar phrase types within a theme. These similar phrase types were denoted as a 'b' version of the original phrase type (e.g. 1a, 1b, 1c) and transitional phrases were removed as per the full protocol described in section 3.2.2. Spectrograms of each theme (including 'b' themes) were created in R using the 'warbleR' package (FFT = 2048, Hop Length = 75). The order of themes was plotted using transition plots in which all theme types (including b themes) were visualised in a cycle. A transition plot was created for each recording and only complete song cycles were included to construct the transition plots.

All phrases identified by a human observer were then entered into a Levenshtein distance analysis (LDA) to verify the relationship of phrase and theme categorisation described above. Please see section 3.2.2 for a complete description of LDA. The resulting pairwise similarity coefficients were then visualised as dendrograms constructed using hierarchical cluster analysis. Each cluster of phrase types in these dendrograms was reduced to one theme type and then labelled with a colour name for ease of reference. These broadly inclusive theme types allowed us to track evolution of units across the season because theme phrase sequences may also evolve over the season (e.g. 1a evolving into 1b and so on). As a further test of how well each dendrogram represented the data, the Cophenetic Correlation Coefficient (CCC) was also calculated. A CCC score of over 0.8 is considered a good representation of the groups present within original the data.

Theme matching between recordings of song captured in Scotland and the Eastern Caribbean was carried out both subjectively by comparing theme spectrograms and quantitatively by separating theme types based on location and performing the Levenshtein Distance Analysis described above. Song strings for each recording were also generated. Song strings for each recording were strings of theme types (rather than units). Here a string was a sequence of phrase types. These song strings were inputted to the Levenshtein distance analysis in R Studio as described above for theme strings.

4.2.3 Unit level analysis

All units were qualitatively assessed for recording quality (any overlap with other sounds or low SNR (< ca. 20 dB) were excluded) and were not taken forward for unit level analysis (‘yes’ for good quality, ‘no’ for bad quality). A further 100 units were included in the subjective ‘yes’ group when the MATLAB code was then unable to produce accurate estimates in MATLAB due to low SNR and these units were removed before progressing the unit analysis. The unit level analysis then followed the full protocol found in section 3.2.3 in which robust signal measurements were generated of each song unit using Raven Pro (v1.6.1). For the reasons outlined in section 3.2.3 a robust measurement (Dur90) was used in place of duration as defined by the placement of the box selection. Start and End frequencies were calculated using custom MATLAB code. This technique was also used to estimate the end frequency (utilising the time at which 95% of the energy in the selection window was cumulatively obtained through to the end of the selection). A full description of this new methodology can be found in section 3.2.3.

The mean, median and standard deviation of each measurement for each unit type was calculated. As per section 3.2.3 a principal component analysis and a heat map of variable importance was applied. All units were input to a random forest analysis to check consistency of the qualitative classification (a full description of the random forest analysis can be found in section 3.2.3).

The analysis aimed to track unit types that occurred in different theme contexts to test the hypothesis of whether or not units evolved differently in different theme contexts. The original transcription of the song data created a fine-scale unit library. Unfortunately, this fine-scale unit library meant that if a unit type evolved into other 'types' during any song change then this unit evolution couldn't be tracked within a continuous measurement series. To avoid missing this significant unit evolution unit types were recombined into larger unit categories, for example, "short" and "long" modulated moans were combined into "modulated moans". To achieve this quantitively values for each measurement of each unit type were calculated. All mean measurements were standardised and then the Euclidean distance was calculated between each fine-scale unit type. Utilising the 'hclust' package in R, the Euclidean distances were then clustered via both the average-linkage method and Ward2 method to create comparative dendrograms. These dendrograms allowed us to view each fine-scale unit type as an end-node. The two linkage methods (Average and Ward2) were compared by calculating the cophenetic correlation coefficient (CCC) to determine the best fit with the original Euclidean distances. The linkage method with the highest CCC and therefore the best fit with the original Euclidean distances was chosen to perform the rest of the analysis.

This dendrogram was then cut into successively smaller number of groups (such that the number of fine-scale units per group increased) as determined by the branches within the dendrogram. As the number of groups decreased the number of fine-scale units within each group increased so that the total number of fine-scale units was held constant. For example, if the if the total number of fine-scale units was 26 we therefore began with 26 'branches' and then the next step was to combine the most similar two branches, as defined by their placement on the dendrogram, so that we then had 25 branches. The next step was then to combine the next most similar two branches so that we had 24 branches. This process was repeated until there remained only one branch containing the complete 26 fine-scale unit types.

Random forest models were created for each number of branches. The random forest model with the lowest error rate was 17.7% (ntree 500, mtry = 5) was applied in a loop to an average-linkage dendrogram of the 26 units. The out of bag error (OOB error) for each iteration was plotted. Conspicuous jumps in OOB error indicated that the number of fine-scale units being allocated to the wrong group significantly increased at this point. The number of branches present before each large jump was investigated through examining the dendrograms with this number of branches. For example, if there was a large jump in OOB error when the number of groups increased from four to five then a dendrogram with four groups was taken forward. If there was another large jump in OOB error between 10 and 11 groups, then a dendrogram with 10 groups was also examined. I wanted to choose a number of groups which allowed fine-scale units to be brought together to allow their evolution to be tracked across the season but that also did not lump very different units together as per the protocol described in section 3.2.3.

When the number of groups was chosen, the number of observations within each group was counted across theme type and recording. Units with more than 100 observations in each theme type were considered for further analysis. Fine-scale units outside of the chosen group that were obviously derived from any of the fine-scale units in the chosen group were added to this group too. This judgement was made based on examination of cluster plots, which showed that fine-scale units that had been placed on a different branch due to a change in length or modulation were close in acoustic space (see Figure 4.16 and Appendix 4.7). For example, if a “trumpet” was within the target group then the "trumpet-sp” (a longer version of the trumpet) fine-scale unit type was also added to the group. Again, this was to encapsulate any song evolution that may occur. This process created a final group of multiple fine-scale units termed a ‘meta-unit’ which was named the ‘Moan’ unit.

4.2.4 Alternative hypotheses analyses

As in Chapter 3, I conducted three additional analyses to check for other mechanisms that could change sound form over time. Firstly, I assessed the influence of Signal to Noise Ratio (SNR) on Start Frequency, End Frequency, and Duration 90 measurements. This examination involved a Pearson correlation test, the complete protocol of which can be found in Section 3.2.4. Secondly, I investigated coarticulation patterns within the 'moan unit' using a linear regression analysis, with the comprehensive protocol detailed in Section 3.2.4. Lastly, I delved into the concept of signal exhaustion by examining the average peak frequency within the initial and final theme renditions within each recording. To determine if there was a significant shift in peak frequency from the first to the last rendition, and whether this shift moved towards the population average, I employed a t-test. The detailed protocol can be referenced in Section 3.2.4.

4.2.5 Statistical analysis of Unit Change over Time

Each theme type was isolated from the dataset and firstly an acoustic distance matrix was generated across all recordings as per the protocol described in section 3.2.4. Secondly, a temporal distance matrix was created as per the protocol described in section 3.2.4. For each theme the data were partitioned into those comparisons that were within the same recording and those comparisons across different recordings, which allowed analysis of variation both within and between individuals.

A symmetrical matrix was required for input into a Mantel test. A Mantel test was chosen to analyse for change of acoustic structure over time because this test allows input of distances in time and space (here defined as acoustic space). Further description of a Mantel test is found in section 3.2.4. In this case the first matrix was the matrix of Euclidean acoustic distances between all possible unit pairs in the study. The second matrix was the temporal distances between all possible unit pairs in the study. To generate a symmetrical matrix of the partitioned observations partitioned datasets required to be a length equal to a triangle number as fully described in section 3.2.4. To achieve this, the closest triangle number below the number of observations within each vector was identified and a random sample equal to this triangle number was derived from the vector. To check for any effect of sampling error on the mantel output a random sample was applied 10,000 times to each partitioned dataset. The frequencies of observations were plotted and checked for normal distribution and no sampling effect was found for any of the randomly sampled vectors. A Mantel test, from the R Package 'vegan' based on Pearson's product-moment correlation with 999 permutations was applied to each dataset using R code "mantel(acousticMATRIX, timeMATRIX, method= "pearson", permutations=999)". The Mantel test was against the null hypothesis that there was no correlation between unit acoustic similarity and time between recordings - this null hypothesis would mean units were not changing detectably over the sampled period. If units are changing, we expect a consistent relationship in which acoustic distance increases with the passage of more time between recordings.

To investigate whether the moan meta-unit (defined above as a group of fine-scale units) changed in different ways in different theme types each comparison between pairs of observations derived from different theme types (either Orange – Indigo, Indigo – Violet and Orange – Violet) were isolated from the dataset. Summary statistics were generated for each theme comparison and the median acoustic distances between each theme pair within each recording were analysed with a linear regression of form "lm(median ~ Time)" [see this link for complete R code: https://figshare.com/s/2a98f777eeb9c55c5f8e].

Table 4.1: Recording and time since first recording (in days to 1 decimal point)

Recording		Days since start of season
ID	Date Time	
100220-000404	10-02-20 00:04:04	0
160220-174516	16-02-20 17:45:16	6.7
270220-190235	27-02-20 19:02:35	17.8
050320-182937	05-03-20 18:29:37	24.8
270221-210004	27-02-21 21:00:04	383.9
050321-000004	05-03-21 00:00:04	389.0
170321-071042	17-03-21 07:10:42	401.3
250321-080005	25-03-21 08:00:05	409.3
300321-090004	30-03-21 09:00:04	414.4

Violin plots of each regression were generated directly from the above models using the R function ‘violinplotter’ (v3.0.1, Paril, 2022) following the protocol described in section 3.2.4. Under this analysis I expected the coefficient for 'Time' to be significantly different from zero, and further I expected that distance would change at different rates in the three models if similar units were evolving independently in the two themes. If so, I would interpret different rate in change as suggesting that the units used in the different themes, despite being the same unit type, had independent change trajectories over time and were unlikely to be drawn from the same cognitive or neural representation when produced.

Discrete acoustic measurements

A linear regression with interaction of theme type (Orange, Indigo, Violet) was applied to the median in the form of ‘lm(median ~ TimeDays * theme, data = measurement type)’. To test whether units in different theme types were changing in different ways across the season and an interaction term was added. Interaction plots were generated using ‘interact plot’ in the ‘interactions’ package (v1.1.5, Long, 2021). Under this analysis, significant interaction terms would provide an explicit test of different trajectories of acoustic change across different themes, this is arguably more robust than fitting individual models.

To determine how each acoustic measurement type changed within song sessions the robust measurement ‘Time5s’ was standardised from start of each recording. Time5s was converted from seconds to minutes for easy interpretation of output plots. Themes were analysed independently. For the Orange and Indigo themes, recording 27/02/20 was removed due to only one iteration of the orange and indigo themes being captured in this song recording (all other recordings had at least X such iterations). A linear regression with interaction term ‘Recording’ in the following form was applied to each theme type dataset: “lm(MeasurementType ~ Time5__s_ * Recording, data = ThemeType)”. The interaction term allowed testing of whether units in different individuals (recordings) were changing in different ways across their song sessions. Visual inspection of the model of the untransformed data showed that data from some measurement types required some transformation in order to accommodate the large positive residuals and produce a better fit of the model. For each measurement type a model utilising raw values and a model utilising log-transformed values was fitted following the protocol in section 3.2.2. For each measurement type a table of how each individual changed their display of each unit in each theme type (positively, negatively or No Significant Change) was created through examining the interaction term outputs of the regressions for each individual in each theme.

4.3 Results

4.3.1 Data Collection

Recordings at each site were chosen to enable separation by at least two days to increase the likelihood that each recording was from a separate individual. The COMPASS project made 196 recordings over 40 days at the Tolsta site in 2020. 69 recordings were found to have humpback whale song present which represented 9 days of the total deployment. Only two recordings at this site were of sufficient quality to enable a theme level analysis to be carried out. None of the recordings at this site were of high enough quality to be taken forward for a full fine-scale analysis. The SAMOSAS project successfully made a total of 22750 recordings across the three outer sites: EL1, N1 and S1 (see Table X for breakdown of recordings per site). 950 recordings across all three sites were found to have humpback whale song present. Five recordings had sufficient quality to be taken forward for fine-scale analysis (2 at EL1, 2 at N1 and 1 at S1). The Eastern Caribbean project successfully made 2259 recordings over 55 days. 245 were found to have humpback whale song present. Four recordings were chosen of sufficient quality for this fine scale analysis.

The recording quality screening resulted in 5 songs being selected from Scotland 2021 and 4 songs from Dominica 2020. The recordings from Scotland 2020 (COMPASS) were not of high enough SNR to enable fine-scale analysis (i.e. measurements of individual units), however two recordings at Tolsta 2020 allowed the song theme structure to be transcribed. The high-quality recordings spanned a time frame of 10/02/20 to 30/03/21 and provide a range of times to explore both song evolution within the peak singing period within the breeding season and on migration to feeding grounds. One song type was identified in all of the recordings. An example of the songs theme structure is presented in Figure 4.7. A transition plot for each recording can be found in Appendix 4.3. A transition plot shows the consistent song cycle but with minor variation in theme order and phrase variant use.

Table 4.2: Percentage of recordings utilised for fine-scale analysis at each site

Location	Site	Survey Type	Survey Dates	Number Recordings	Number positive HB recording	Number days	Number positive days	Number recordings utilised	Number days utilised
SAMOSAS 2021	EL1	ST	18/10/2020 - 23/08/2021	7390	1189	309	81	2(0.2%)	2(2.5%)
	N1	ST	21/09/2020 - 22/08/2021	8050	1100	336	86	2(0.2%)	2(2.3%)
	S1	ST	18/10/2020 - 19/08/2021	7310	985	305	70	1(0.1%)	1(1.4%)
Caribbean 2020	Transect	H-P	15/01/20 – 14/03/20	2259	245	54	35	4(1.6%)	4(7.3%)
COMPASS 2020	Tolsta	ST	20/02/20 – 30/03/20	196	69	40	9	2(2.9%)	2(22.2%)

Table 4.3: Songs utilised for this study

Date	Site	Sub-site	Song Type	Themes present	Song Recording length	Number of complete song cycles
10/02/20	EC	W.Grenada	1	1a, 1b, 2a, 3a, 4a, 5b, 5c	28 minutes	2
16/02/20	EC	W.Martinique	1	1a, 1b, 2a, 3a, 4a, 5a, 5b	29 minutes	2
27/02/20	EC	W.Grenada	1	1a, 2a, 3a, 4a, 5b	30 minutes	1
05/03/20	EC	W.Martinique	1.5	1a, 4a, 5a, 5b, 5c	30 minutes	3
26/02/20	SC	TOLSTA	1	1a, 1b, 2a, 3b?, 4a, 5d, 5a, 5b, 5c	20 minutes	1
13/03/20	SC	TOLSTA	1	1a, 1b, 2a, 3b?, 4a, 5d, 5a, 5b, 5c	13 minutes	1
27/02/21	SC	EL1	1.5	1a, 1c, 4a, 5a, 5d, 5c	25 minutes	2
05/03/21	SC	S1	1.5	1a, 1c, 1d, 4a, 4b, 5a, 5d, 5b, 5c	25 minutes	2
17/03/21	SC	N1	1.5	1a, 1c, 1d, 4a, 5a, 5b, 5c	14 minutes	1
25/03/21	SC	N1	1.5	1a, 1c, 1d, 4a, 5a, 5b, 5c	20 minutes	2
30/03/21	SC	EL1	1.5	1a, 1c, 1d, 4a, 5a, 5d, 5c	25 minutes	3

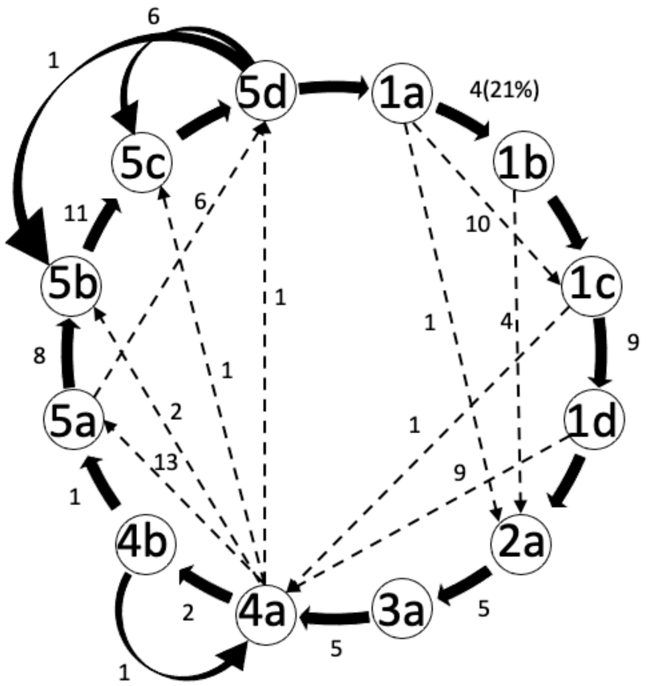


Figure 4.7: Complete transition diagram of the 20/21 North Atlantic song. The transition diagram includes relevant 'b' themes (in which similar phrase types are grouped together).

4.3.2 Song analysis: Are the songs in Scotland and the Eastern Caribbean the same song type?

Across both sites five core themes were identified. A clear match in song type has been identified between these locations (Figure 4.7 and Appendix 4.2). Not only is there a clear match between theme types (see spectrograms in Appendix 4.2) but in the Eastern Caribbean 2020 the latest recording has evolved to match the theme transitions of Scotland 2021 (see Eastern Caribbean transition diagram Figure 4.8 and Scotland transition diagram Figure 4.9). The earlier song in the Eastern Caribbean is comprised of five core themes, two themes (theme 2a and 3a) have dropped out by the 5th of March in Dominica and from all of the song recordings present in Scotland 2021. It is clear that the late song of Eastern Caribbean is more similar to the song of Scotland 2021 than it is to the song of early 2020 in the Eastern Caribbean (Figure 4.10 shows a dendrogram of the similarity of all of the recordings analysed in both the Eastern Caribbean in 2020 and Scotland 2021).

Two recordings in the COMPASS Scotland 2020 recordings allowed a broadscale theme analysis (i.e. themes were identified however individual units were not analysed). In Scotland 2020 there is some evidence that the song matches the earlier version of the song in Eastern Caribbean 2020 (comprised of five rather than three core themes). It appears that the song in Scotland in 2021 is more similar to the late song of Eastern Caribbean 2020 (dropping theme 2a and 3a), than it is to the late song of Scotland 2020 (includes theme 2a and a version of theme 3a) (see Figures 4.8; 4.9).

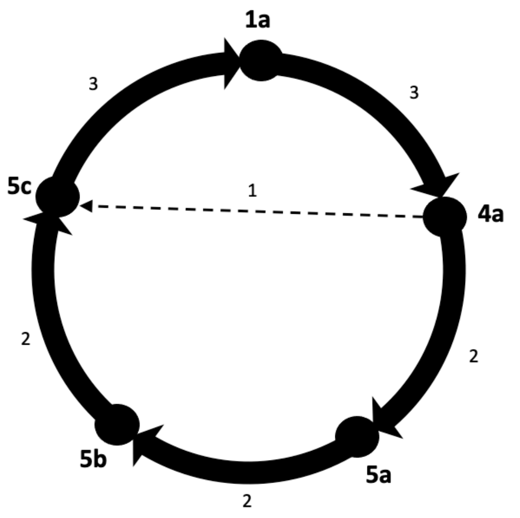


Figure 4.8: Transition diagram for Dominica – 05/03/20 – 3 complete cycles

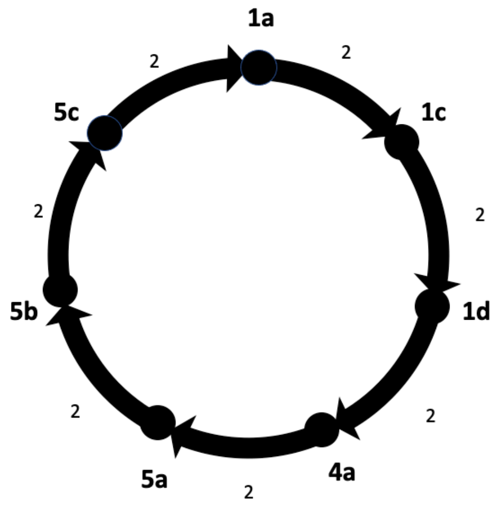


Figure 4.9: Transition diagram for Scotland – 25/03/21 – 2 complete cycles

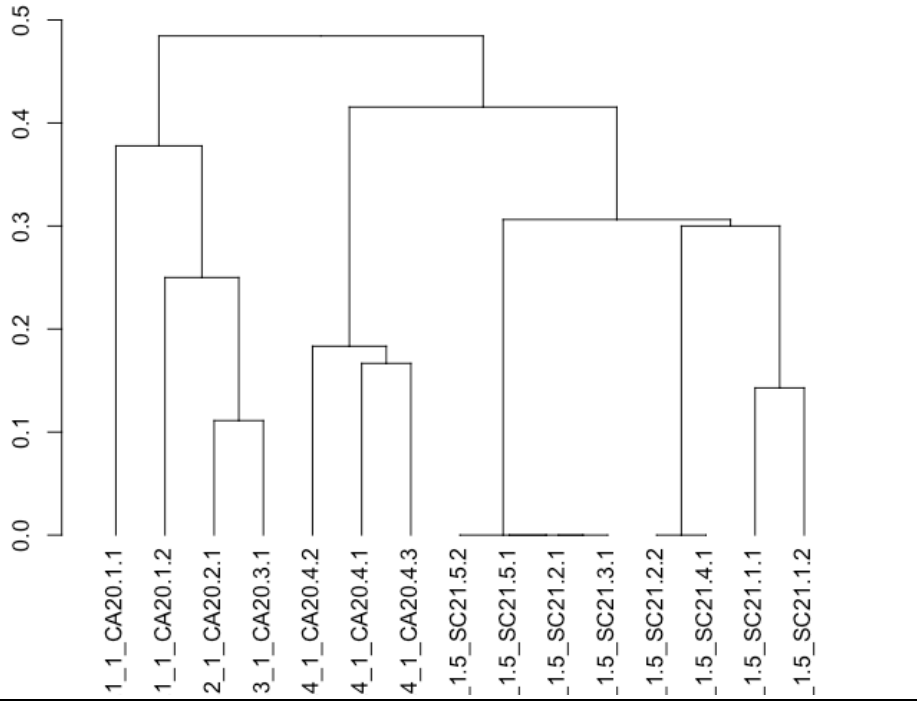


Figure 4.10: Song cycle similarity: Song dendrogram average-linkage hierarchical clustered median unit sequences for each theme all Eastern Caribbean 2020 and Scotland 2021 Song recordings (CCC = 0.815). A CCC score of over 0.8 is considered a good representation of the groups present within the data. Branches with high bootstrap values (AU significance P > 95% and bootstrap probability significance P > 70%) are strongly supported by the data, whereas lower values suggest uncertainty in their division.

4.3.3 Theme analysis: How is Song 1 structured into different theme types?

The North Atlantic 2020/2021 song was composed of five core themes, evidenced by the Levenshtein analysis and dendrogram outputs, which supported the qualitative classification of five core themes with 1-4 theme variants within each (Figure 4.8 and 4.9; see Appendix 4.2 for complete spectrograms of the core themes). Theme five was split into two groups (5a and 5d together and 5b and 5c together) but due to the consistent transitions between these four phrase types within the songs I have chosen to group as one core theme type. Due to the similarity of theme 5a and 5d I took this sub theme forward for further analysis. The theme composition was supported by both the weighted (Figure 4.11; Figure 4.12) and unweighted (see Appendix 4.4) analyses. All spectrograms of each core theme variant can be viewed in Appendix 4.2. Each core theme type was given a colour name: Orange (theme 1a, 1b, 1c, 1d), Indigo (theme 4a, 4b) or Violet (theme 5a, 5d).

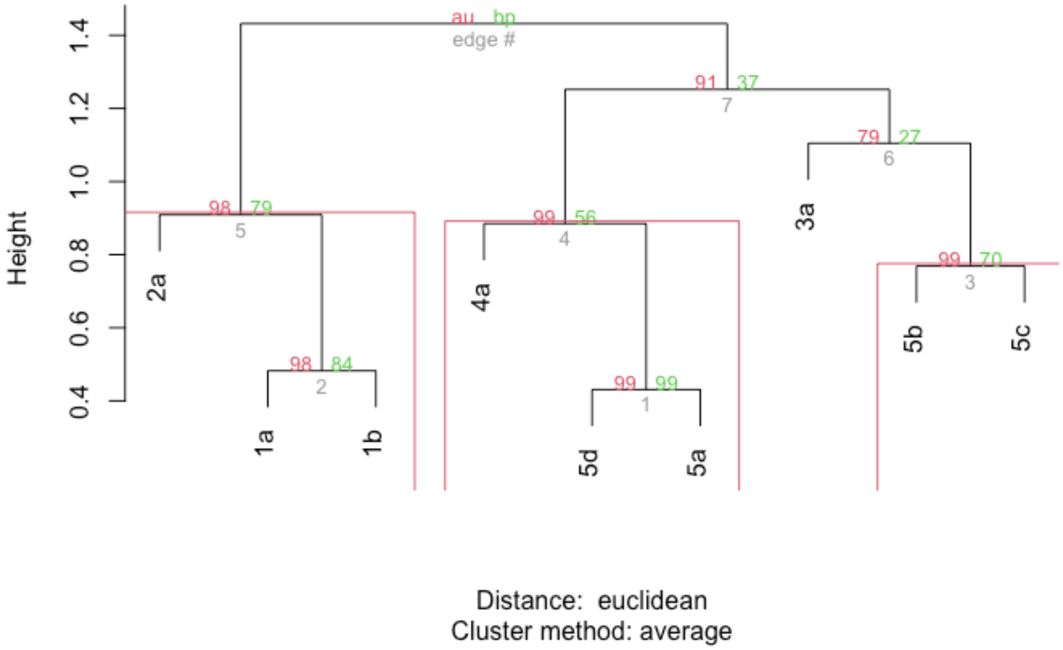


Figure 4.11: Eastern Caribbean 2020 Theme dendrogram Weighted dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Eastern Caribbean 2020 Song (CCC = 0.916). Branches with high bootstrap values (AU significance P > 95% and bootstrap probability significance P > 70%) are strongly supported by the data, whereas lower values suggest uncertainty in their division.

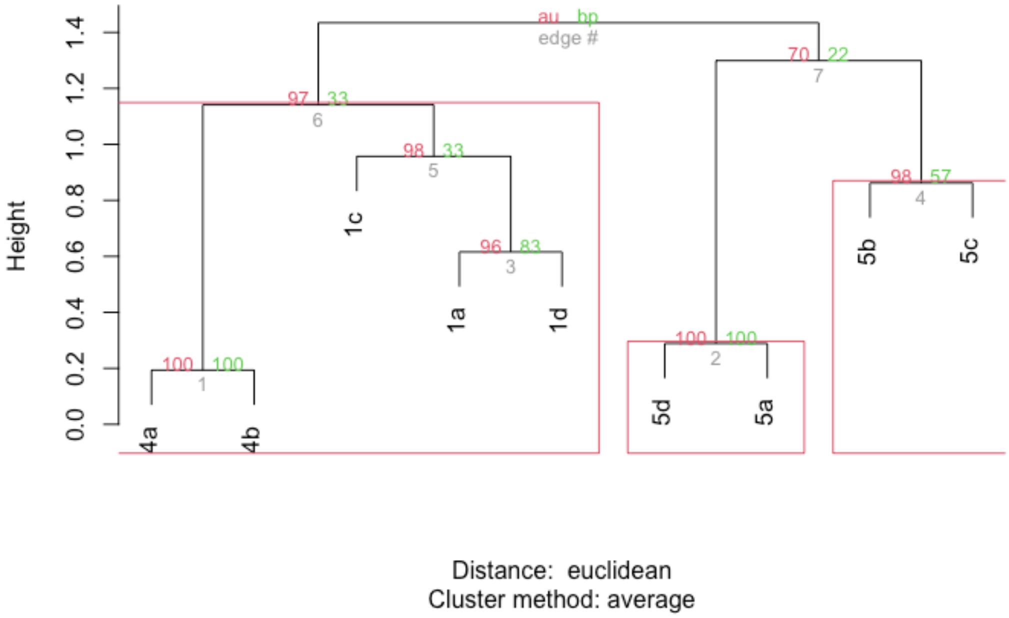


Figure 4.12: Scotland 2021 Theme Weighted dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for Scotland 2021 Song (CCC = 0.940). Branches with high bootstrap values (AU significance P > 95% and bootstrap probability significance P > 70%) are strongly supported by the data, whereas lower values suggest uncertainty in their division.

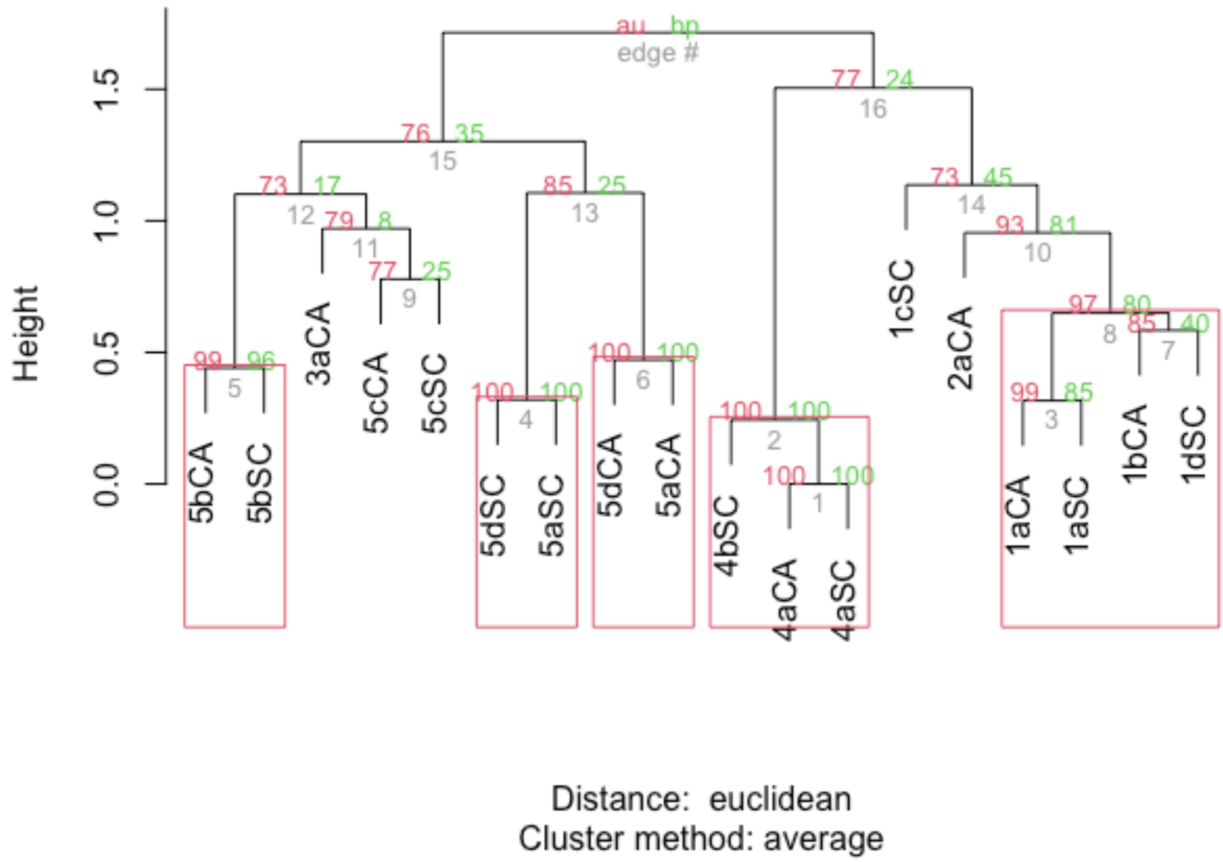


Figure 4.13: Eastern Caribbean 2020 and Scotland 2021: Weighted dendrogram of bootstrapped (1,000) similarity matrices of average-linkage hierarchical clustered median unit sequences for each theme for the Eastern Caribbean 2020 and Scotland 2021 song themes (CCC = 0.854). Branches with high bootstrap values (AU significance P > 95% and bootstrap probability significance P > 70%) are strongly supported by the data, whereas lower values suggest uncertainty in their division. Red rectangles indicate clusters of significant probability. Note how similar themes from both Scotland and the Caribbean cluster together, indicating the common song.

4.3.4 Unit analysis: What fine-scale and broad-scale unit types are present in the North Atlantic 2020/2021 song?

Transcription of the North Atlantic 2020/2021 song identified 26 units (Appendix 4.1). The random forest models applied to each branch level in the unit dendrogram revealed two clear jumps in out-of-bag error (at 4 and 10 groups) (Figure 4.14). My visual inspection of the groupings revealed that the dendrogram with 10 groups of fine-scale units more realistically showed variation in the unit types (Figure 4.15 and see Appendix 4.4 for a comparison of 4 and 10 groups). Of these 10 meta-unit types, one was able to be tracked over all three core themes (orange, indigo and violet) (see Table 4.4) and across the season (Table 4.5). This meta-unit – named the 'moan' unit – was therefore chosen for further analysis. The additional units "tsp" and "t-sp" were added to this meta-unit because they were simply longer versions of fine-scale units within the moan group and could represent evolution of the unit over the season or within song sessions (Figure 4.16 and see Appendix 4.7 for complete list of original unit types committed to the meta-unit 'Moan'). In total 1798 observations were analysed in the final analysis.

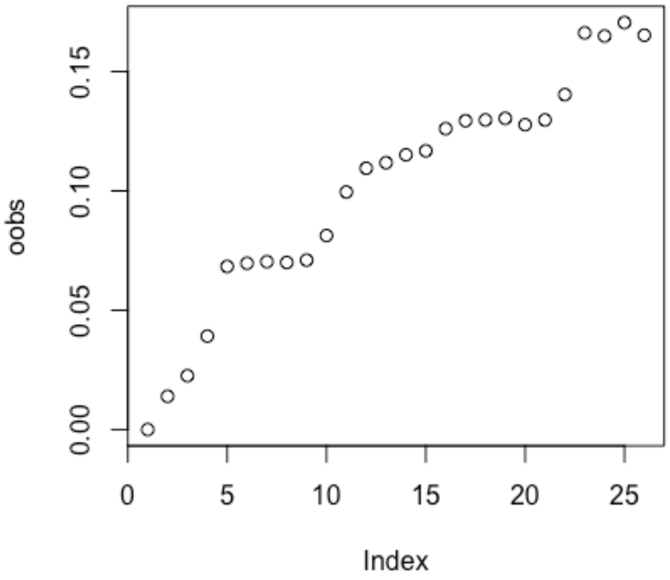


Figure 4.14: OOB error scores of original 26 fine-scale units The plot of OOB error scores per number of unit groups revealed two jumps in OOB error at four and ten groups. The number of groups was how many categories the total 26 fine-scale units were split into. A large jump in OOB meant that more unit observations were incorrectly assigned to a group. The OOB error score for 4 groups was just over 4% and the OOB error score for 16 groups was 8%.

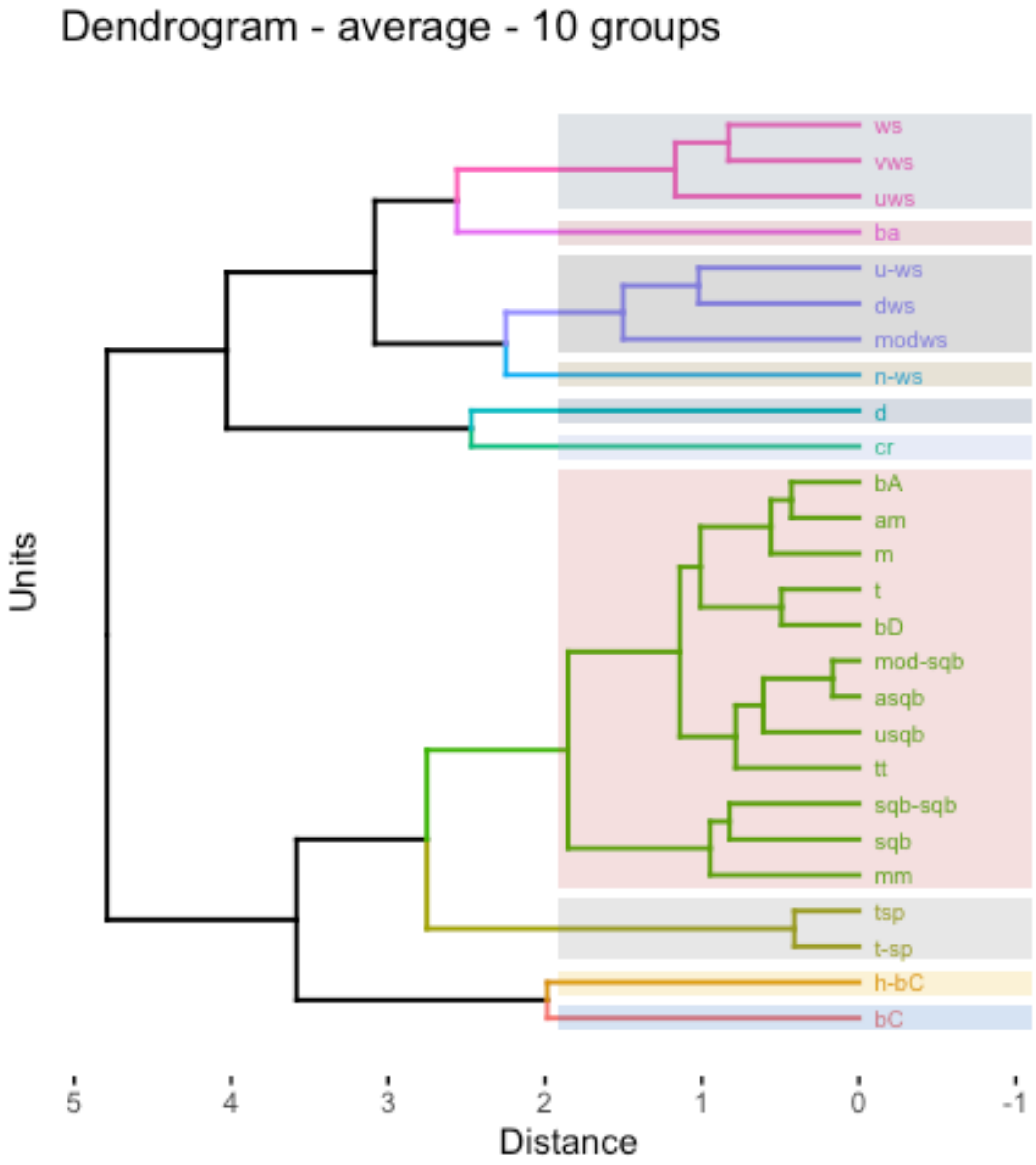


Figure 4.15: 10 group dendrogram: Average linkage dendrograms in 10 groups. The large green group in the middle of the dendrogram represents the meta-unit 'moan'

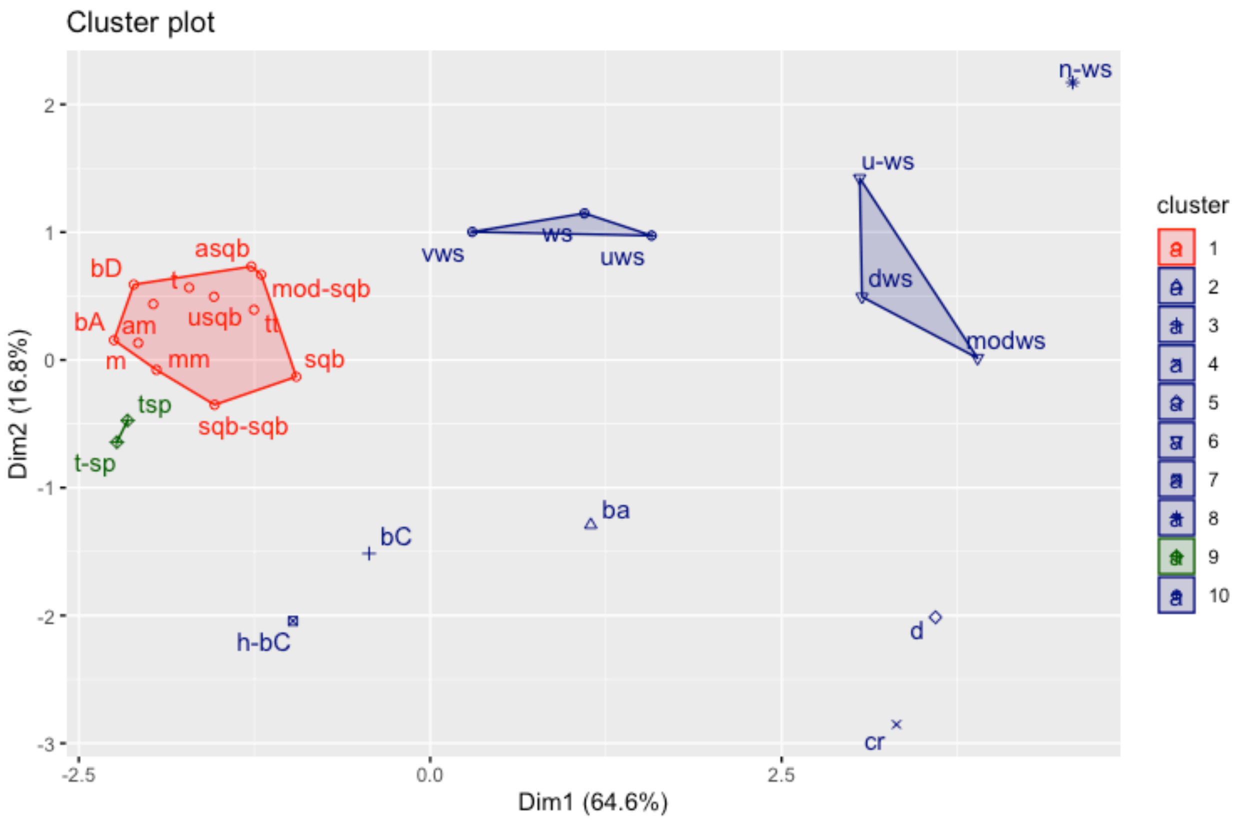


Figure 4.16: 10 group cluster plot: Cluster plot visualising the song units partitioned into 10 groups. Cluster 1 (red cluster) represents the meta-unit 'moan'. The longer versions of these units were also included in the analysis and can be seen to overlap with this group (see cluster 9 – green cluster) including the tsp/t-sp unit – a longer version of the t unit resent in cluster 1).

Table 4.4: Number of observations in new unit categories

Theme	Meta-unit type							
	moan	eight	ten	two	one	three	nine	four	seven
Orange	314	0	0	0	0	312	0	0	338
Yellow	0	0	0	0	106	0	0	1	70
Grey	0	48	0	27	0	0	0	0	0
Indigo	997	0	0	0	0	0	0	0	0
Violet	487	0	0	0	0	0	0	0	0
Navy	0	0	116	0	0	0	162	0	0

Table 4.5: Number of observations of meta-unit moan in each core theme type across each recording

Theme	Recording								
	100220 CA	160220 CA	270220 CA	050320 CA	270221 SC	050321 SC	170321 SC	250321 SC	300321 SC
Orange	15	24	4	40	25	72	32	63	39
Indigo	26	129	7	141	201	158	70	105	160
Violet	0	9	0	11	47	88	60	77	195

4.3.5 Statistical analysis results

4.3.5.1 Across seasons change: do units change and if so, do the same unit types change in the same way in different themes?

Across seasons, units were found to change significantly in both individual measurement types and overall acoustic change and with differences between theme types. Across the seasons change in acoustic distance was found in all themes with variation in degree. Significant but small changes were found in the indigo theme (Indigo: Mantel statistic 0.09186, p = 0.001) while in the orange and violet themes larger magnitude correlations between acoustic distance and time were detected (Orange: Mantel statistic R: 0.3024, p = 0.001, see Figure. 4.17, and Violet: Mantel statistic R: 0.6449, p = 0.001) (see Appendix 4.8 for all Mantel test summaries over the season). The divergence test did not detect any aggregate acoustic change over the season between units produced in the context of different theme pairs, for any pair of themes (Figure 4.18, see Appendix 4.9 for complete divergence outputs). Change was detected in all eight individual measurement types in at least one theme type. Six of eight discrete measurements displayed a change that was significantly different across theme types. Peak frequency and Frequency 5 both showed similar decreases over the season in all three theme types. On the other hand, Frequency 95, Bandwidth 90, Duration, Start Frequency, End Frequency and Frequency Ratio all changed in different ways across the seasons depending on the theme type. For example, duration of moans in the indigo and violet themes did not change over the seasons but moans in the orange theme (which were already significantly higher than the indigo and violet themes to begin with) showed an almost 50% increase in duration (from around 1 second to around 1.5 seconds). The acoustic feature 'Frequency Ratio' also showed distinct differences across theme types with moans from the orange theme remaining the same but those from the indigo and violet themes decreasing in frequency ratio across seasons (see Figure 4.19). Furthermore, Start Frequency in the orange theme was significantly higher than both the indigo and violet themes (Figure 4.20). See Table 4.6 and Appendix 4.10 for complete discrete measurement outputs.

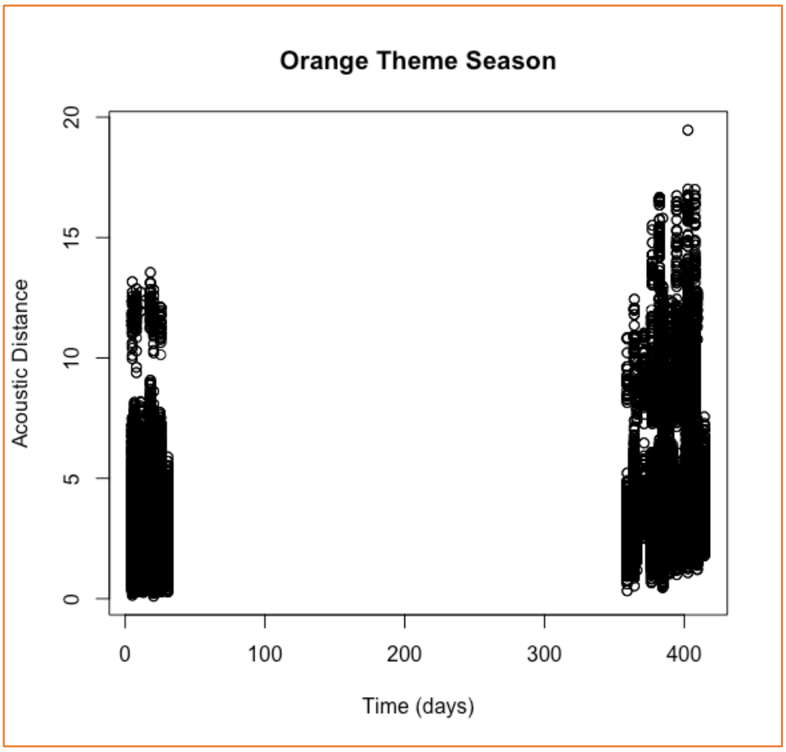


Figure 4.17: Orange Theme Acoustic Distance over time – over Seasons: There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.3024, p value = 0.001). In other words, as units became further apart in time they became noticeably more dissimilar in structure.

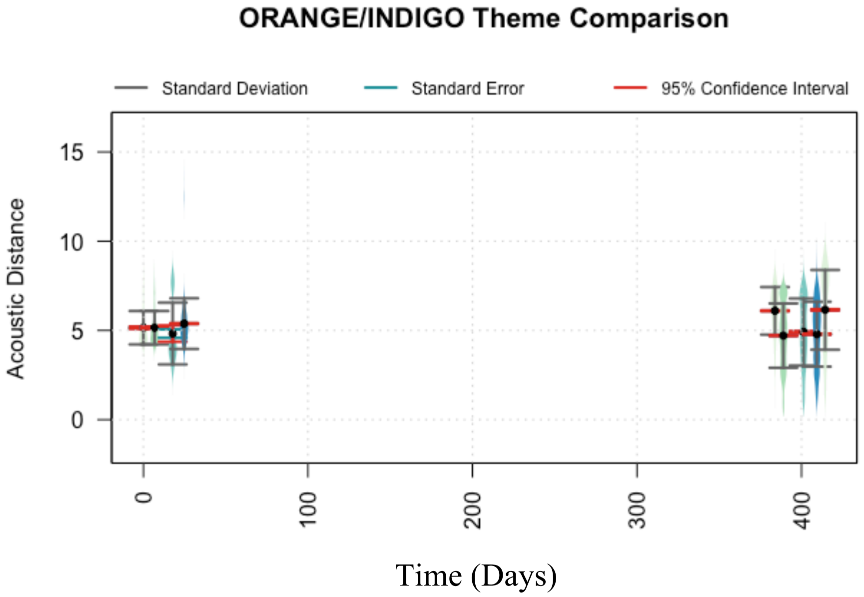


Figure 4.18: Test for Call Divergence. Orange Vs Indigo Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryIndigoVioletComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant (R^2 = 0.1378, F(1, 4) = 6.28, p = 0.1749).

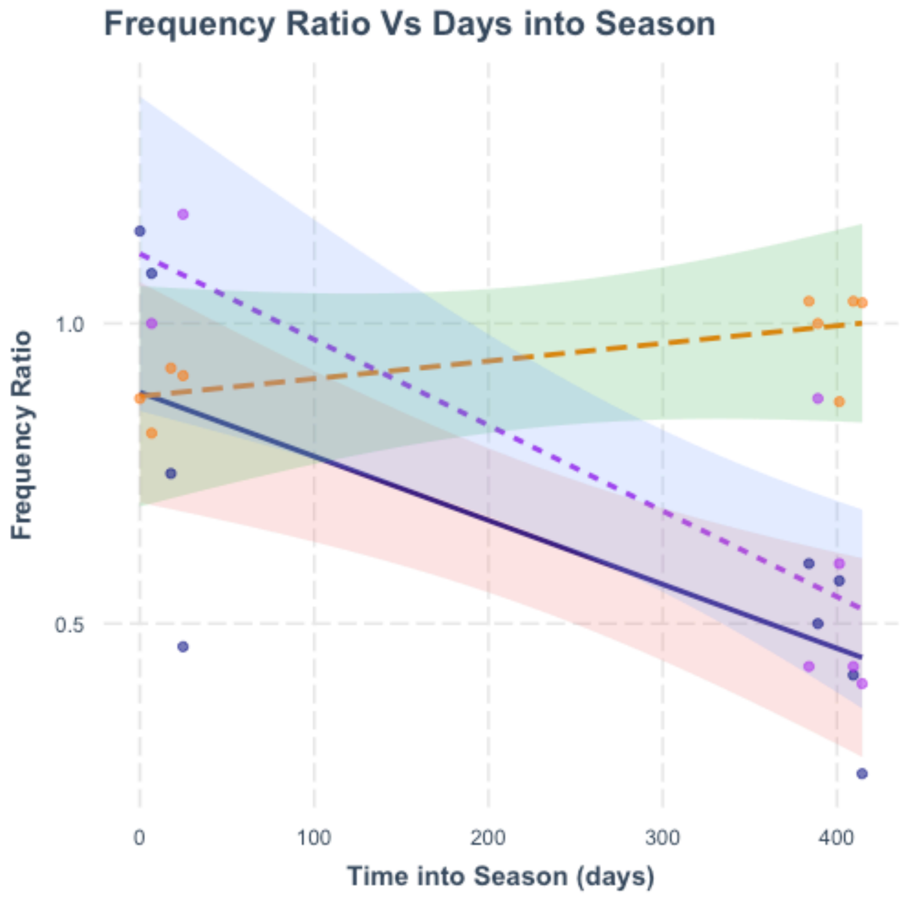


Figure 4.19: Across Season: the acoustic measure 'Frequency Trend' in moans from the indigo and violet themes decreased while moans from the orange theme type show much less evidence of change. Frequency Trend in moans from each theme type were not significantly different from each other at the beginning of the season but in the second season moans from orange theme were significantly different from the moans from the indigo and violet themes

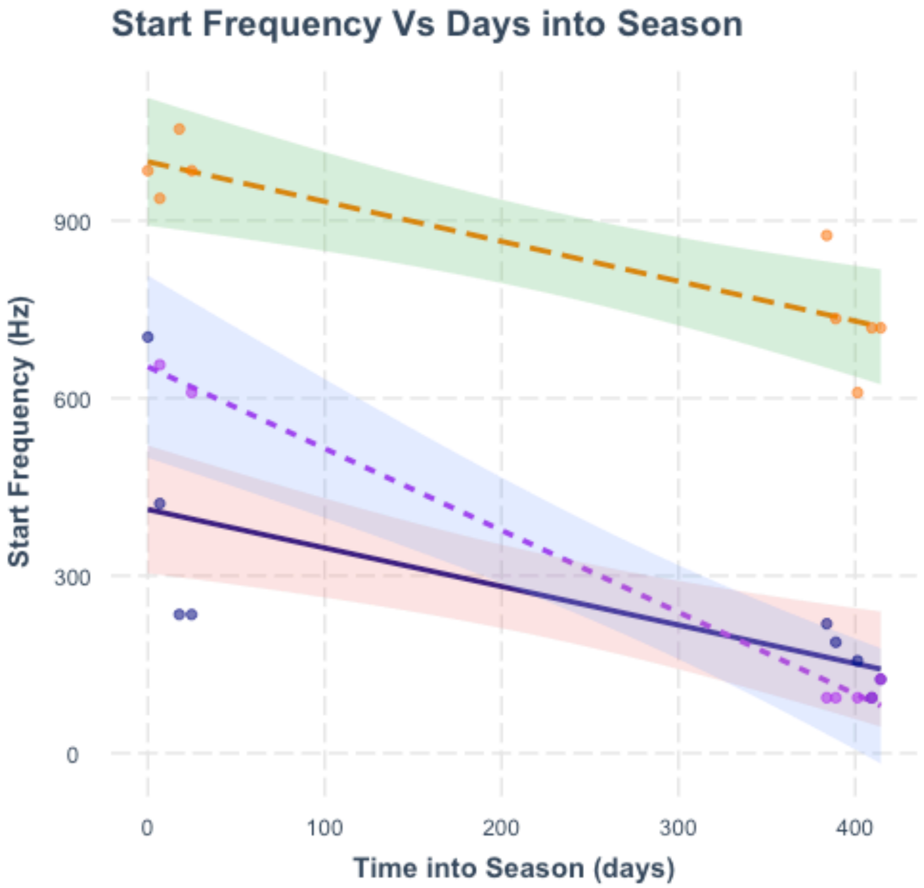


Figure 4.20: Across Season: Start Frequency. Start frequency was found to significantly decrease across seasons in all theme types with moans from the violet theme type decreasing at a faster rate than the indigo or orange themes. Start Frequency in moans from the orange theme type were found to be significantly higher than the indigo and violet theme types.

Table 4.6: Discrete measurement test results across seasons: Model estimate followed by standard error and p value in brackets. Significant changes are in bold.

Acoustic Measurement	Indigo	Orange	Violet
Peak Frequency	**-0.410**** (0.130, 0.005)	-0.208 (0.184, 0.272)	-0.266 (0.209, 0.219)
Frequency 95	0.036 (0.184, 0.848)	**-1.150***** (0.261, 0.000)	**-1.004**** (0.296, 0.003)
Frequency 5	**-0.400*****,** (0.091, 0.000)	-0.146, (0.128, 0.270)	0.165, (0.146, 0.273)
BW 90	0.335 (0.217, 0.139)	**-0.914**** (0.307, 0.008)	**-1.049**** (0.349, 0.007)
Duration 90	0.000 (0.000, 0.653)	**0.001+** (0.001, 0.061)	0.000 (0.001, 0.525)
Start Frequency	**-0.651**** (0.173, 0.001)	0.022 (0.244, 0.929)	**-0.731*** (0.278, 0.016)
End Frequency	-0.093, (0.179, 0.610)	**-0.847**,** (0.253, 0.003)	**-0.853**** (0.288, 0.008)
Frequency Trend	**-0.001**** (0.000, 0.002)	**0.001**** (0.000, 0.004)	0.000 (0.000, 0.463)
	+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001		

4.3.5.2 Within song session change: do you units change, and if so, do the same unit types change in the same way in different themes?

Within song sessions acoustic change was detected across individuals with idiosyncratic variation between theme types. Individuals changed their moan units in different ways across theme types at both the level of overall acoustic change (Euclidean distance) (Table 4.7 for Mantel outputs) and also within discrete measurement types e.g. Start Frequency (Figure 4.22, 4.23 and 4.24, and Appendix 4.11 for complete outputs across all discrete measurements within song sessions).

For example, a significant change in overall acoustic distance was found in all of the themes of individual 2608 (Table 4.7) however, significant acoustic change was found in only one or two themes of the three total themes in the remaining four individuals (Table 4.7).

Discrete measurements also displayed this variability in moan unit change across themes and individuals within song sessions. For example, individual 160220 decreased Start Frequency of their moans in the orange theme during their song performance while all other individuals remained the same. Furthermore, individual 160220 started with a significantly higher Start frequency and by the end of the recording better matched the other individuals. Across themes, individuals can be seen to change their units in different ways for example individual 100220 did not show any change in the orange theme but increased start frequency in the indigo theme (Table 4.8) (see Appendix 4.11 for complete outputs for discrete measurements within song sessions).

Table 4.7: Individual mantel results

	Mantel	Sig	Mantel	Sig	Mantel	Sig
	Orange		**Indigo**		**Violet**	
100220	**-0.01448**	0.576	**0.4498**	0.001*	**ND**	ND
160220	0.06115	0.1	**0.2692**	0.001*	0.01332	0.419
270220	**0.9552**	0.008*	-0.3103	0.984	ND	ND
050320	**0.01929**	0.21	**0.1637**	0.001*	**0.3639**	0.001*
270221	0.06475	0.046*	**0.0877**	0.001*	**0.3508**	0.001*
050321	0.0157	0.152	**0.07661**	0.001*	**0.5722**	0.001*
170321	0.08763	0.006*	**-0.09126**	1	**0.431**	0.001*
250321	0.009236	0.263	**0.1987**	0.001*	**0.08174**	0.001*
300321	0.04357	0.05	**0.07896**	0.001*	**0.2031**	0.001*

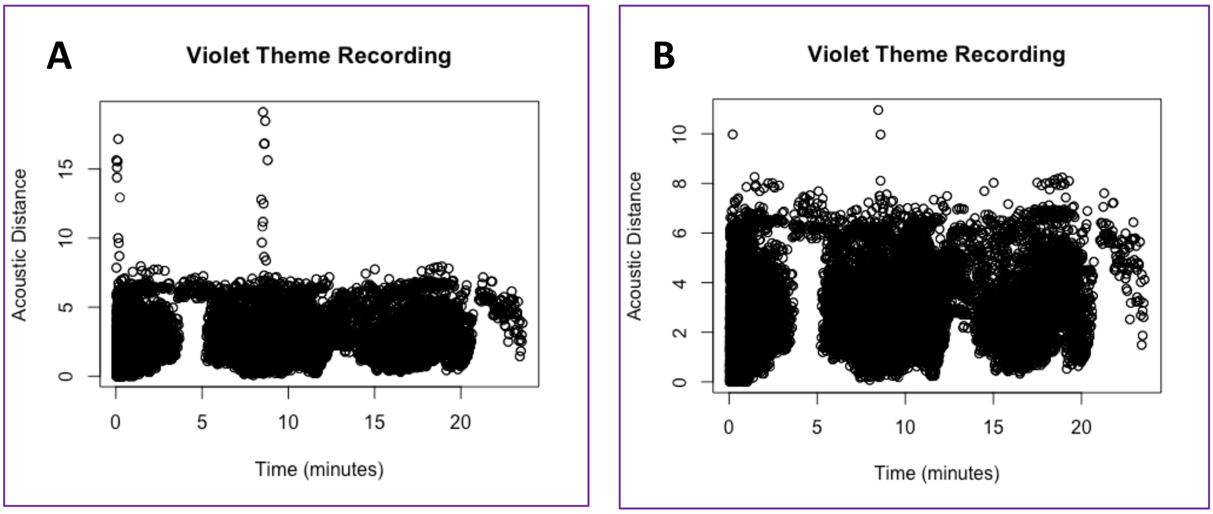


Figure 4.21: Violet Theme Acoustic Distance over time – within recording. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.2617, p-value.= 0.001). In other words, as units became further apart in a song session they became noticeably more dissimilar in structure. The positive outliers observed in this study correspond to two specific instances of the unit type exhibiting unusual characteristics, such as a large frequency ratio. Nevertheless, these occurrences were infrequent enough that they did not significantly impact the overall results. Subsequently, the analysis was recalculated after removing these outliers, resulting in a Mantel statistic of 0.2658. In 4.21 (B), the acoustic distance over the duration of the recording is depicted without the presence of outliers, clearly demonstrating a distinct change over the length of the recording.

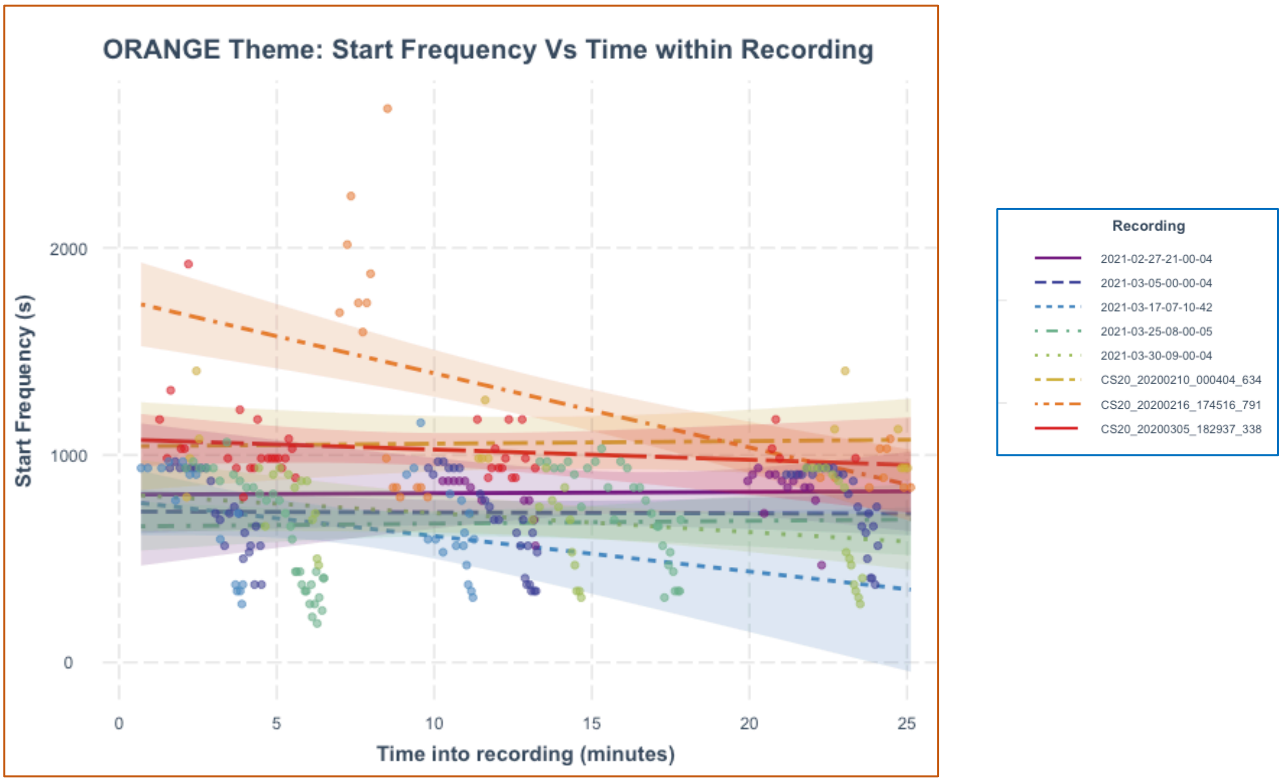


Figure 4.22: Orange theme: All individuals showed no significant change in start frequency except ID 160220 who displayed a decrease. Similarly, to Frequency 5, this individual started producing this unit with a significantly higher start frequency than the other individuals, so the decrease over the song session brought the individual closer to the start frequency of other individuals.

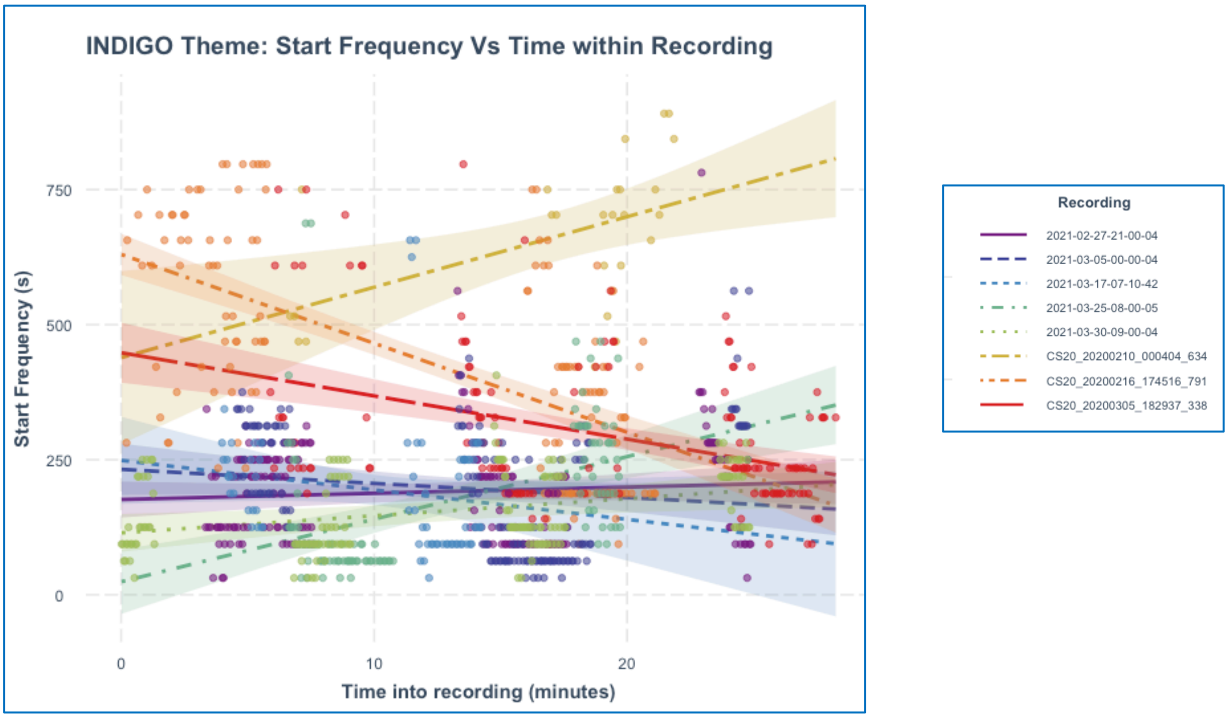


Figure 4.23: There was variation across individuals. Most individuals (4) decreased the start frequency of their units while two individuals increased and two individuals remained the same. All of the individuals displaying songs in the Caribbean started with a higher start frequency but interestingly only ID 100220 continued to increase the start frequency of their moan unit making it even more different from the other individuals displaying the moan unit in this theme.

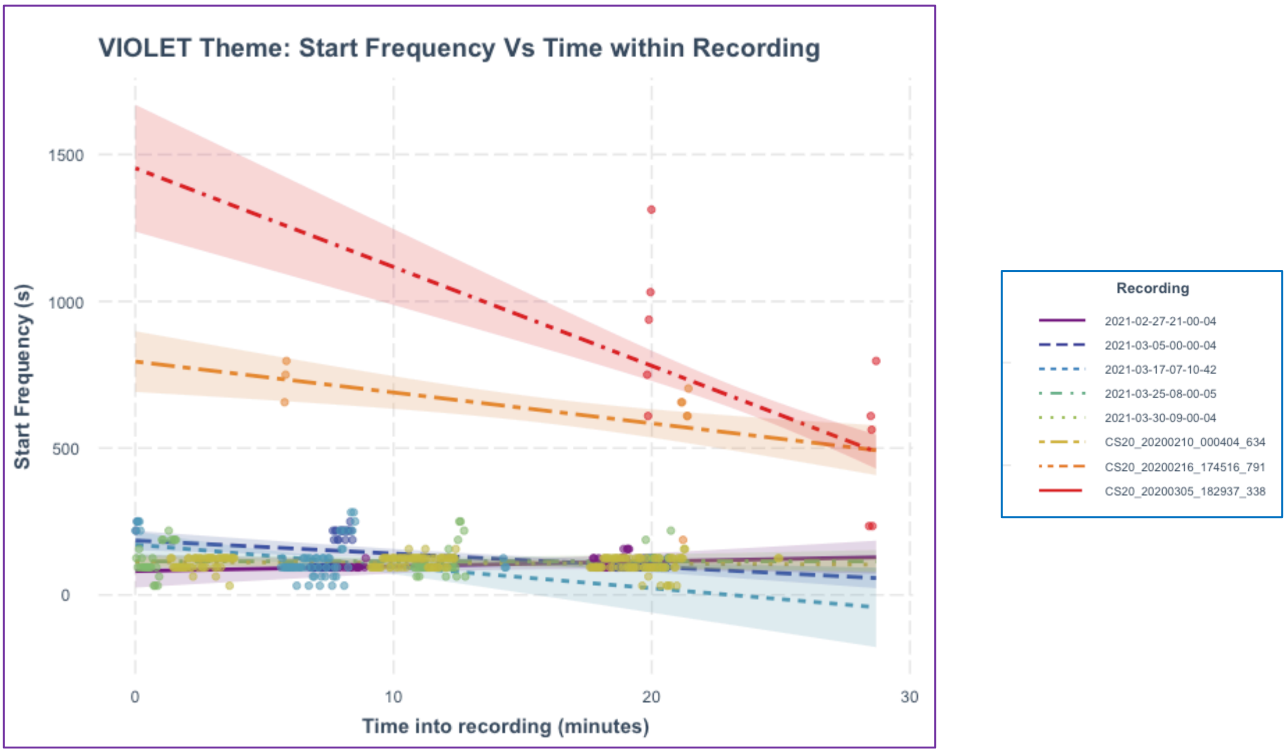


Figure 4.24: Individuals either showed no significant change in start frequency or a decrease over their song sessions. Interestingly again, individuals from the Caribbean in 2020 displayed significantly higher start frequencies than those displayed in Scotland in 2021.

Table 4.8: Individual across theme change – Start Frequency

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	NSC	NSC	no
050321	NSC	Decrease	Decrease	yes
170321	NSC	Decrease	Decrease	yes
250321	NSC	Increase	NSC	yes
300321	NSC	NSC	NSC	no
100220	NSC	Increase	ND	yes
160220	Decrease	Decrease	Decrease	no
050320	NSC	Decrease	Decrease	yes

4.3.5.3 Alternative hypotheses

The additional explorations of possible change in unit structure over time due to signal quality as quantified by Signal to Noise Ratio, coarticulation or exhaustion did not yield any consistent effects and are therefore unlikely to affect the main analysis interpretation (please see Appendix 4.15 for full results).

4.4 Discussion

My study aimed to better understand the potential matching of humpback whale songs between feeding, migrating and breeding locations in the North Atlantic through fine-scale analysis of humpback whale song recordings in the Eastern Caribbean and Scottish waters. My study aimed to track the evolution of the songs present over the breeding season and migration at these locations in two years. Furthermore, this study aimed to build on chapter 3 study in furthering our understanding of humpback whale song unit learning and production. This chapter looked for evidence of change in acoustic structure of one unit type – named the 'moan' - at two time-scales, within individual song sessions and more widely across the span of two seasons (including a breeding season in 2020 and on migration to feeding locations in 2021).

The clear match in song type and concurrent evolution of this song between both locations (eastern Caribbean and Scotland) makes it likely that this is the same population present at both sites, in different parts of their migration cycle in the north Atlantic. This is supported by at the temporal distribution of song changes. For example, the last recording in the eastern Caribbean in 2020 has evolved to the updated song state in which themes 2a and 3a are dropped from the song structure. This matches what is observed in Scotland in 2021. Interestingly, in Scotland 2020 there is still evidence of theme 2a and 3a being sung (after the whales at the breeding site switched). It is therefore likely that individuals who switched their song in the Eastern Caribbean in March 2020 (late in the breeding season) then carried this updated song version to Scotland to be expressed there in 2021.

Previous research has shown that the north Atlantic and north Pacific populations generally conform to one song type (Payne and Guinee, 1983; Vu *et al*., 2012; Darling *et al*., 2019; Kowarski *et al*., 2019; Magnusdottir *et al*., 2019; Kowarski *et al*., 2022). This is very different from the song dynamics in the South Pacific Ocean, in which different breeding populations can sing completely different songs in any one year (Garland *et al*., 2011; Noad *et al*., 2000). Individuals from the Cape Verdes (the eastern breeding site in the North Atlantic) have also been observed migrating to eastern feeding grounds in the North Atlantic. It is possible that the evolution of song in the Cape Verdes matches that in the Caribbean, however the timing of song evolution in the Caribbean and Scotland suggests a clear connection between these two sites. Future research could also include concurrent recordings in Cape Verdes to analyse any similarities or differences in song evolution between the eastern and western breeding sites in the North Atlantic.

Furthermore, the quality of sound recordings across the three recording projects differed so much so that a fine-scale song analysis was not possible for song recordings collected under the COMPASS project. Both higher shipping traffic close to mainland Scotland and lower occurrence of individuals in close proximity to the sound recorders severely affected the song quality captured at the COMPASS sites. Future effort should therefore be focused at the outer SAMOSAS sites on the Scottish Atlantic Frontier. Full fine-scale song analysis could be performed from recordings at these sites and future ongoing recordings would allow population connectivity in the North Atlantic to be monitored.

The fine-scale analysis of the ‘moan’ unit present in the North Atlantic song revealed that over two seasons the unit appeared to change considerably in some but not all theme types. The ‘moan’ unit in one theme (Indigo) showed evidence of very small change while in the Orange and Violet themes much larger change was detected over the two seasons. Surprisingly then, the divergence test did not detect any aggregate acoustic change over the seasons between units produced in the context of different theme pairs, for any pair of themes. This change detected within multiple themes but not amounting to divergence between themes indicates that units in each theme could be changing in the same way, or that the divergence test was not powerful enough to detect any divergence. For the former, investigating particular discrete measurements could provide a clue as to how similar the change across theme types is.

When considering individual acoustic measures, the discrete measurement types ‘Peak frequency’ and ‘Frequency 5%’ (the frequency above which 90% of the unit energy occurs) showed similar decreases across all three theme types as the seasons progressed. On the other hand, the remaining six discrete measurements were found to change differently depending on the theme type they belonged to. This was particularly evident for call duration, where moans in the Indigo and Violet themes did not change, but those in the orange theme increased in duration by 50% over the study period, which is particularly interesting as the Orange theme moans already began as longer than those expressed in the Indigo and Violet themes. This was also the case for ‘Frequency Ratio’. As a reminder, ‘Frequency Ratio’ refers to the comparison between two frequencies, representing the relationship or proportion between them. For example, If the Start frequency is of 440 Hz (hertz) and the end frequency is 660 Hz, the frequency ratio between them would be 3:2. This means that the end frequency is 1.5 times higher than the start frequency. Therefore, if the Frequency ratio is above one then the end frequency is higher than the start frequency. Moans from the Indigo and Violet themes decreased in Frequency Ratio across the season while those from the Orange theme did not. The discrepancy between the observed differences in discrete measurement trajectories among theme types, which were not detected in the divergence test, could be attributed to the concurrent changes in certain measurements that explain a significant portion of the overall acoustic distance variation. Specifically, the analysis using Principal Component Analysis (PCA) demonstrated that frequency characteristics, such as peak frequency, accounted for a considerably larger amount of variation in unit type compared to duration. Consequently, the distinct evolutionary trajectories in duration may have been overshadowed by similar trajectories in frequency changes during the calculation of the overall acoustic distance.

Analysing the same song type over two seasons has revealed that much larger magnitude changes in unit types can be detected than in one season. These changes show that the unit is changing significantly as the season goes on. While we might not be able to detect this change between themes at overall acoustic distance, we are able to detect significant differences in trajectories of discrete measurements in 6 out of 8 discrete measurements between the two seasons. These different trajectories in discrete measurement types between themes is evidence that these units cannot be stored in the same place in an individual whale's brain, as they are changing in different ways. This would be evidence against possessing an innate template in accordance with the Vocal production Hypothesis (Janik & Knornschild, 2021; Tyack, 2019).

My study detected change in the same unit in multiple themes across the two seasons. Concurrent change but with no overall divergence between unit types in separate themes would be compelling evidence for a unit that is stored as a single template. This builds on Deecke *et al*.'s (2000) study in killer whales in which acoustic contact between matrilines was detected through change but not overall divergence between call types. I have detected change across the season but no overall divergence which supports that these may be the same unit. On the other hand, the discrete measurement types reveal that there are changes between theme types in different trajectories. This is in contrast to the findings utilising recordings within one season in the South Pacific. This shows that a longer time period can detect changes in a unit type that within season evolution may not.

Similar to the study in the Cook Islands reported in Chapter 3, it was not possible to conduct a within subject design which would arguably be more powerful for detecting fine scale unit changes. Currently, researchers do not have the resources to conduct a within subject project in song evolution because this would require a massive amount of photo ID and recording effort to collect resightings of individuals. However, four recordings in the Eastern Caribbean and five recordings in Scotland show multiple time points that are showing an overall change in discrete measurement values.

This study analysed song recordings from two seasons and from two locations (Eastern Caribbean in 2020 and Scotland in 2021) therefore location and season is somewhat confounded. However, I have multiple recordings from each location and over each season. Whales from different parts of the Caribbean may go to different feeding grounds and there is evidence of this from satellite tag surveys (Kennedy *et al*., 2013). My study focuses on the North Atlantic population and there is clear evidence of individuals from the Eastern

Caribbean moving through Scotland to eastern feeding grounds (Pix, 2020). Therefore, while we have a between location design, we are confident that this is one population due to photo ID matches between these locations and satellite tag studies that match our song analysis.

Change in the moan unit across the season was also observed within song sessions. Change within song sessions was detected at both overall acoustic distance and in discrete measurement types. For example, an overall change within song sessions was detected in the Violet theme. Discrete measurements also showed significant differences in trajectories at two levels, both between individuals and between theme types. For example, this is most evident in Start Frequency in which individual 160220 was the only individual to decrease start frequency of their moans over the song session, while all other individuals remained the same. Interestingly, this individual also started with a significantly higher start frequency than all other individuals and this decrease meant that this individual then matched the other individuals. This was evident in other discrete measurements, in which individuals that started off significantly different changed their signals to be more similar to the overall group. There is consensus in whale song literature that individuals update their song to maintain conformity with individuals in their population. This could be evidence of this at the unit level. However, in the indigo theme this was not the case, in which two individuals started higher and then decreased to be more similar to the majority of individuals. Individual 100220 started at a higher start frequency in the indigo theme and then increased start frequency over the duration of the recording. Clear differences can be noted between individuals singing in the Eastern Caribbean in 2020 and those individuals recorded singing in Scotland 2021. This is most evident in the violet theme for start frequency in which individual 160220 and 050320 begin higher and decrease their start frequencies over the duration of the song session. Therefore, it can be seen here that changes at the individual level *do* eventually add up to changes at the seasonal level.

The same methodology as Chapter 3 was utilised here, in which an automatic method was used to determine start and end frequency of each unit using custom written MATLAB code. Fine-scale research on humpback whale song has been hampered by large processing time and this automatic method again proved to be a useful way for analysing large datasets. An additional step was required in the Scotland and Eastern Caribbean datasets as compared to the Cook Island data set due to generally lower SNR and signal overlap in the North Atlantic datasets. At the SAMOSAS site it was possible that multiple singers were recorded at the same time, therefore any units that portrayed an overlap in song units had to be be removed from the dataset before unit measurement. I carried out a qualitative screening of all song units, applying 'yes' (for high SNR and inclusion in the data set) or 'no' (implying low SNR and exclusion from dataset). A further 100 units which were originally committed to the 'yes' group were further excluded at the data processing stage as either a start or end frequency could not be computed from the MATLAB code. This was due to a low SNR of these units and furthermore all the units suffering from this problem were from the 'moan' discrete unit category, which is a unit that is more difficult than other unit to pinpoint the start and of the unit. However, this 100 units was a very small proportion to the 3000 units that were processed for the fine-scale analysis. Furthermore, previous methodologies of unit measurements have only utilised a small number of the very highest quality units meaning that dozens rather than thousands of units were analysed, Therefore, excluding 100 units from the analysis is very small.

In Chapter 3 I asked whether some units may be subject to learning and others are innate and I found that the unit analysed was generally stable over the duration of one season. In this chapter I have analysed a unit type over two seasons. I have detected significant changes in this unit type across seasons however this did not add up to significant divergence between theme types. On the other hand, discrete measurement types showed significantly different trends between theme types across the season which supports the vocal production learning hypothesis. Furthermore, I matched the song type present in two locations, the Eastern Caribbean in 2020 and Scotland in 2021 supporting photographic data of individuals migrating from the Eastern Caribbean to north-eastern feeding grounds. Further research would seek to establish whether the same song is also being sung in the Cape Verdes breeding population to establish the link between these sites. Furthermore, comparisons of units recorded in acoustically isolated populations (e.g. North Atlantic and South Pacific) would allow further insight into whether humpback whales have an inheritable repertoire of species-specific sound types or whether they are subject to complex vocal production learning (as defined by Tyack, 2020). This study has initiated fine-scale cultural evolutionary analyses as a useful vehicle for elucidating the mechanisms of song learning in the humpback whale's brain. Our understanding of humpback whale song learning is far behind our understanding of bird song learning and neural mechanisms. Passive and experimental analysis such as this can aid our ability to understand large, wild animal learning mechanisms in an ethical way while furthering existing datasets.

Chapter 4: Appendices

Appendix 4.1 Units and abbreviations

Unit Short Code	Full Unit Name
am	Ascending moan
asqb	Ascending squeaky balloon
ba	bark
bA	Bark 'A' type
bC	Bark – 'C' type
bD	Bark 'D' type
cr	croak
d	door
dws	Down whistle
h-bC	High-bC
m	moan
mm	modulated moan
mod-sqb	Modulated squeaky balloon
modws	Modulated whistle
nws	n-shaped whistle
sqb	Squeaky balloon
sqb-sqb	Squeaky balloon – squeaky balloon (connected)
t	trumpet
t-sp	Trumpet with tail
tsp	Trumpet with tail
tt	trumpet
u-ws	u-shaped whistle
usqb	u-shaped squeaky balloon
uws	u-shaped whistle
vws	v-shaped whistle
ws	whistle

Appendix 4.2- Theme Spectrograms

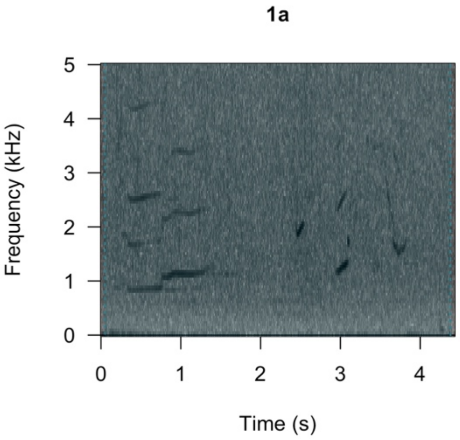


Figure A4.1: 1a: Eastern Caribbean – (taken from recording 10/02/20)

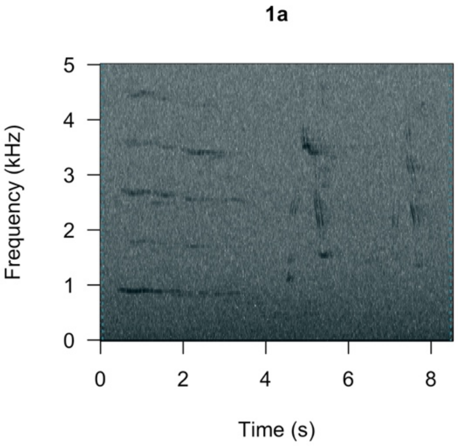


Figure A4.2: 1a: Scotland 2021 (taken from recording 27/02/21)

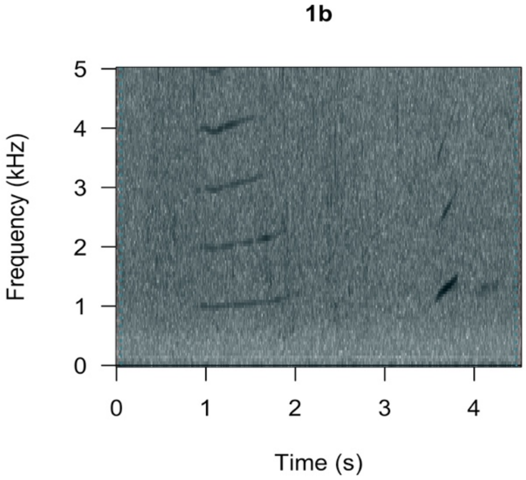


Figure A4.3: 1b Eastern Caribbean – taken from 10/02/20

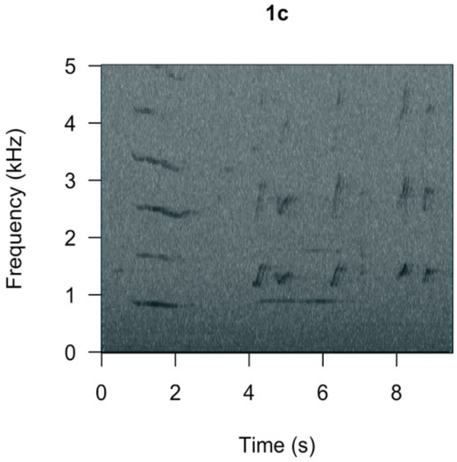


Figure A4.4: 1c: Scotland 2021 (taken from recording 27/02/21)

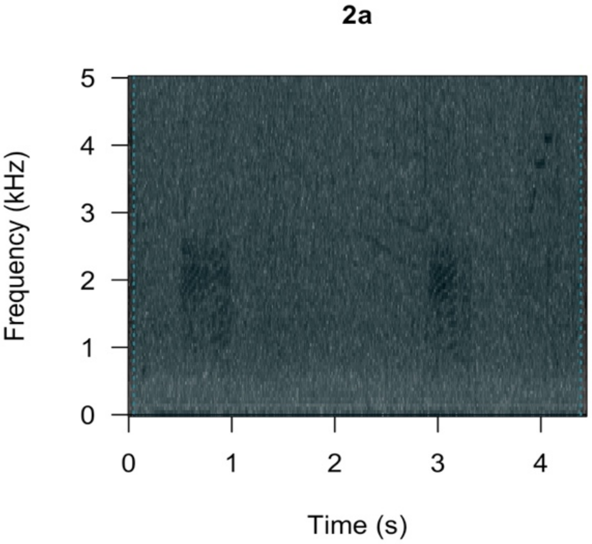


Figure A4.5: 2a Eastern Caribbean

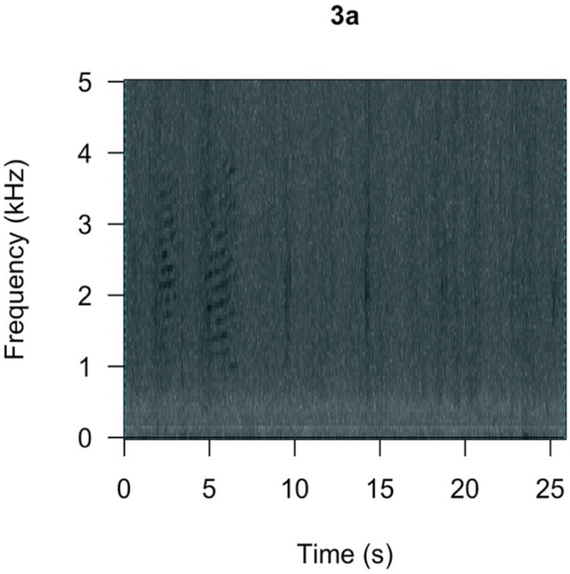


Figure A4.6: 3a Eastern Caribbean

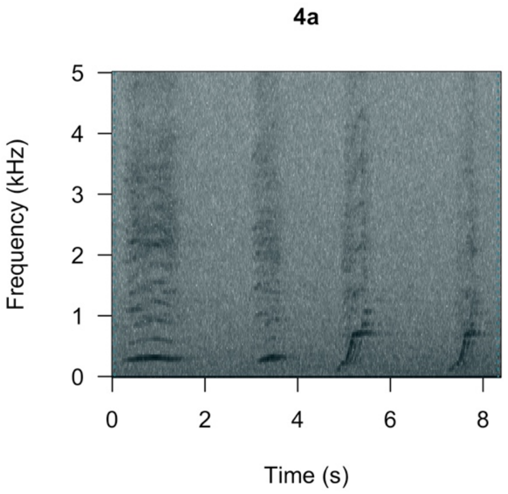


Figure A4.7: 4a Scotland 2021 (taken from recording 27/02/21)

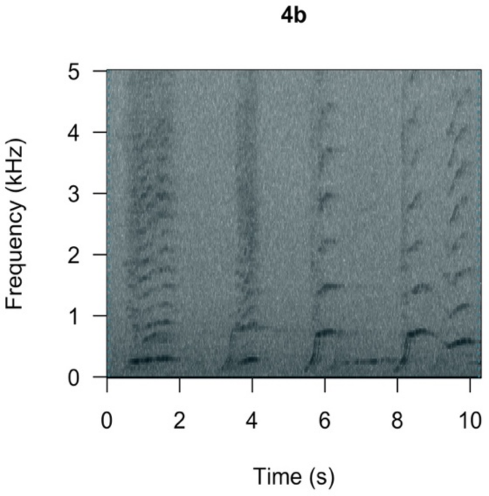


Figure A4.8: 4b: Scotland 2021 (taken from recording 27/02/21)

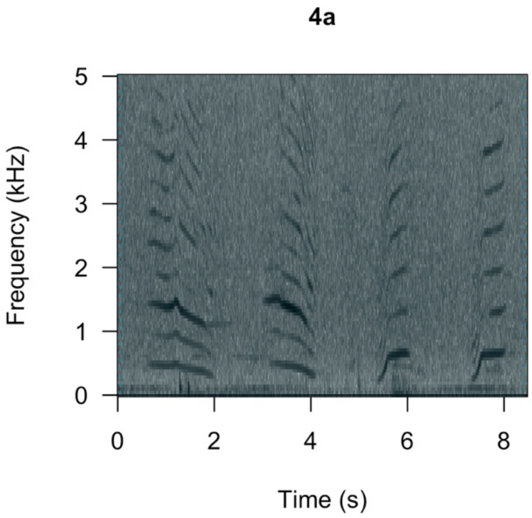


Figure A4.9: 4a Eastern Caribbean (taken from recording 05/03/20)

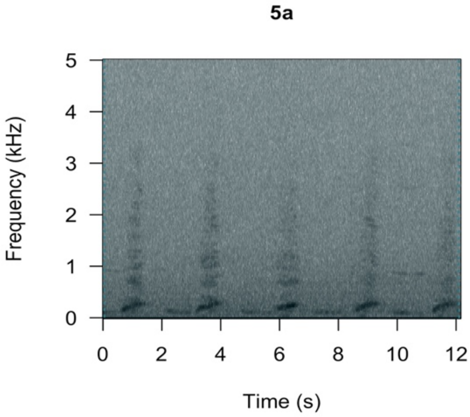


Figure A4.10: 5a Scotland (taken from recording 27/02/21)

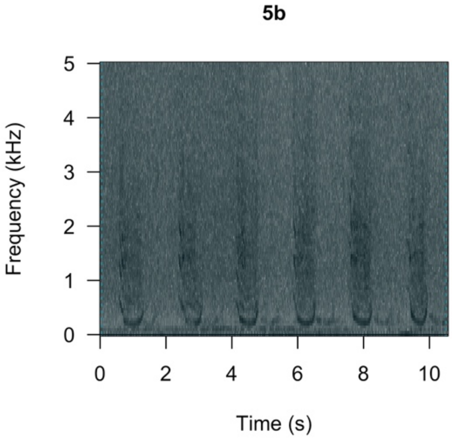


Figure A4.11: 5b Eastern Caribbean (taken from recording 05/03/20)

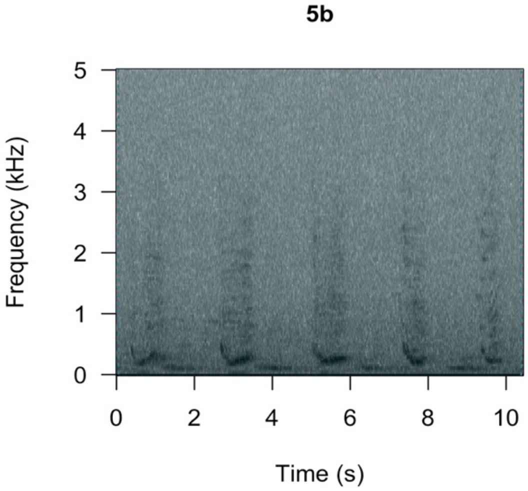


Figure A4.12: 5b: Scotland 2021 (taken from recording 27/02/21)

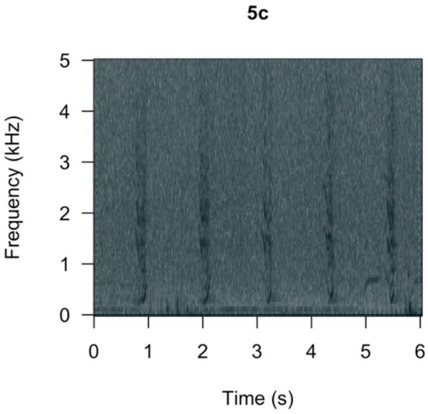


Figure A4.13: 5c Eastern Caribbean (taken from recording 05/03/20)

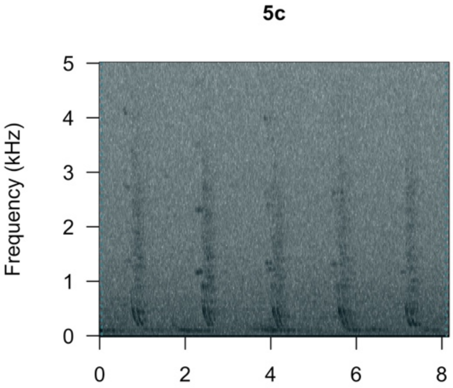


Figure A4.14: 5c: Scotland 2021 (taken from recording 27/02/21)

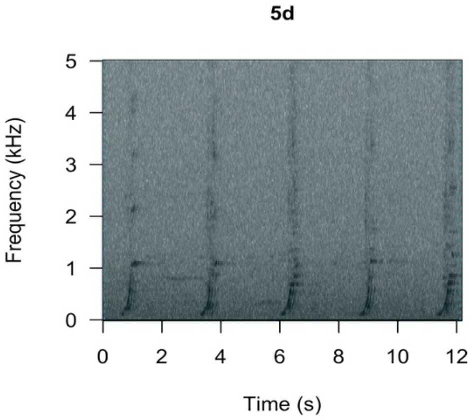
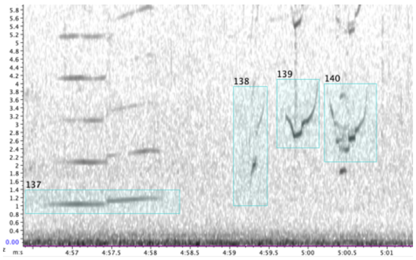
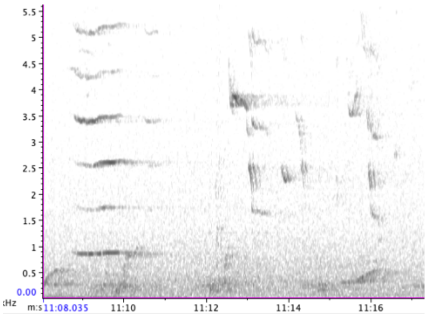
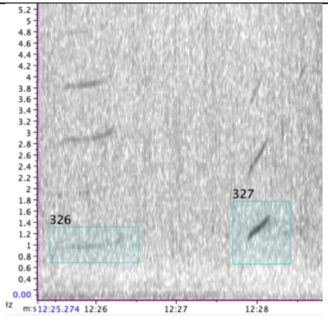
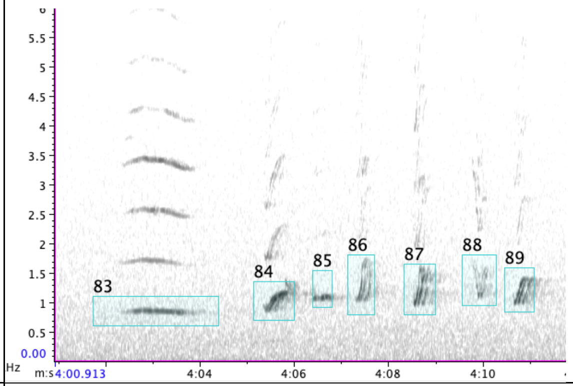
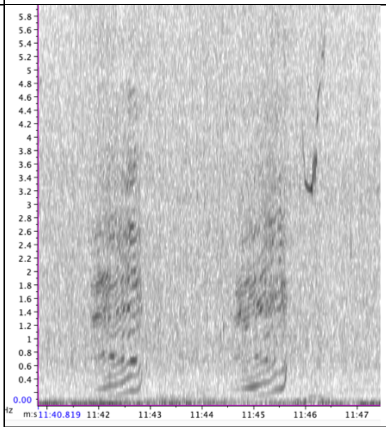
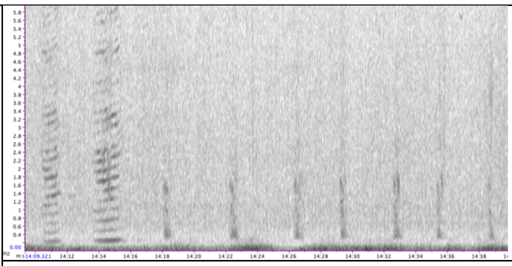
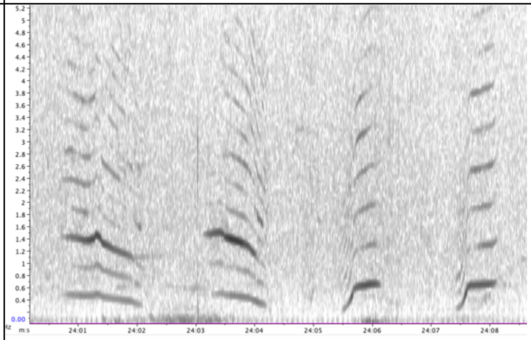
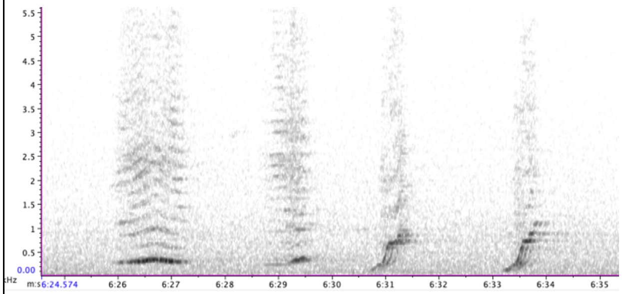
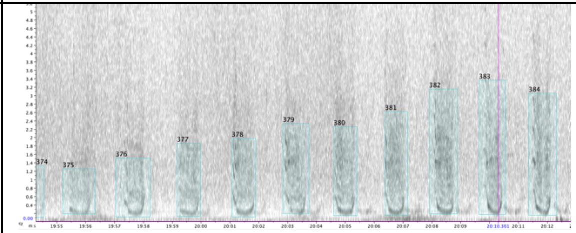
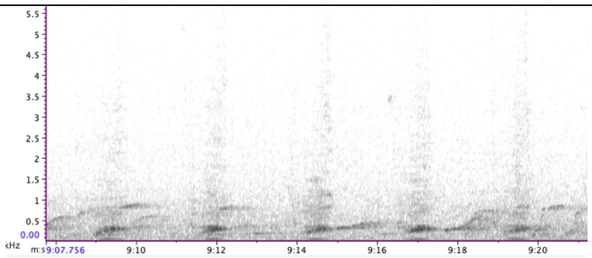
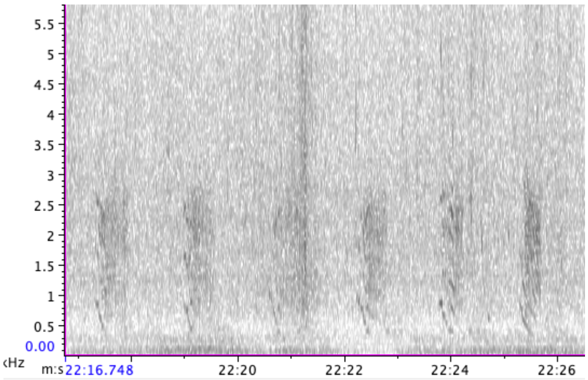
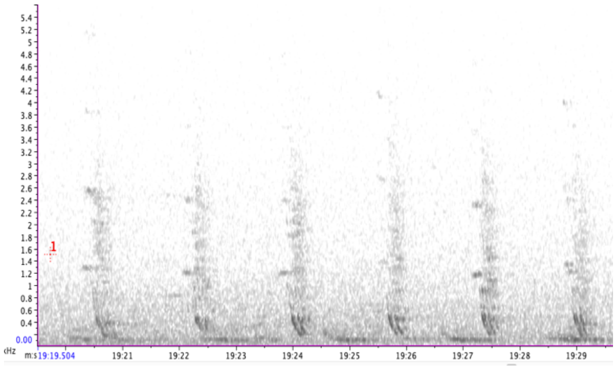
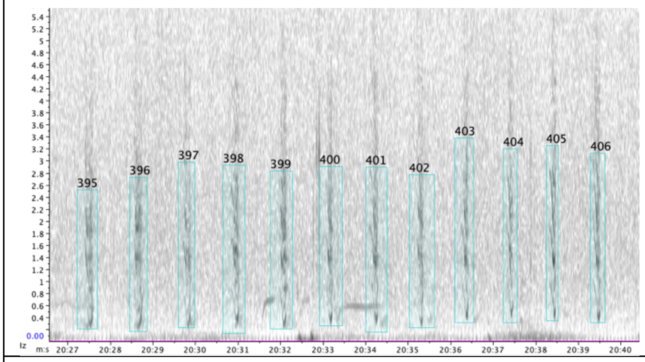
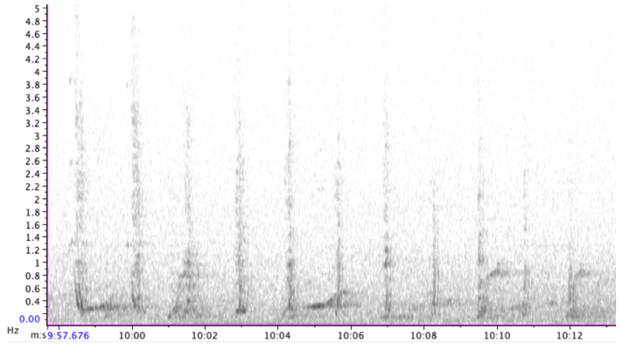
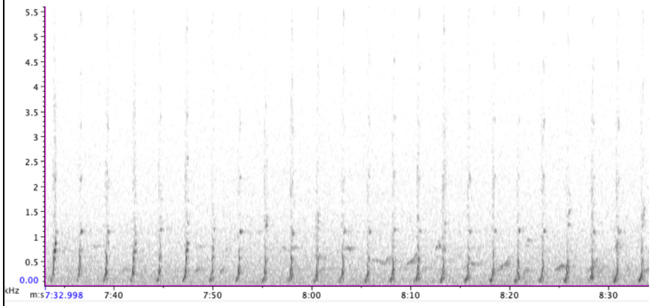


Figure A4.16: 5d Scotland (taken from recording 27/02/21)

Theme Type	**Dominica 2020**	**Scotland 2021**
1a		
	sqb modws modws modws	sqb modws modws modws
1b		**Not present**
	sqb uws	
1c	**Not present**	
		sqb uws uws uws uws uws uws
1d		
2a		**Not present**
	d d uws	

3a		**Not present**
	cr cr ba ba ba ba ba ba	
4a		
	m m t t	m m t t
4b	m m t t-sp	
5a		
	bA	bA
5b		
	h-bC	h-bC

5c		
	bC	bC
5d	I	
		bD

Appendix 4.3 – Transitional Diagrams

Dominica transition diagrams 2020

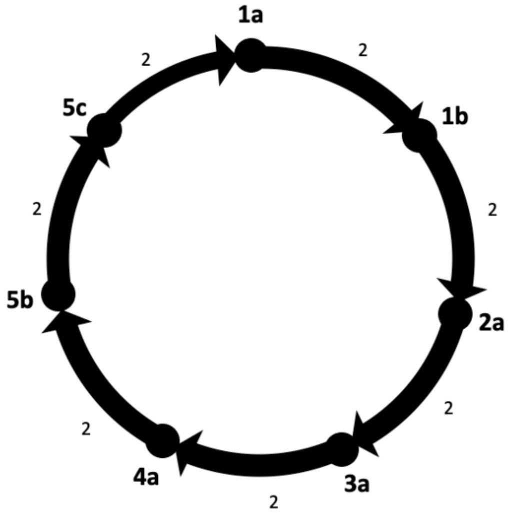


Figure A4.17: Dominica – 10/2/20 -2 complete cycles

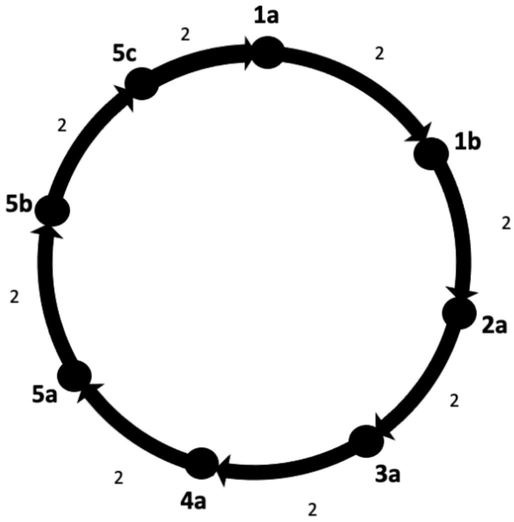


Figure A4.18: Dominica – 16/2/20 – 2 complete cycles

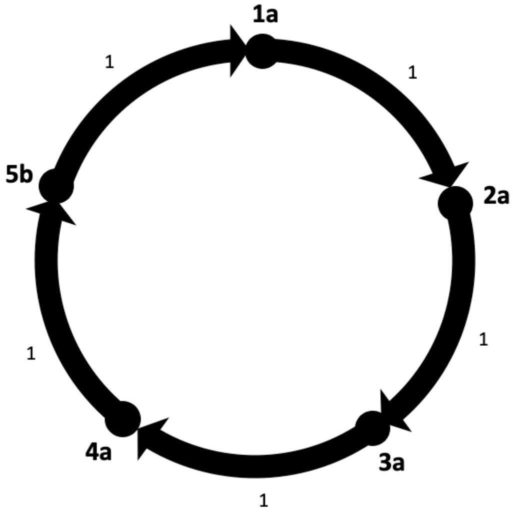


Figure A4.19: Dominica – 27/02/20 – 1 complete cycle

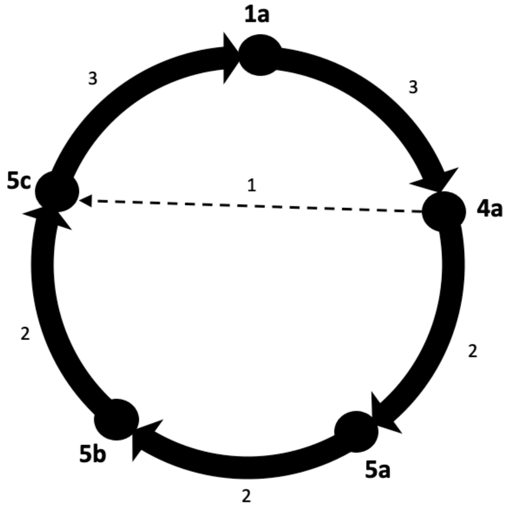


Figure A4.20: Dominica – 05/03/20 – 3 complete cycles

Scotland 2021 Transition diagrams

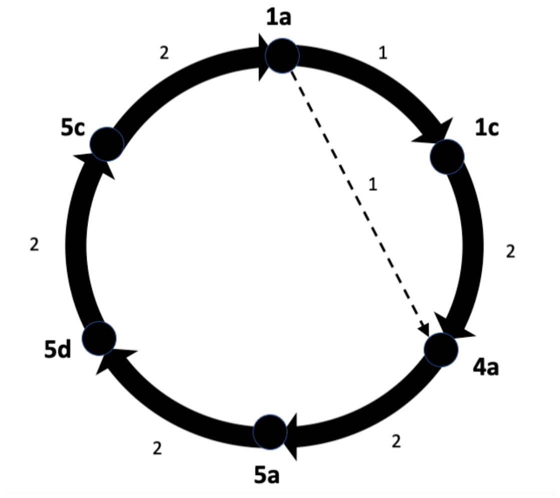


Figure A4.21: Scotland – 27/02/21 - 2 complete cycles

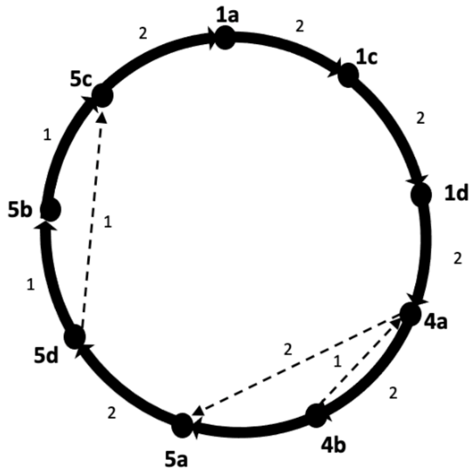


Figure A4.22: Scotland – 05/03/21 – 2 complete cycles

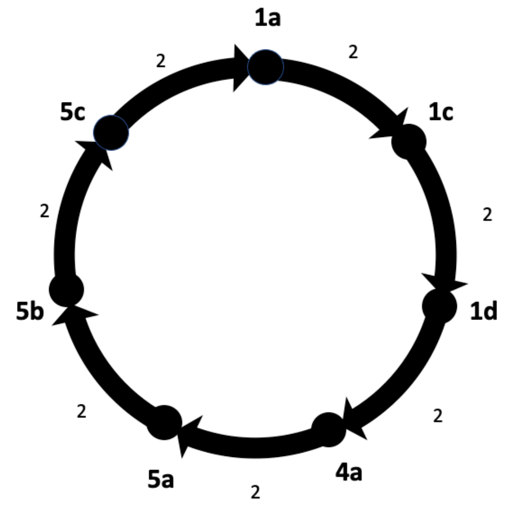


Figure A4.23: Scotland – 17/03/21 – 1 complete cycle

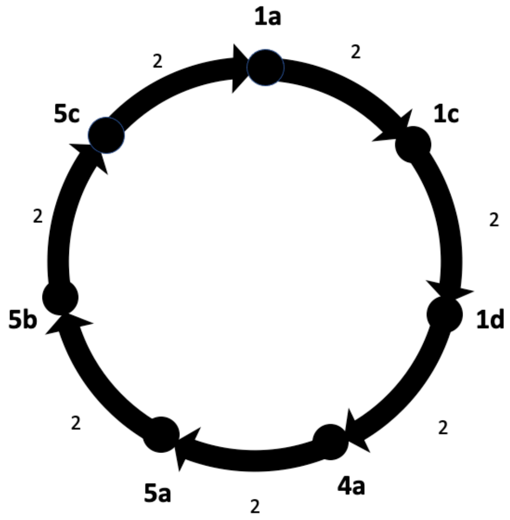


Figure A4.24: Scotland – 25/03/21 – 2 complete cycles

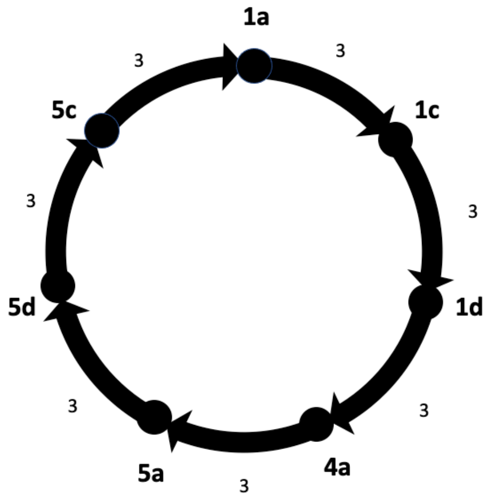


Figure A4.25: Scotland – 30/03/21 – 3 complete cycles

Scotland 2020 Transition diagrams

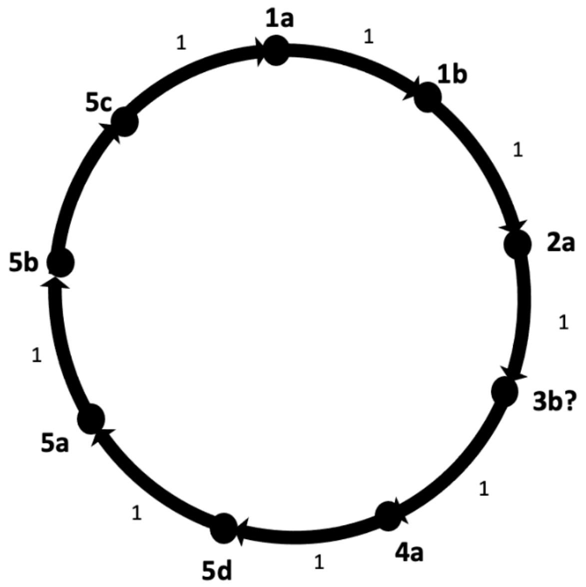


Figure A4.26: Scotland: Tolsta – 26/02/20 – 1 complete cycle

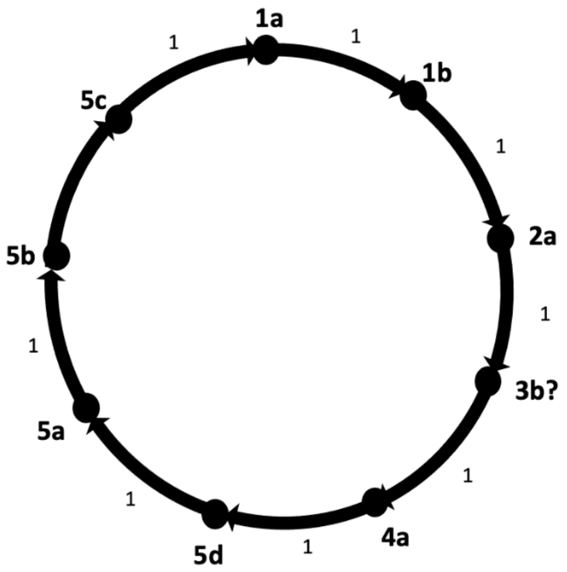


Figure A4.27: Scotland: Tolsta – 13/03/20 – 1 complete cycle

Appendix 4.4 – Levenshtein Distance Analysis Dendrograms

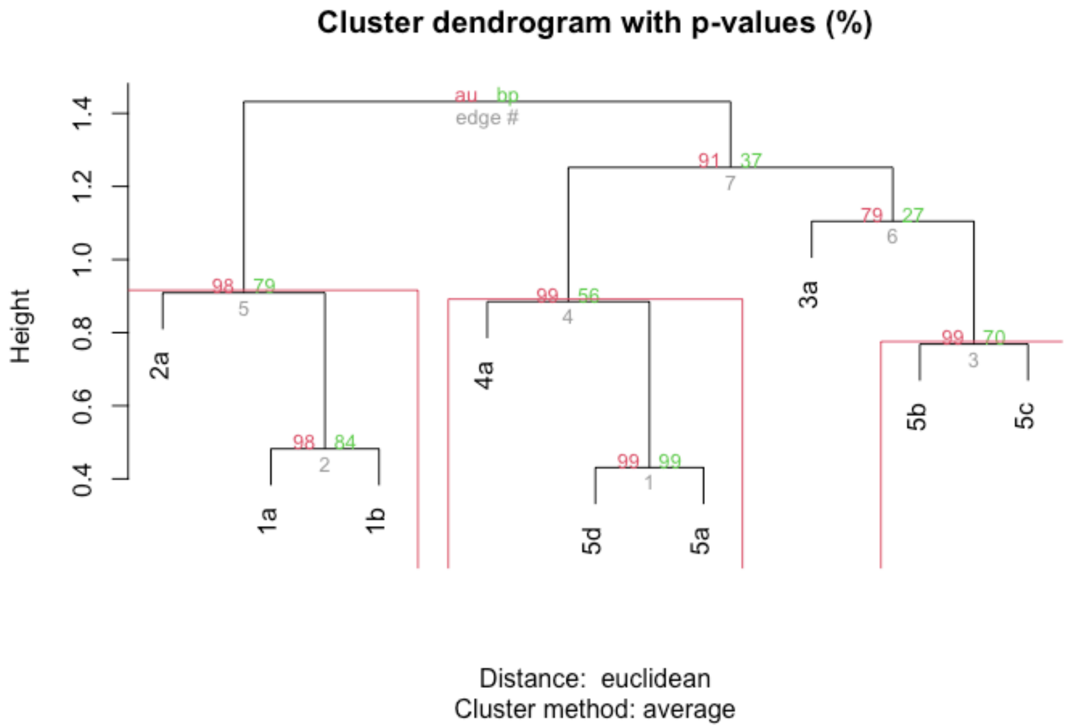


Figure A4.28: Eastern Caribbean 2020 Theme dendrogram

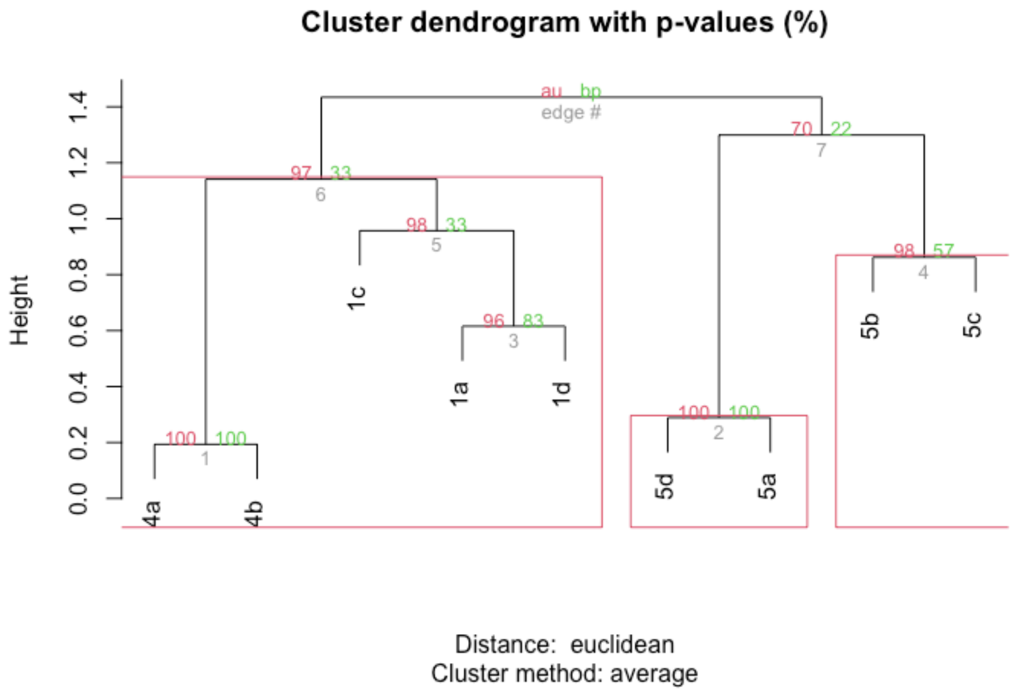


Figure A4.29: Scotland 2021 Theme dendrogram

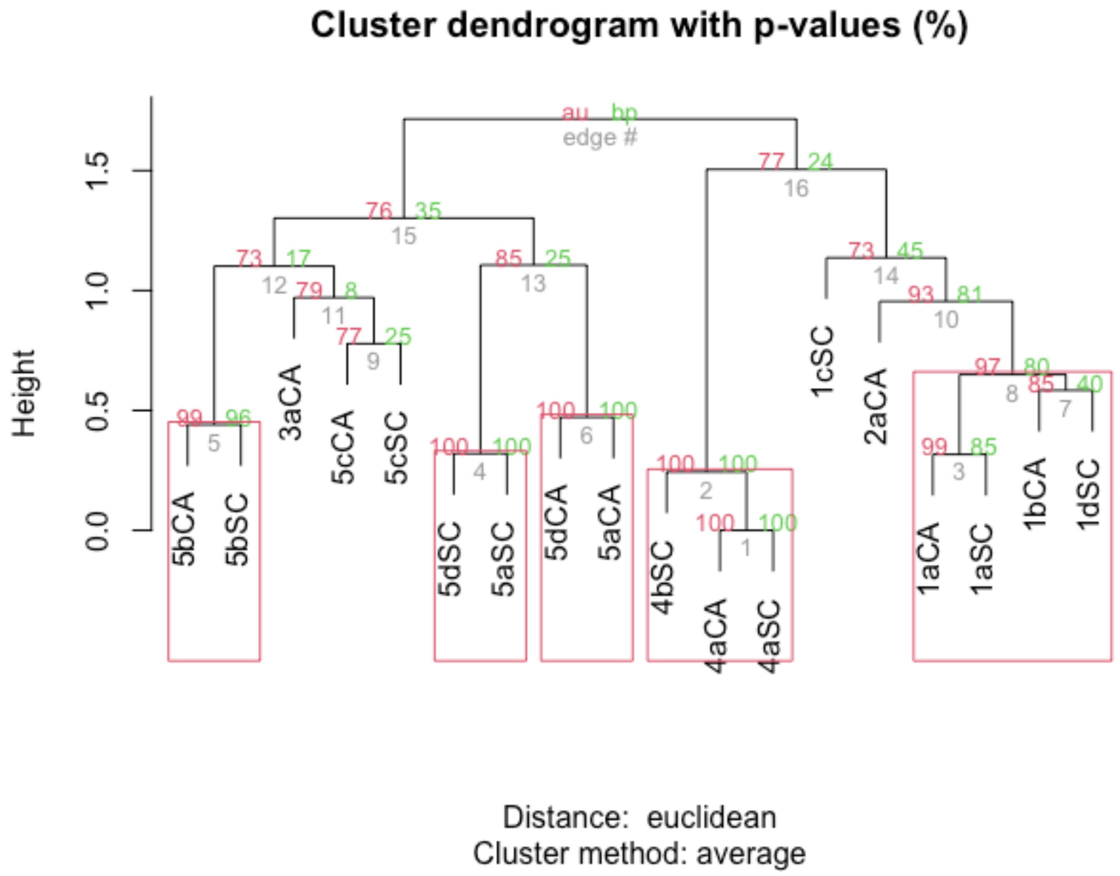


Figure A4.30: Scotland (SC) and Caribbean (CA) themes

Table 23: Phrases assigned to large theme type

Phrase Code	New Theme Name
1a, 1b, 1c, 1d	ORANGE
4a, 4b	INDIGO
5a, 5d	VIOLET

Appendix 4.6 – PCA and heatmaps of original units

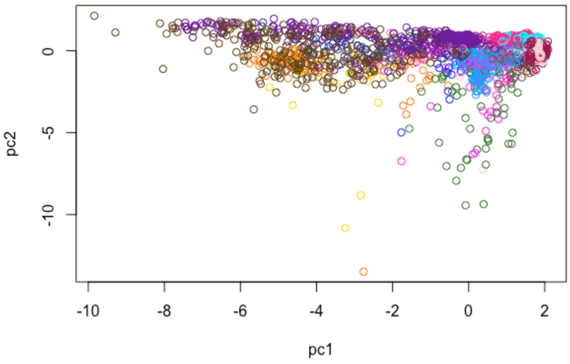


Figure A4.31: PC1 vs PC2

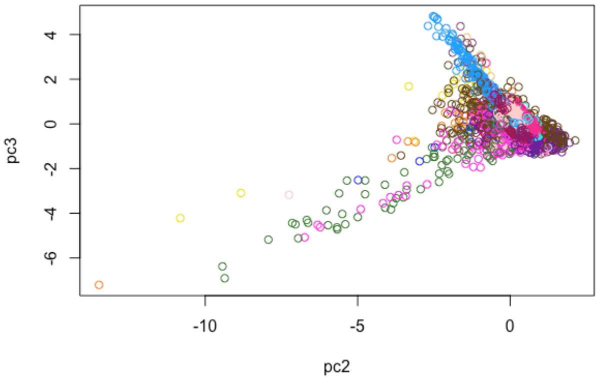


Figure A4.32: PC2 vs PC3

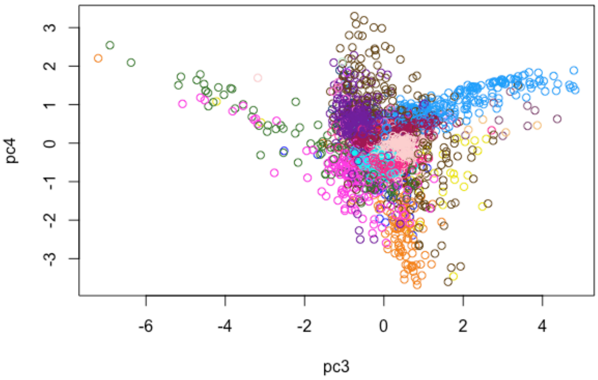


Figure A4.33: PC3 vs PC4

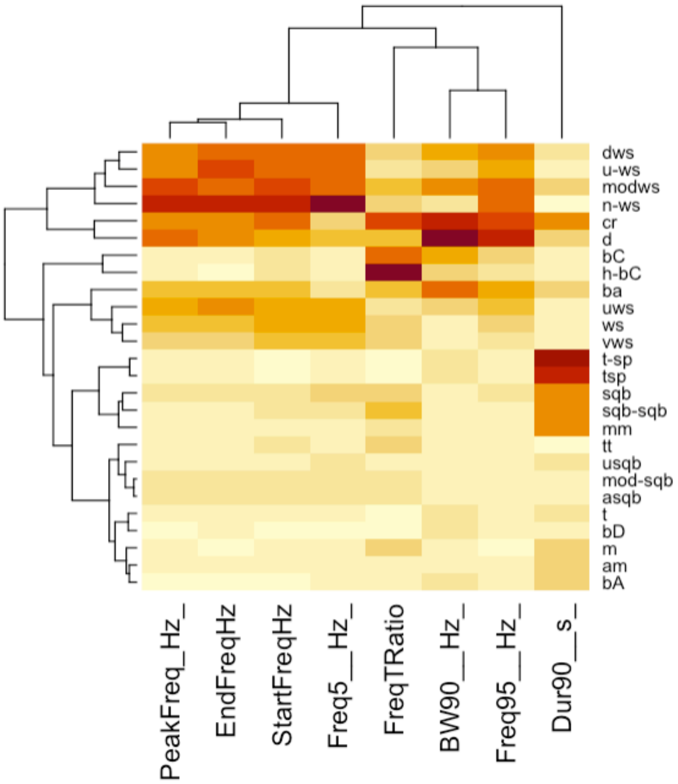


Figure A4.34: Dendrogram and heat map showing the relationship between unit types and the measurements taken

Appendix 4.6– Unit dendrograms and unit cluster plots

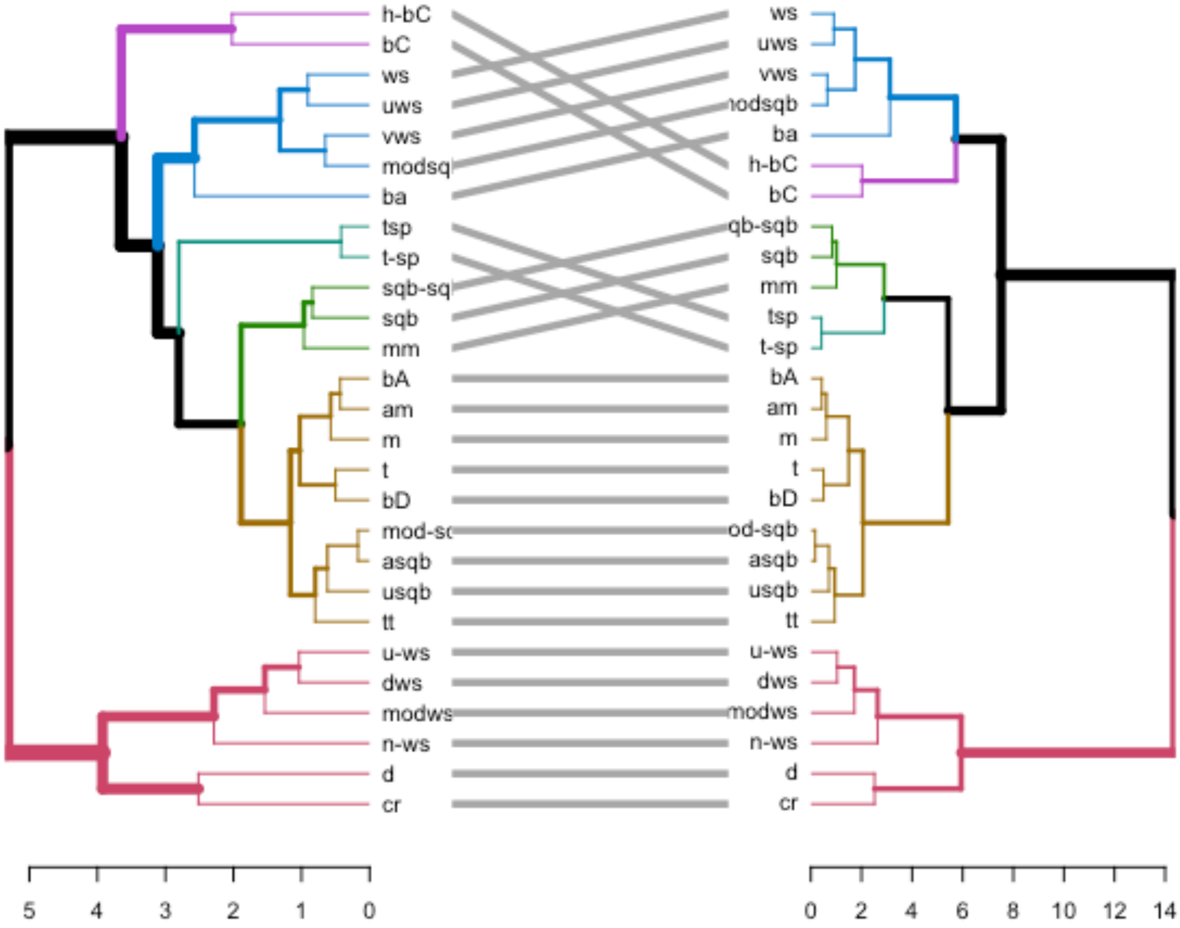


Figure A4.35: Linkage diagram of two dendrograms created by different linkage methods – WARD2 or Average-linkage.

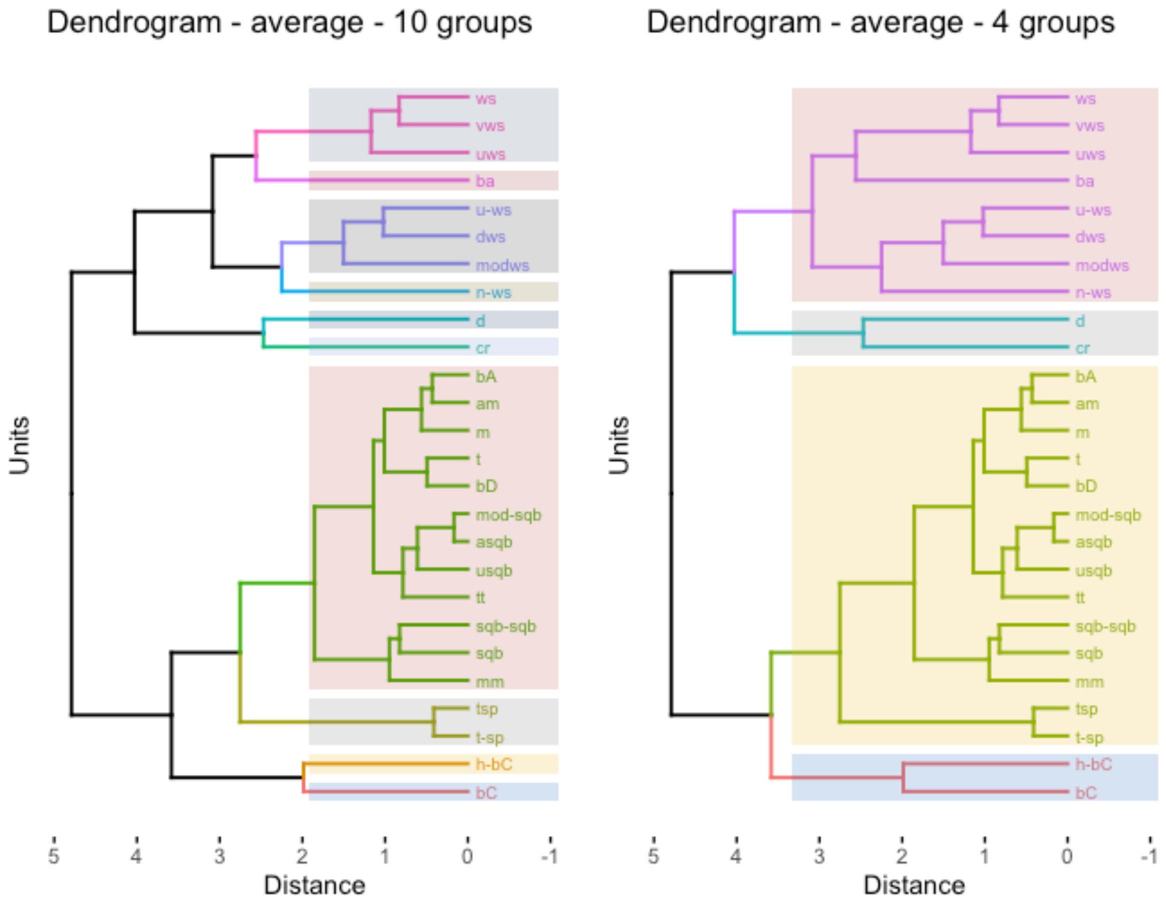


Figure A4.36:: Average linkage dendrograms partitioned into 10 (left) or 4 groups (right)

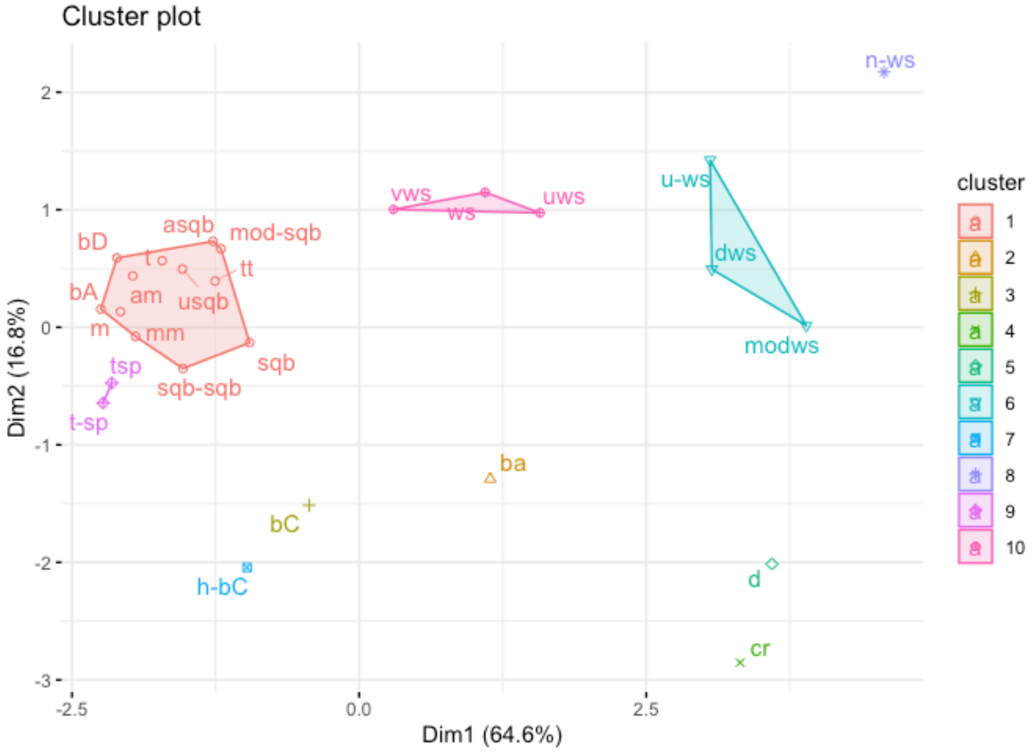


Figure A4.37: 10 group cluster plot

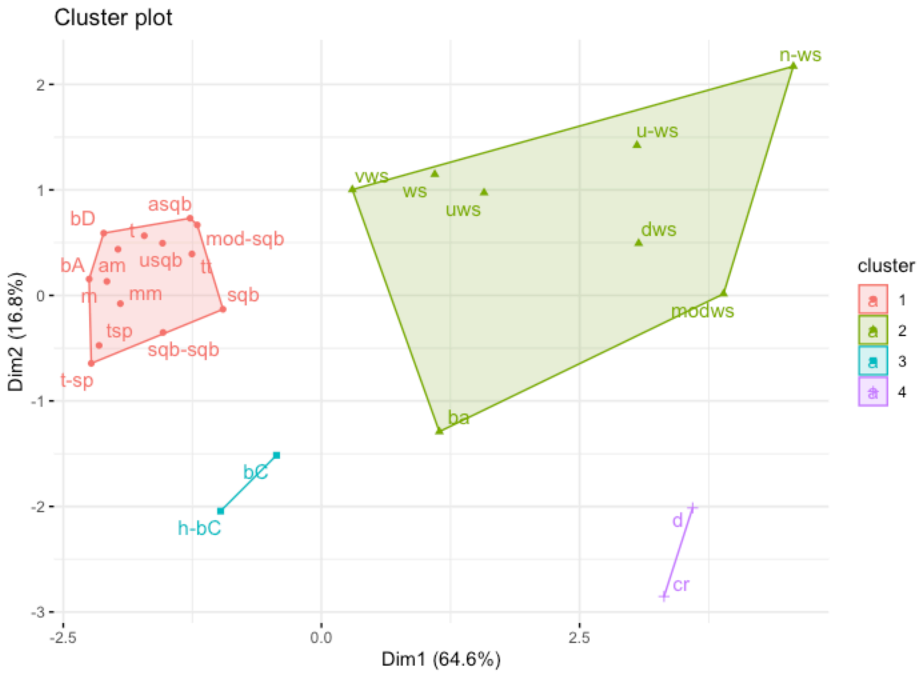


Figure A4.38

Appendix 4.7 – Complete list of original unit types committed to the meta-unit “Moan”

Original Unit	Full name	New Category
bA	Look back at notes for this	MOAN
am	Ascending-moan	
m	moan	
t	trumpet	
bD	Look back at notes for this	
mod-sqb	Modulated-squeaky balloon	
asqb	Ascending squeaky balloon	
usqb	u-shaped squeaky balloon	
tt	trumpet	
sqb-sqb	Two connected squeaky balloons	
sqb	Squeaky balloon	
mm	Modulated moan	
tsp	Trumpet connected to (look back at notes for this)	
t-sp	Trumpet connected to (variation in code)	

Appendix 4.8 – Mantel test outputs

Orange Theme

Within hour

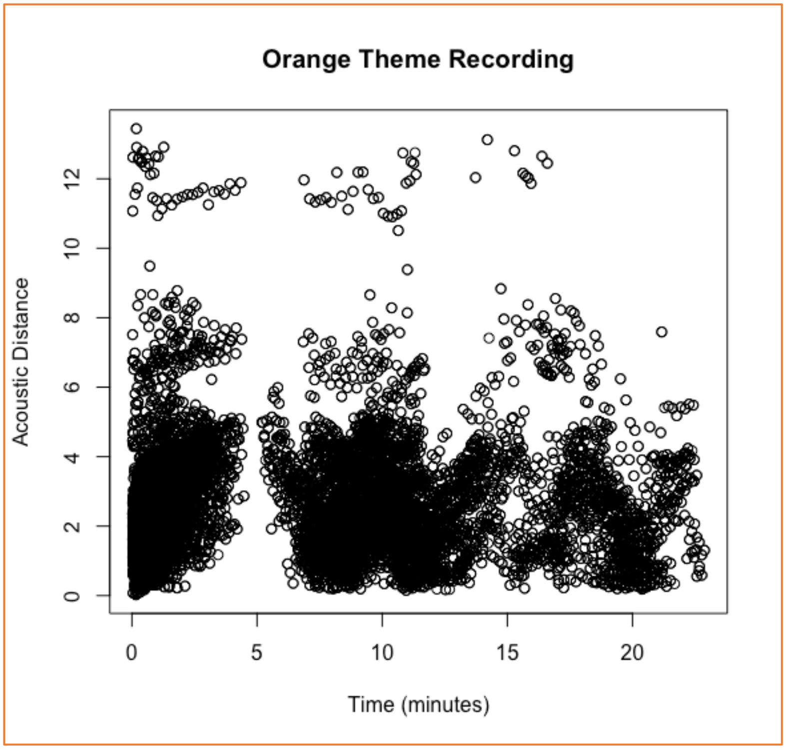


Figure A4.39: Orange theme Acoustic Distance over time – within recording. There was no relationship between acoustic distance of units and time (Mantel statistic R: -0.005345, p = 0.726). In other words, when units became further apart in time across the recording they did not become more dissimilar in structure.

Over seasons

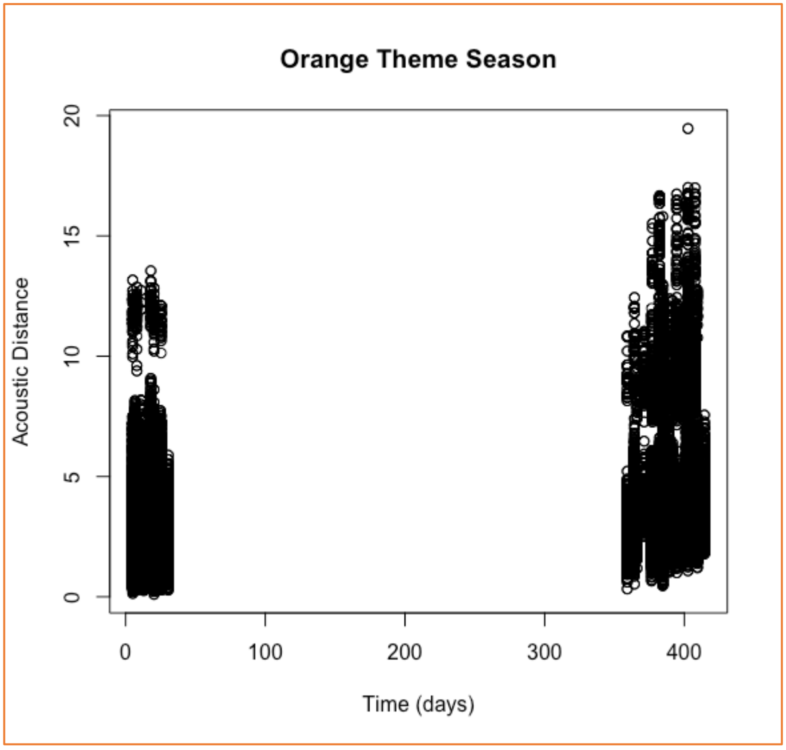


Figure A4.40: Orange Theme Acoustic Distance over time – over Seasons: There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.3024, p value.= 0.001). In other words, as units became further apart in time they became noticeably more dissimilar in structure.

Indigo Theme

Within hour

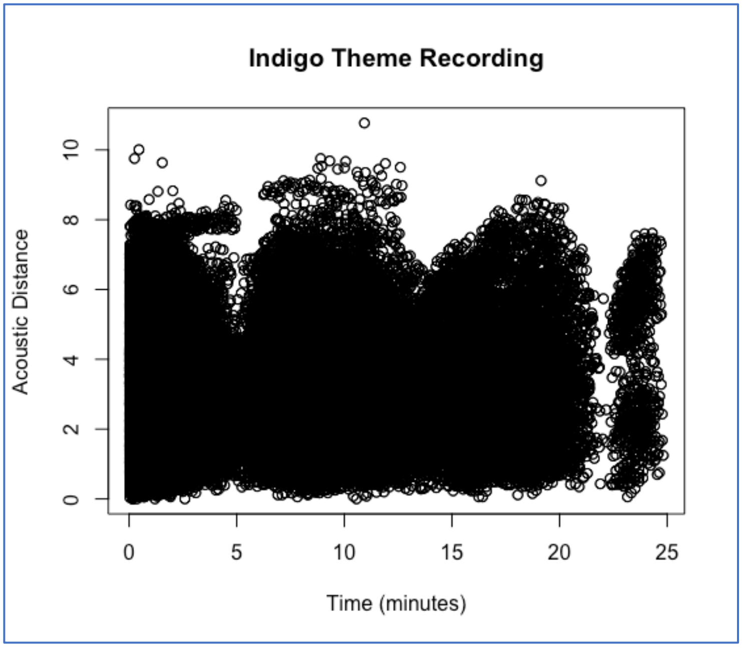


Figure A4.41: Indigo theme Acoustic Distance over time – within recording. Although weak there are some points occurring at higher points later in the seasons, which suggests that at least some productions of that unit are getting a bit more different. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.08909, p value = 0.001). However, this change was negligible being close to 0. In other words when units became further apart in time across the recording they did not become noticeably dissimilar in structure.

Over seasons

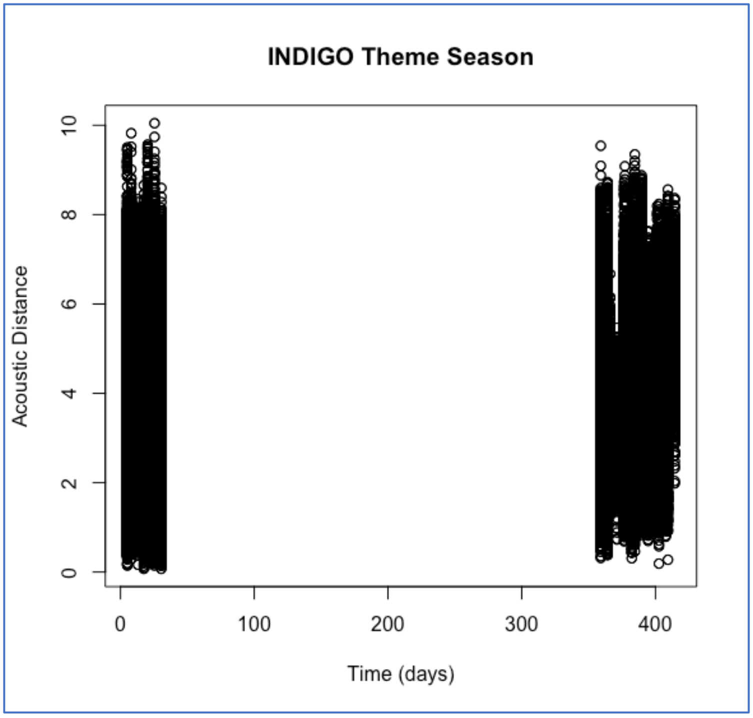


Figure A4.42: Indigo Theme Acoustic Distance over time – over Seasons: Although weak there are some points occurring at higher points later in the seasons which suggests that at least some productions of that unit are getting a bit more different. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.09186, p value = 0.001). However, this change was negligible being close to 0. In other words when units became further apart in time across the seasons they did not become noticeably dissimilar in structure

Violet Theme

Within hour

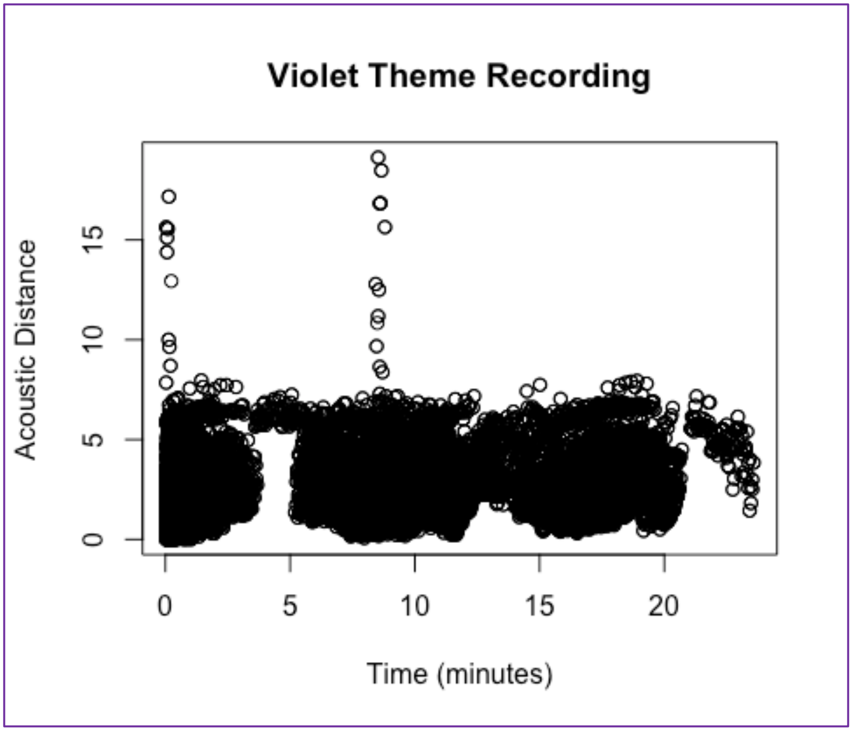


Figure A4.43: Violet Theme Acoustic Distance over time – within recording. There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.2617, p value.= 0.001). In other words, as units became further apart in a song session they became noticeably more dissimilar in structure.

Over seasons

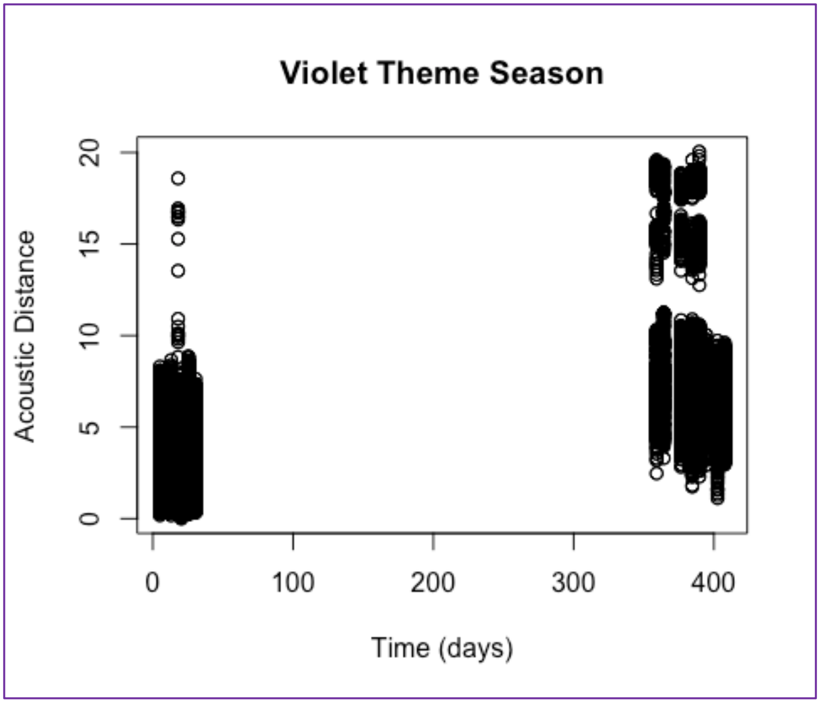


Figure A4.44: Violet Theme Acoustic Distance over time – over Seasons: There was a relationship between acoustic distance of units and time (Mantel statistic R: 0.6449, p value.= 0.001). In other words, as units became further apart in time they became noticeably more dissimilar in structure.

Appendix 4.9 – Test for Call Divergence

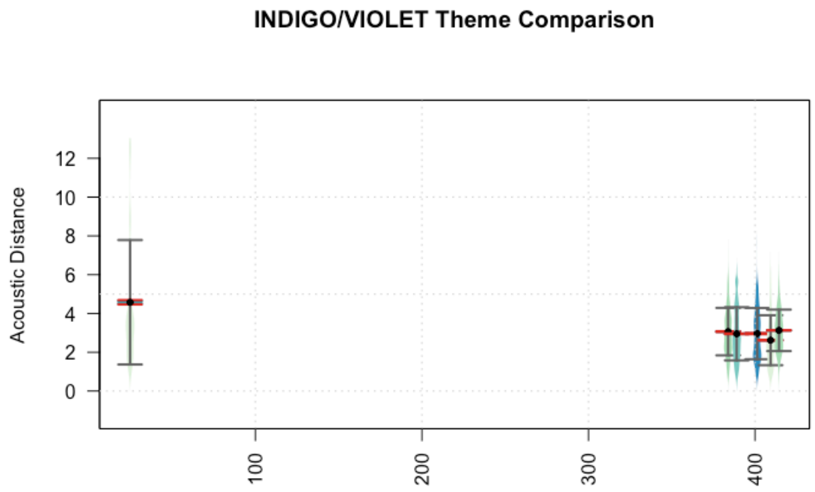


Figure A4.45: Test for Call Divergence. Indigo Vs Violet Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryIndigoVioletComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant ($R^2 = 0.5136$, $F(1, 4) = 6.28$, $p = 0.06633$).

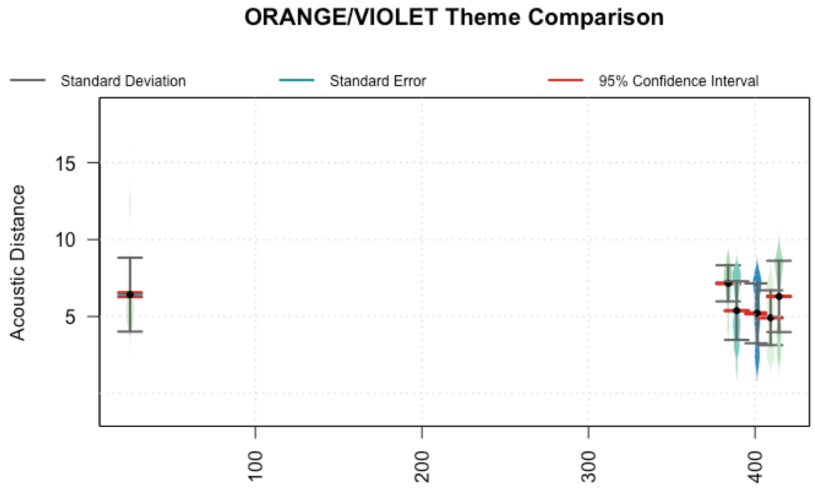


Figure A4.46: Test for Call Divergence. Orange Vs Violet Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryOrangeVioletComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant ($R^2 = -0.2212$, $F(1, 4) = 0.09423$, $p = 0.06633$).

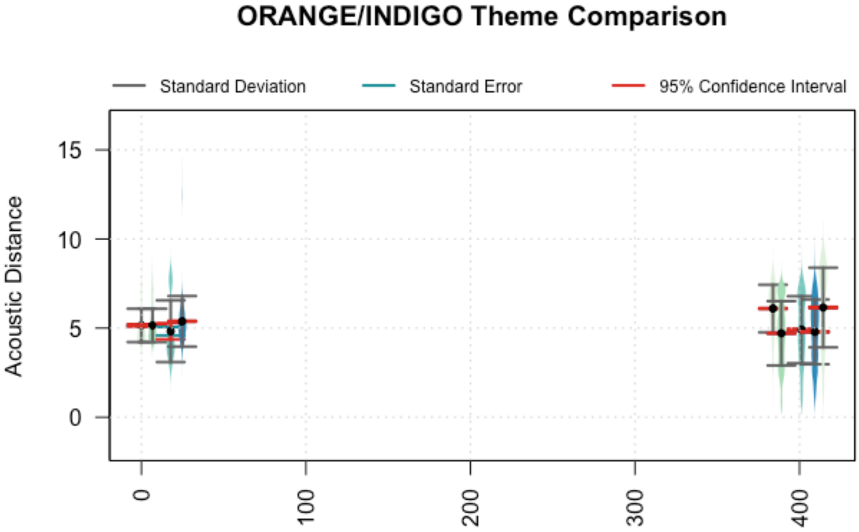


Figure A4.47: Test for Call Divergence. Orange Vs Indigo Theme: The fitted regression model was: lm(formula = median ~ TimeSeconds, data = SummaryIndigoVioletComp1). Simple linear regression was used to test if time significantly predicted acoustic distance. The overall regression was statistically insignificant (R^2 = 0.1378, F(1, 4) = 6.28, p = 0.1749).

Appendix 4.10: Test for Call Modification – Discrete Measurements

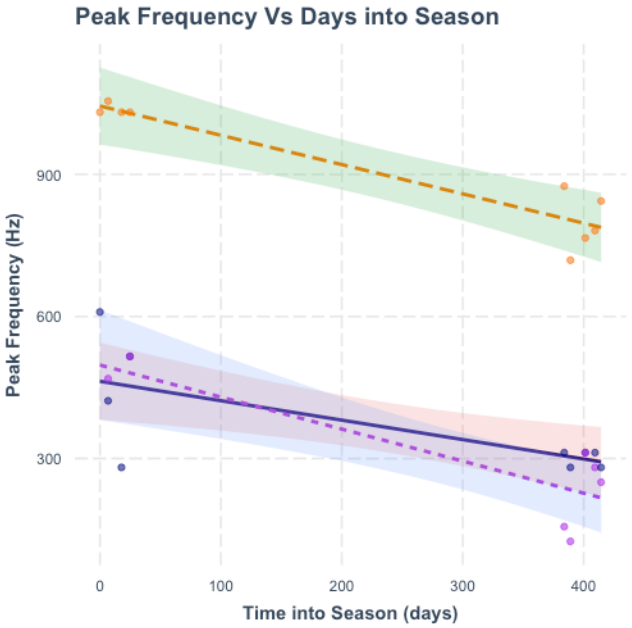


Figure A4.48: Across Season: Peak Frequency: Peak frequency was found to decrease over the seasons in all theme types. Peak Frequency in groans from the orange theme type were found to be significantly higher than the indigo and violet theme types

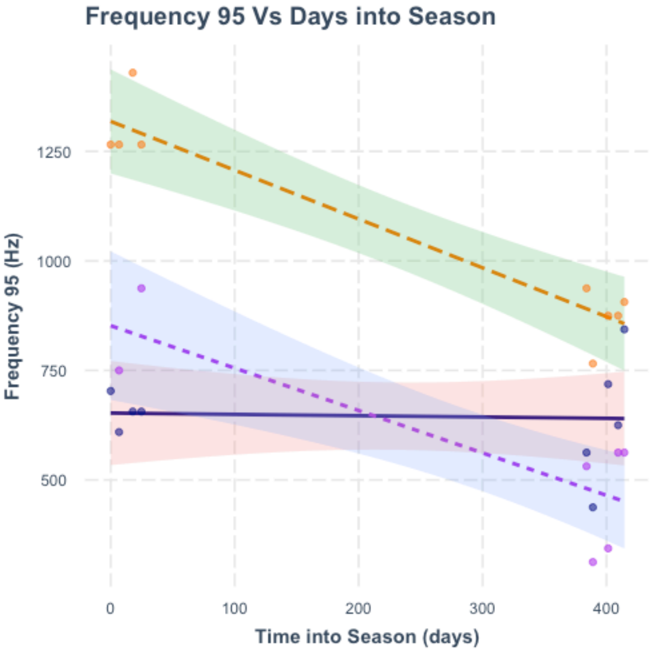


Figure A4.49: Across Season: Frequency 95: Frequency 95 was found to decrease over the seasons in two theme types (orange and violet) but not in the indigo theme type. Frequency 95 in the orange theme type was found to be significantly higher than the violet or indigo theme types.

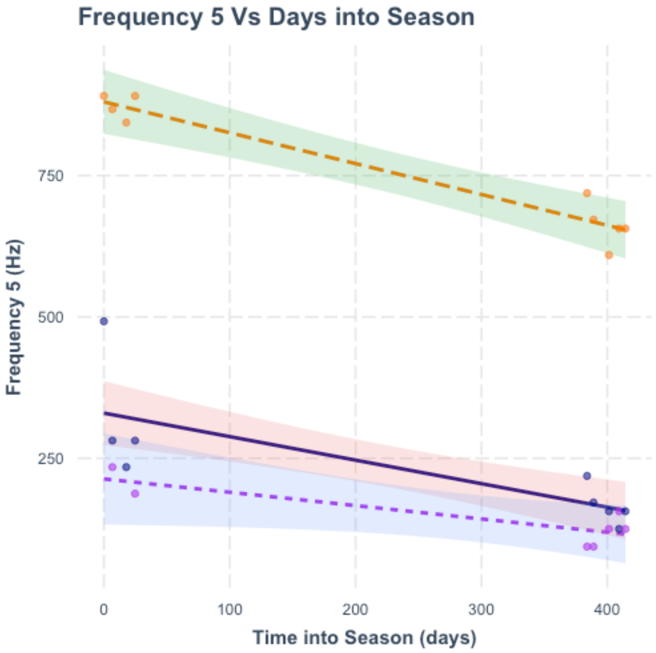


Figure A4.50: Across Season: Frequency 5: Frequency 5 was found to decrease over the season in all theme types. Frequency 5 in the orange theme type was found to be significantly higher than the violet or indigo theme types.

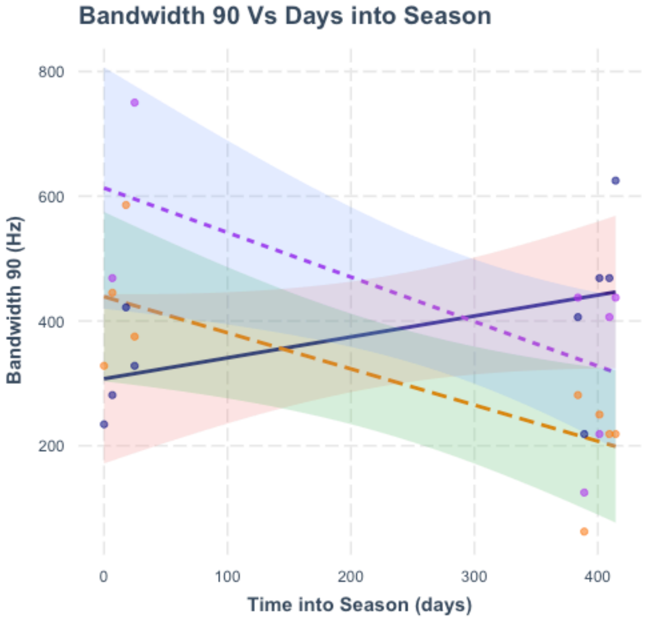


Figure A4.51: Across Season: Bandwidth 90: Bandwidth 90 was found to significantly change over the season with significant changes between themes types in which the indigo theme moans did not significantly change over seasons and the orange a violet theme moans significantly decreased.

First half Across Season

Table 24

	Peak Frequency	**Frequency 95**	**Frequency 5**	**Bandwidth**
(Intercept)	463.132***	653.302***	329.801***	307.421***
	[381.959, 544.305]	[538.188, 768.416]	[273.224, 386.378]	[171.795, 443.047]
	s.e. = 38.783	s.e. = 54.999	s.e. = 27.031	s.e. = 64.799
	t = 11.942	t = 11.878	t = 12.201	t = 4.744
	p = 0.000	p = 0.000	p = 0.000	p = 0.000
TimeDays	**-0.410****	0.036	**-0.400*****	0.335
	[-0.683, -0.138]	[-0.350, 0.422]	[-0.590, -0.211]	[-0.120, 0.790]
	s.e. = 0.130	s.e. = 0.184	s.e. = 0.091	s.e. = 0.217
	t = -3.155	t = 0.194	t = -4.417	t = 1.542
	p = 0.005	p = 0.848	p = 0.000	p = 0.139
Themeorange	**581.212*****	**665.333*****	**550.481*****	131.587
	[466.416, 696.008]	[502.537, 828.129]	[470.469, 630.493]	[-60.217, 323.391]
	s.e. = 54.847	s.e. = 77.780	s.e. = 38.228	s.e. = 91.640
	t = 10.597	t = 8.554	t = 14.400	t = 1.436
	p = 0.000	p = 0.000	p = 0.000	p = 0.167
Themeviolet	34.241	198.849+	-116.321*	305.694*
	[-107.134, 175.616]	[-1.640, 399.338]	[-214.859, -17.784]	[69.481, 541.908]
	s.e. = 67.546	s.e. = 95.789	s.e. = 47.079	s.e. = 112.858
	t = 0.507	t = 2.076	t = -2.471	t = 2.709
	p = 0.618	p = 0.052	p = 0.023	p = 0.014
TimeDays × Themeorange	-0.208	**-1.150*****	-0.146	**-0.914****
	[-0.593, 0.177]	[-1.697, -0.604]	[-0.414, 0.123]	[-1.558, -0.271]
	s.e. = 0.184	s.e. = 0.261	s.e. = 0.128	s.e. = 0.307
	t = -1.132	t = -4.410	t = -1.136	t = -2.975
	p = 0.272	p = 0.000	p = 0.270	p = 0.008
TimeDays × Themeviolet	-0.266	**-1.004****	0.165	**-1.049****
	[-0.703, 0.172]	[-1.625, -0.384]	[-0.140, 0.469]	[-1.780, -0.318]
	s.e. = 0.209	s.e. = 0.296	s.e. = 0.146	s.e. = 0.349
	t = -1.272	t = -3.387	t = 1.129	t = -3.003
	p = 0.219	p = 0.003	p = 0.273	p = 0.007
Num.Obs.	25	25	25	25
R2	0.952	0.892	0.974	0.502
+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001				

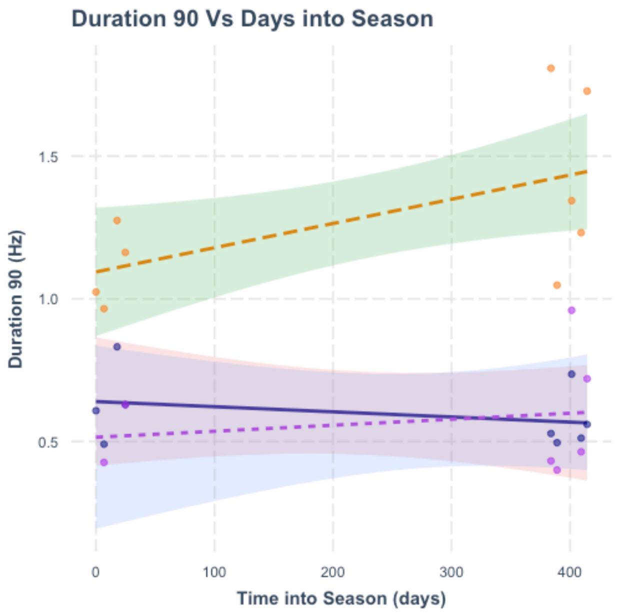


Figure A4.52: Across Season: Duration: No change in median duration over the season was detected in any theme type. Duration in moans from the orange theme type were found to be significantly longer than those in the violet and indigo theme types.

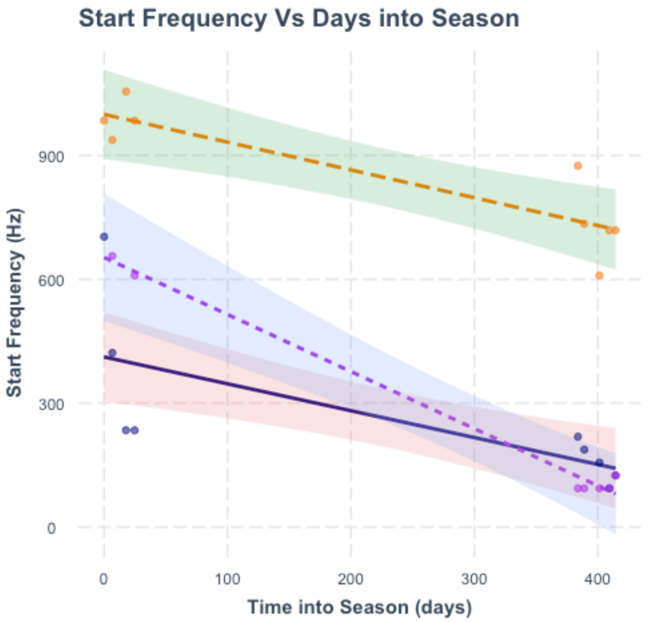


Figure A4.53: Across Season: Start Frequency. Start frequency was found to significantly decrease across seasons in all theme types with moans from the violet theme type decreasing at a faster rate than the indigo or orange themes. Start Frequency in moans from the orange theme type were found to be significantly higher than the indigo and violet theme types.

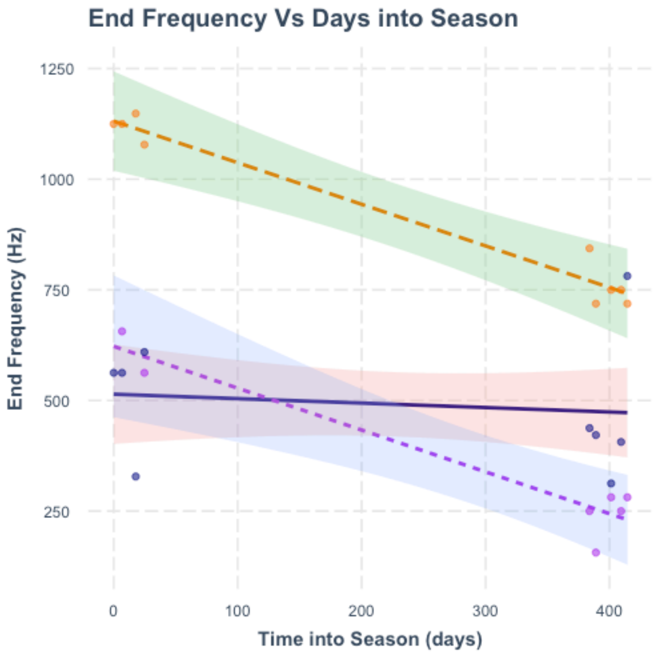


Figure A4.54: Across Season: End Frequency. End frequency was found to significantly decrease across seasons in the orange and violet theme types but remain the same in the indigo theme type. End Frequency in moans from the orange theme type were found to be significantly higher than the indigo and violet theme types.

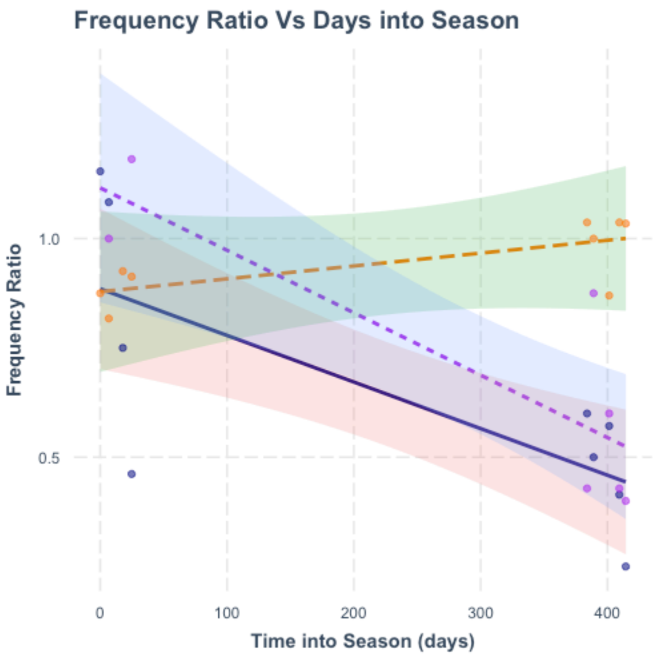


Figure A4.55: Across Season: Frequency Trend in the indigo and violet themes decreased while moans from the orange theme type stayed the same. Frequency Trend in moans from each theme type were found not to be significantly different from each other at the beginning of the season but were in the second season.

Secondhalf Across Season

Table 25

	Duration	Start Frequency	End Frequency	Frequency Ratio
(Intercept)	0.640***	411.967***	514.211***	0.885***
	[0.415, 0.865]	[304.137, 519.796]	[402.377, 626.045]	[0.702, 1.069]
	s.e. = 0.107	s.e. = 51.519	s.e. = 53.432	s.e. = 0.088
	t = 5.958	t = 7.996	t = 9.624	t = 10.082
	p = 0.000	p = 0.000	p = 0.000	p = 0.000
TimeDays	0.000	**-0.651****	-0.093	**-0.001****
	[-0.001, 0.001]	[-1.013, -0.289]	[-0.468, 0.282]	[-0.002, 0.000]
	s.e. = 0.000	s.e. = 0.173	s.e. = 0.179	s.e. = 0.000
	t = -0.456	t = -3.767	t = -0.519	t = -3.645
	p = 0.653	p = 0.001	p = 0.610	p = 0.002
Themeorange	**0.454****	**587.505*****	**617.214*****	-0.007
	[0.136, 0.772]	[435.011, 739.999]	[459.057, 775.371]	[-0.267, 0.253]
	s.e. = 0.152	s.e. = 72.858	s.e. = 75.564	s.e. = 0.124
	t = 2.989	t = 8.064	t = 8.168	t = -0.055
	p = 0.008	p = 0.000	p = 0.000	p = 0.957
Themeviolet	-0.125	241.062*	108.165	0.231
	[-0.517, 0.266]	[53.260, 428.864]	[-86.611, 302.941]	[-0.089, 0.551]
	s.e. = 0.187	s.e. = 89.727	s.e. = 93.059	s.e. = 0.153
	t = -0.669	t = 2.687	t = 1.162	t = 1.508
	p = 0.512	p = 0.015	p = 0.259	p = 0.148
TimeDays × Themeorange	0.001+	-0.022	**-0.847****	**0.001****
	[0.000, 0.002]	[-0.534, 0.489]	[-1.378, -0.317]	[0.000, 0.002]
	s.e. = 0.001	s.e. = 0.244	s.e. = 0.253	s.e. = 0.000
	t = 1.989	t = -0.091	t = -3.343	t = 3.284
	p = 0.061	p = 0.929	p = 0.003	p = 0.004
TimeDays × Themeviolet	0.000	**-0.731***	**-0.853****	0.000
	[-0.001, 0.002]	[-1.313, -0.150]	[-1.455, -0.250]	[-0.001, 0.001]
	s.e. = 0.001	s.e. = 0.278	s.e. = 0.288	s.e. = 0.000
	t = 0.648	t = -2.634	t = -2.961	t = -0.749
	p = 0.525	p = 0.016	p = 0.008	p = 0.463
Num.Obs.	25	25	25	25
R2	0.787	0.934	0.905	0.703

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Appendix 4.11– Discrete Measurements – Within Song Session – Test outputs

Peak Frequency over song session:

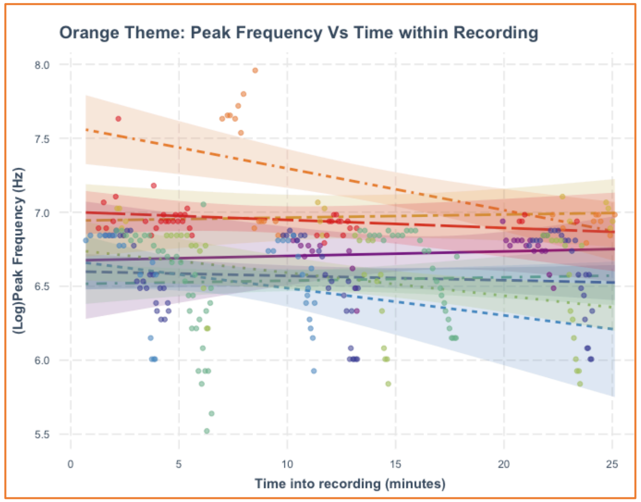


Figure A4.56: Significant difference in trend between individuals within song session. 160220 significantly decreases while all other individuals remain the same.

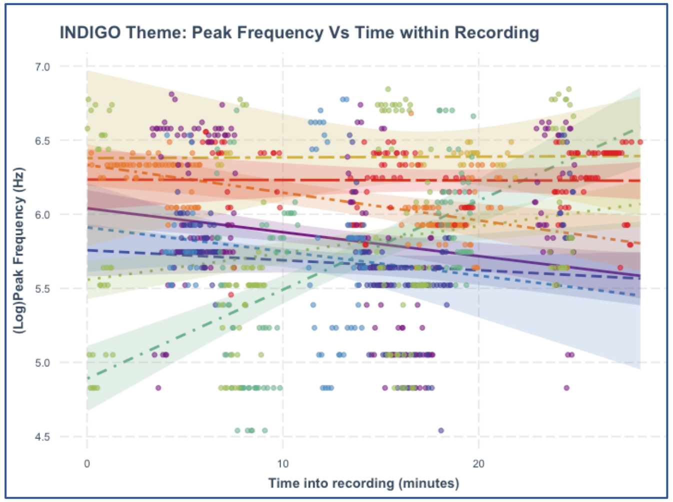


Figure A4.57: Significant difference in trend between individuals within song session. Individuals 270221, 050321, 170321, 100220 and 160220 decrease slightly in peak frequency over the song session while individuals 250321 and 300321 increases in peak frequency over the song session. Individual 050320 does not change peak frequency across the song session.

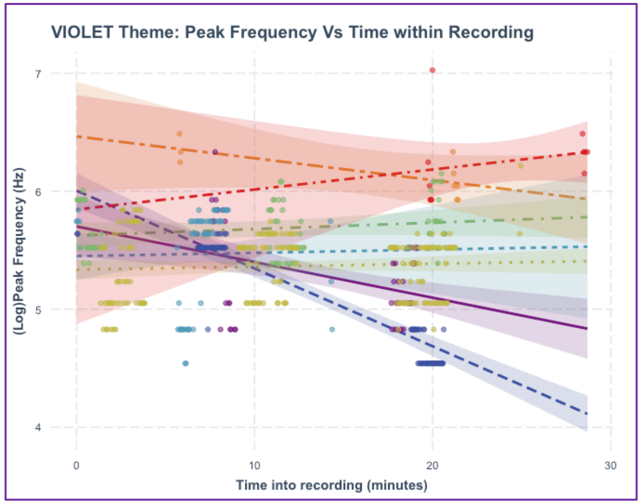
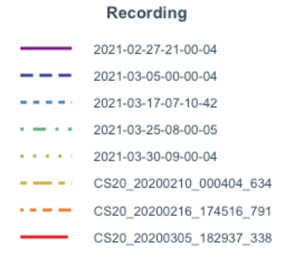
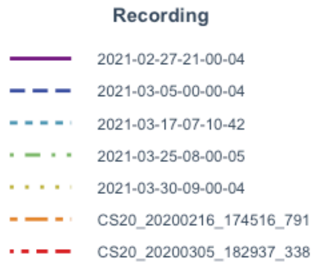


Figure A4.58: Significant difference in trend between individuals within song session. Individual 270221 and 160220 decreases in peak frequency over the song session at half the rate of individual 050321 individuals 050320 increases while there is no significant difference in peak frequency for the other individuals.



ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	Decrease	Decrease	yes
050321	NSC	Decrease	Decrease	yes
170321	NSC	Decrease	NSC	yes
250321	NSC	Increase	NSC	yes
300321	NSC	Increase	NSC	yes
100220	NSC	Decrease	ND	yes
160220	Decrease	Decrease	Decrease	no
050320	NSC	NSC	Increase	yes



Peak Frequency Within Recording Across Individuals

	ORANGE	INDIGO	VIOLET
(Intercept)	6.674***	6.040***	5.701***
	[6.262, 7.085]	[5.916, 6.163]	[5.450, 5.953]
	s.e. = 0.209	s.e. = 0.063	s.e. = 0.128
	t = 31.911	t = 95.964	t = 44.479
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	0.003	**-0.016*** **	**-0.030*** **
	[-0.020, 0.026]	[-0.025, -0.007]	[-0.047, -0.014]
	s.e. = 0.012	s.e. = 0.004	s.e. = 0.008
	t = 0.259	t = -3.613	t = -3.564
	p = 0.796	p = 0.000	p = 0.000
Recording2021-03-05-00-00-04	-0.073	**-0.283***	**0.304***
	[-0.503, 0.357]	[-0.498, -0.068]	[0.011, 0.596]
	s.e. = 0.218	s.e. = 0.110	s.e. = 0.149
	t = -0.336	t = -2.579	t = 2.041
	p = 0.737	p = 0.010	p = 0.042
Recording2021-03-17-07-10-42	-0.002	-0.129	-0.252
	[-0.457, 0.453]	[-0.452, 0.195]	[-0.574, 0.071]
	s.e. = 0.231	s.e. = 0.165	s.e. = 0.164
	t = -0.009	t = -0.780	t = -1.533
	p = 0.993	p = 0.435	p = 0.126
Recording2021-03-25-08-00-05	-0.159	**-1.149*** **	-0.077
	[-0.595, 0.277]	[-1.402, -0.896]	[-0.352, 0.199]
	s.e. = 0.221	s.e. = 0.129	s.e. = 0.140
	t = -0.718	t = -8.914	t = -0.546
	p = 0.473	p = 0.000	p = 0.585
Recording2021-03-30-09-00-04	0.074	**-0.482*** **	**-0.366** **
	[-0.386, 0.534]	[-0.661, -0.303]	[-0.631, -0.101]
	s.e. = 0.234	s.e. = 0.091	s.e. = 0.135
	t = 0.315	t = -5.276	t = -2.713
	p = 0.753	p = 0.000	p = 0.007
RecordingCS20_20200210_000404_634	0.269	0.338	
	[-0.214, 0.753]	[-0.267, 0.944]	
	s.e. = 0.246	s.e. = 0.309	
	t = 1.097	t = 1.096	
	p = 0.274	p = 0.273	
RecordingCS20_20200216_174516_791	**0.904*** **	**0.293** **	**0.763** **
	[0.427, 1.381]	[0.105, 0.480]	[0.235, 1.291]
	s.e. = 0.242	s.e. = 0.096	s.e. = 0.269
	t = 3.728	t = 3.065	t = 2.839
	p = 0.000	p = 0.002	p = 0.005
RecordingCS20_20200305_182937_338	0.328	0.194	0.144
	[-0.111, 0.768]	[-0.046, 0.433]	[-0.859, 1.147]

	s.e. = 0.223	s.e. = 0.122	s.e. = 0.510
	t = 1.471	t = 1.585	t = 0.281
	p = 0.142	p = 0.113	p = 0.778
Time5__s_ × Recording2021-03-05-00-00-04	-0.006	0.009	**-0.036*** **
	[-0.031, 0.019]	[-0.005, 0.024]	[-0.055, -0.017]
	s.e. = 0.013	s.e. = 0.007	s.e. = 0.010
	t = -0.483	t = 1.262	t = -3.649
	p = 0.629	p = 0.207	p = 0.000
Time5__s_ × Recording2021-03-17-07-10-42	-0.022	0.000	**0.033***
	[-0.055, 0.012]	[-0.029, 0.028]	[0.001, 0.065]
	s.e. = 0.017	s.e. = 0.015	s.e. = 0.016
	t = -1.253	t = -0.011	t = 2.009
	p = 0.211	p = 0.992	p = 0.045
Time5__s_ × Recording2021-03-25-08-00-05	-0.001	**0.076*** **	**0.036*** **
	[-0.027, 0.026]	[0.058, 0.095]	[0.017, 0.054]
	s.e. = 0.013	s.e. = 0.009	s.e. = 0.010
	t = -0.060	t = 8.107	t = 3.716
	p = 0.952	p = 0.000	p = 0.000
Time5__s_ × Recording2021-03-30-09-00-04	-0.019	**0.034*** **	**0.033*** **
	[-0.045, 0.008]	[0.022, 0.047]	[0.015, 0.050]
	s.e. = 0.013	s.e. = 0.006	s.e. = 0.009
	t = -1.387	t = 5.404	t = 3.631
	p = 0.167	p = 0.000	p = 0.000
Time5__s_ × RecordingCS20_20200210_000404_634	-0.001	0.017	
	[-0.029, 0.027]	[-0.017, 0.051]	
	s.e. = 0.014	s.e. = 0.017	
	t = -0.070	t = 0.956	
	p = 0.944	p = 0.339	
Time5__s_ × RecordingCS20_20200216_174516_791	**-0.031***	-0.003	0.012
	[-0.059, -0.003]	[-0.016, 0.011]	[-0.019, 0.043]
	s.e. = 0.014	s.e. = 0.007	s.e. = 0.016
	t = -2.216	t = -0.381	t = 0.739
	p = 0.027	p = 0.703	p = 0.460
Time5__s_ × RecordingCS20_20200305_182937_338	-0.008	**0.016***	**0.047***
	[-0.036, 0.019]	[0.002, 0.029]	[0.004, 0.091]
	s.e. = 0.014	s.e. = 0.007	s.e. = 0.022
	t = -0.600	t = 2.286	t = 2.132
	p = 0.549	p = 0.022	p = 0.033
Num.Obs.	310	990	487
R2	0.404	0.259	0.534

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Frequency 95 over song session

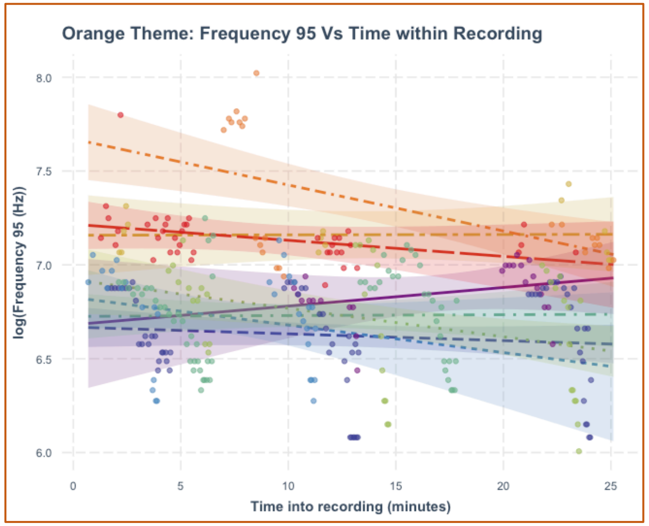


Figure A4.59: Most individuals show no significant change in Frequency 95 over their song sessions, except individuals 300321 and 160220 who decrease Frequency 95 over the song session.

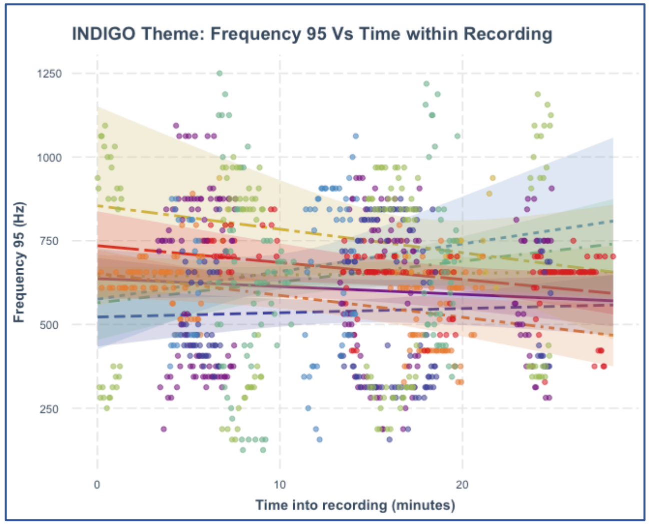


Figure A4.60: All individuals do not significantly change Frequency 95 across their song sessions in moans in the indigo theme

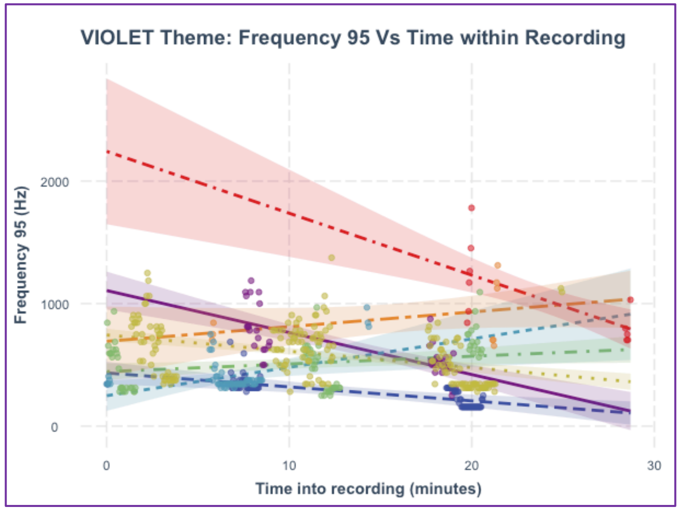


Figure A4.61: There is variation across individuals with some individuals decreasing Frequency 95 and others increasing Frequency 95.

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	NSC	Decrease	yes
050321	NSC	NSC	Decrease	yes
170321	NSC	NSC	Increase	yes
250321	NSC	NSC	Increase	yes
300321	Decrease	NSC	Decrease	yes
100220	NSC	NSC	ND	no
160220	Decrease	NSC	Increase	yes
050320	NSC	NSC	Decrease	yes

Frequency 95 Within Recording Across Individuals

	ORANGE	INDIGO	VIOLET
(Intercept)	6.681***	636.706***	1106.920***
	[6.324, 7.038]	[574.905, 698.507]	[952.662, 1261.177]
	s.e. = 0.181	s.e. = 31.492	s.e. = 78.503
	t = 36.860	t = 20.218	t = 14.100
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	0.010	-2.337	**-34.289*** **
	[-0.010, 0.030]	[-6.718, 2.045]	[-44.486, -24.091]
	s.e. = 0.010	s.e. = 2.233	s.e. = 5.190
	t = 0.963	t = -1.047	t = -6.607
	p = 0.336	p = 0.296	p = 0.000
Recording2021-03-05-00-00-04	-0.012	**-114.399* **	**-672.575*** **
	[-0.385, 0.360]	[-222.037, -6.761]	[-851.706, -493.444]
	s.e. = 0.189	s.e. = 54.850	s.e. = 91.161
	t = -0.066	t = -2.086	t = -7.378
	p = 0.948	p = 0.037	p = 0.000
Recording2021-03-17-07-10-42	0.145	-61.228	**-858.582*** **
	[-0.249, 0.539]	[-223.051, 100.594]	[-1056.159, -661.005]
	s.e. = 0.200	s.e. = 82.461	s.e. = 100.548
	t = 0.725	t = -0.743	t = -8.539
	p = 0.469	p = 0.458	p = 0.000
Recording2021-03-25-08-00-05	0.044	-72.005	**-662.057*** **
	[-0.333, 0.422]	[-198.604, 54.594]	[-830.720, -493.394]
	s.e. = 0.192	s.e. = 64.512	s.e. = 85.834
	t = 0.231	t = -1.116	t = -7.713
	p = 0.817	p = 0.265	p = 0.000
Recording2021-03-30-09-00-04	0.239	5.816	**-362.912*** **
	[-0.159, 0.638]	[-83.908, 95.539]	[-525.355, -200.470]
	s.e. = 0.203	s.e. = 45.721	s.e. = 82.668
	t = 1.182	t = 0.127	t = -4.390
	p = 0.238	p = 0.899	p = 0.000
RecordingCS20_20200210_000404_634	**0.477* **	217.880	
	[0.058, 0.896]	[-85.223, 520.983]	
	s.e. = 0.213	s.e. = 154.455	
	t = 2.240	t = 1.411	
	p = 0.026	p = 0.159	
RecordingCS20_20200216_174516_791	**0.990*** **	15.607	**-414.683* **
	[0.576, 1.403]	[-78.178, 109.391]	[-738.037, -91.329]
	s.e. = 0.210	s.e. = 47.791	s.e. = 164.557
	t = 4.708	t = 0.327	t = -2.520
	p = 0.000	p = 0.744	p = 0.012
RecordingCS20_20200305_182937_338	**0.535** **	98.501	**1136.145*** **
	[0.155, 0.916]	[-21.477, 218.478]	[521.953, 1750.337]
	s.e. = 0.193	s.e. = 61.138	s.e. = 312.567

	t = 2.767	t = 1.611	t = 3.635
	p = 0.006	p = 0.107	p = 0.000
Time5__s_ × Recording2021-03-05-00-00-04	-0.014	3.604	__22.887***__
	[-0.035, 0.008]	[-3.684, 10.892]	[11.088, 34.686]
	s.e. = 0.011	s.e. = 3.714	s.e. = 6.005
	t = -1.241	t = 0.970	t = 3.812
	p = 0.215	p = 0.332	p = 0.000
Time5__s_ × Recording2021-03-17-07-10-42	-0.025+	10.594	__57.470***__
	[-0.054, 0.005]	[-3.686, 24.874]	[37.721, 77.220]
	s.e. = 0.015	s.e. = 7.277	s.e. = 10.051
	t = -1.653	t = 1.456	t = 5.718
	p = 0.099	p = 0.146	p = 0.000
Time5__s_ × Recording2021-03-25-08-00-05	-0.009	8.555+	__40.571***__
	[-0.032, 0.013]	[-0.673, 17.782]	[29.040, 52.102]
	s.e. = 0.012	s.e. = 4.702	s.e. = 5.868
	t = -0.813	t = 1.819	t = 6.914
	p = 0.417	p = 0.069	p = 0.000
Time5__s_ × Recording2021-03-30-09-00-04	__-0.025*__	2.855	__21.000***__
	[-0.048, -0.002]	[-3.361, 9.072]	[10.165, 31.835]
	s.e. = 0.012	s.e. = 3.168	s.e. = 5.514
	t = -2.153	t = 0.901	t = 3.808
	p = 0.032	p = 0.368	p = 0.000
Time5__s_ × RecordingCS20_20200210_000404_634	-0.010	-4.678	
	[-0.034, 0.015]	[-21.758, 12.402]	
	s.e. = 0.012	s.e. = 8.704	
	t = -0.790	t = -0.537	
	p = 0.430	p = 0.591	
Time5__s_ × RecordingCS20_20200216_174516_791	__-0.034**__	-4.204	__46.265***__
	[-0.058, -0.010]	[-10.915, 2.506]	[27.246, 65.285]
	s.e. = 0.012	s.e. = 3.420	s.e. = 9.679
	t = -2.815	t = -1.229	t = 4.780
	p = 0.005	p = 0.219	p = 0.000
Time5__s_ × RecordingCS20_20200305_182937_338	-0.018	-2.701	-16.246
	[-0.043, 0.006]	[-9.511, 4.109]	[-42.847, 10.354]
	s.e. = 0.012	s.e. = 3.470	s.e. = 13.537
	t = -1.510	t = -0.778	t = -1.200
	p = 0.132	p = 0.437	p = 0.231
Num.Obs.	310	990	487
R2	0.500	0.055	0.513

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Frequency 5 over song session

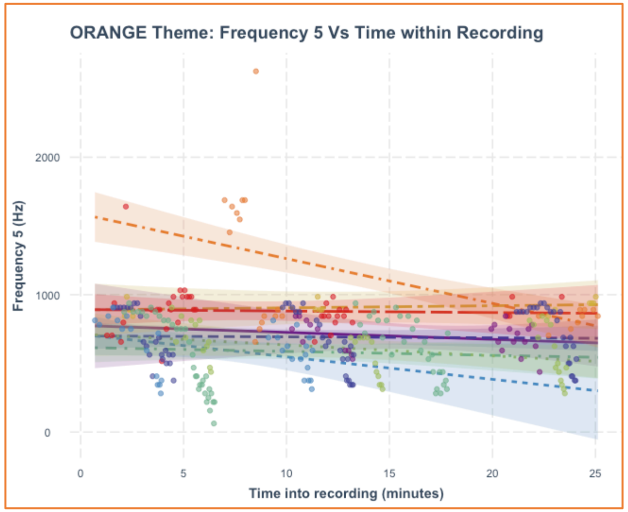


Figure A4.62: All individuals show no significant change of Frequency 5 except individual 160220 who decreases Frequency 5. Interestingly this 160220 is also the only individual to begin with a significantly higher Frequency 5 (as compared to ID 270221) and decrease their Frequency 5 allows a match to the other individuals

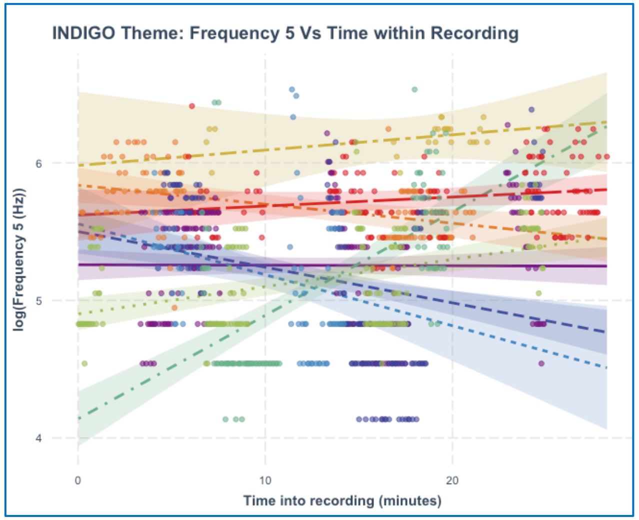


Figure A4.63: There is variation across individuals with some individuals (3) showing no significant change in Frequency 5 across their song session while some increase (2) and some decrease (3)

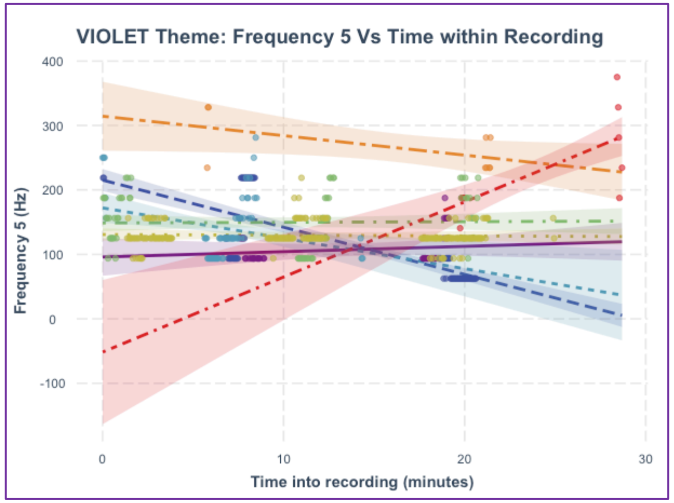


Figure A4.64: There is variation across individuals with ID 270221 showing no significant change in Frequency 5 while three individuals increase and three individuals decrease Frequency 5 as compared to ID 27021. There is no data for individual 100220 for the violet theme.

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	NSC	NSC	no
050321	NSC	Decrease	Decrease	yes
170321	NSC	Decrease	Decrease	yes
250321	NSC	Increase	Increase	yes
300321	NSC	Increase	Increase	yes
100220	NSC	NSC	ND	no
160220	Decrease	Decrease	Decrease	no
050320	NSC	NSC	Increase	yes

Frequency 5 Within Recording Across Individuals

	ORANGE	INDIGO	VIOLET
(Intercept)	775.720***	5.259***	95.928***
	[456.587, 1094.853]	[5.148, 5.371]	[66.920, 124.936]
	s.e. = 162.156	s.e. = 0.057	s.e. = 14.763
	t = 4.784	t = 92.577	t = 6.498
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	-5.061	0.000	0.826
	[-23.190, 13.069]	[-0.008, 0.008]	[-1.092, 2.744]
	s.e. = 9.212	s.e. = 0.004	s.e. = 0.976
	t = -0.549	t = -0.091	t = 0.846
	p = 0.583	p = 0.927	p = 0.398
Recording2021-03-05-00-00-04	-76.253	**0.241***	**119.344*****
	[-409.661, 257.154]	[0.047, 0.435]	[85.658, 153.030]
	s.e. = 169.409	s.e. = 0.099	s.e. = 17.143
	t = -0.450	t = 2.434	t = 6.962
	p = 0.653	p = 0.015	p = 0.000
Recording2021-03-17-07-10-42	-64.530	**0.297***	**76.189*****
	[-417.184, 288.123]	[0.005, 0.589]	[39.035, 113.344]
	s.e. = 179.188	s.e. = 0.149	s.e. = 18.908
	t = -0.360	t = 1.999	t = 4.029
	p = 0.719	p = 0.046	p = 0.000
Recording2021-03-25-08-00-05	-160.161	**-1.121*****	**52.817****
	[-498.003, 177.682]	[-1.349, -0.892]	[21.099, 84.534]
	s.e. = 171.662	s.e. = 0.116	s.e. = 16.141
	t = -0.933	t = -9.632	t = 3.272
	p = 0.352	p = 0.000	p = 0.001
Recording2021-03-30-09-00-04	-62.282	**-0.358*****	**34.846***
	[-418.907, 294.342]	[-0.519, -0.196]	[4.299, 65.394]
	s.e. = 181.205	s.e. = 0.082	s.e. = 15.546
	t = -0.344	t = -4.336	t = 2.242
	p = 0.731	p = 0.000	p = 0.025
RecordingCS20_20200210_000404_634	112.955	**0.722****	
	[-261.841, 487.752]	[0.175, 1.268]	
	s.e. = 190.439	s.e. = 0.279	
	t = 0.593	t = 2.590	
	p = 0.554	p = 0.010	
RecordingCS20_20200216_174516_791	**811.705*****	**0.578*****	**218.411*****
	[441.658, 1181.753]	[0.409, 0.747]	[157.604, 279.218]
	s.e. = 188.026	s.e. = 0.086	s.e. = 30.945
	t = 4.317	t = 6.704	t = 7.058
	p = 0.000	p = 0.000	p = 0.000
RecordingCS20_20200305_182937_338	115.850	**0.361****	**-147.550***
	[-224.778, 456.478]	[0.144, 0.577]	[-263.050, -32.050]
	s.e. = 173.077	s.e. = 0.110	s.e. = 58.779

	t = 0.669	t = 3.272	t = -2.510
	p = 0.504	p = 0.001	p = 0.012
Time5__s_ × Recording2021-03-05-00-00-04	4.373	-0.026***	-8.143***
	[-14.820, 23.567]	[-0.039, -0.012]	[-10.361, -5.924]
	s.e. = 9.752	s.e. = 0.007	s.e. = 1.129
	t = 0.448	t = -3.814	t = -7.211
	p = 0.654	p = 0.000	p = 0.000
Time5__s_ × Recording2021-03-17-07-10-42	-11.312	-0.037**	-5.541**
	[-37.514, 14.890]	[-0.062, -0.011]	[-9.255, -1.827]
	s.e. = 13.314	s.e. = 0.013	s.e. = 1.890
	t = -0.850	t = -2.795	t = -2.932
	p = 0.396	p = 0.005	p = 0.004
Time5__s_ × Recording2021-03-25-08-00-05	2.200	0.076***	-0.727
	[-18.312, 22.711]	[0.059, 0.092]	[-2.896, 1.441]
	s.e. = 10.422	s.e. = 0.008	s.e. = 1.103
	t = 0.211	t = 8.919	t = -0.659
	p = 0.833	p = 0.000	p = 0.510
Time5__s_ × Recording2021-03-30-09-00-04	-2.892	0.020***	-0.932
	[-23.427, 17.642]	[0.009, 0.031]	[-2.970, 1.105]
	s.e. = 10.434	s.e. = 0.006	s.e. = 1.037
	t = -0.277	t = 3.528	t = -0.899
	p = 0.782	p = 0.000	p = 0.369
Time5__s_ × RecordingCS20_20200210_000404_634	6.589	0.012	
	[-15.105, 28.283]	[-0.019, 0.042]	
	s.e. = 11.023	s.e. = 0.016	
	t = 0.598	t = 0.734	
	p = 0.550	p = 0.463	
Time5__s_ × RecordingCS20_20200216_174516_791	-27.489*	-0.013*	-3.846*
	[-49.020, -5.958]	[-0.026, -0.001]	[-7.423, -0.269]
	s.e. = 10.940	s.e. = 0.006	s.e. = 1.820
	t = -2.513	t = -2.182	t = -2.113
	p = 0.013	p = 0.029	p = 0.035
Time5__s_ × RecordingCS20_20200305_182937_338	3.968	0.007	10.827***
	[-17.565, 25.501]	[-0.005, 0.019]	[5.825, 15.830]
	s.e. = 10.941	s.e. = 0.006	s.e. = 2.546
	t = 0.363	t = 1.106	t = 4.253
	p = 0.717	p = 0.269	p = 0.000
Num.Obs.	310	990	487
R2	0.401	0.403	0.519

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Bandwidth within song session

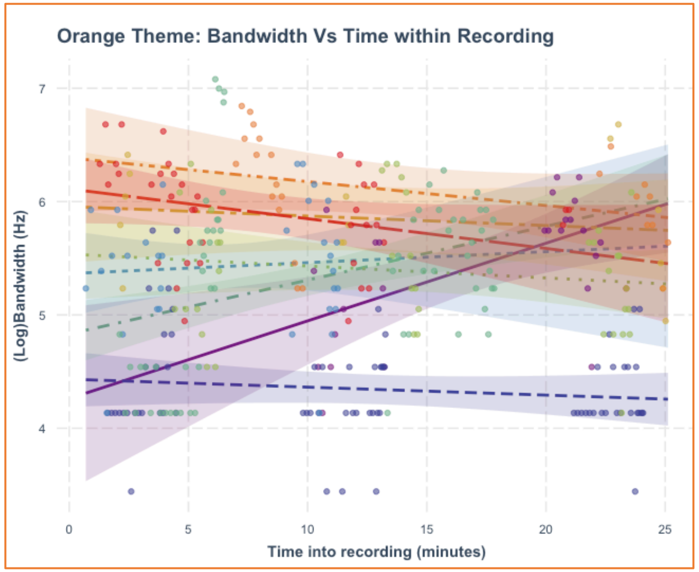


Figure A4.65: There is variation across individuals with two individuals increasing bandwidth, four showing no significant change and two individuals slightly decreasing the bandwidth of their moans in the Orange theme.

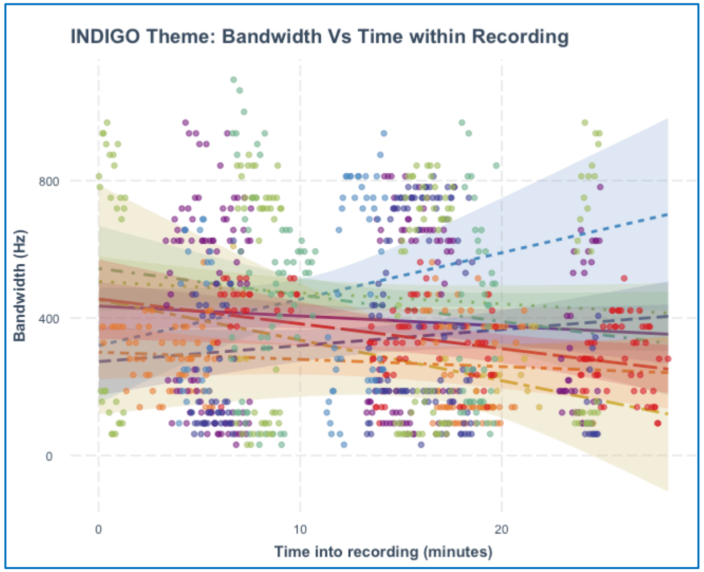


Figure A4.66: Most individuals did not show a significant change in the bandwidth of their moans in the Indigo theme except two individuals which displayed an increase over their song session (IDs 050321, 170321)

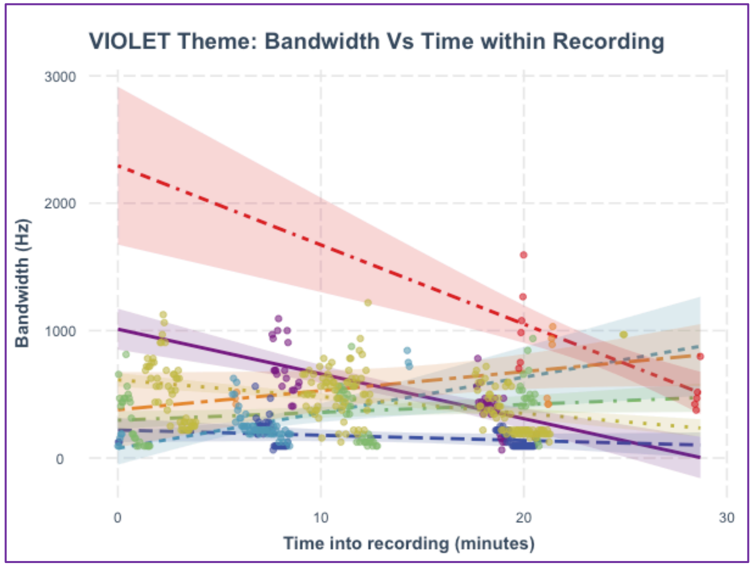


Figure A4.67: There is variation across individuals as three individuals decreased the bandwidth of their moan units and three individuals slightly increased bandwidth while one individual showed no significant change.

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	Increase	NSC	Decrease	yes
050321	NSC	Increase	Decrease	yes
170321	NSC	Increase	Increase	yes
250321	Increase	NSC	Increase	yes
300321	NSC	NSC	NSC	no
100220	NSC	NSC	ND	no
160220	Decrease	NSC	Increase	yes
050320	Decrease	NSC	Decrease	yes

Bandwidth Within Recording Across Individuals

	ORANGE	INDIGO	VIOLET
(Intercept)	4.262***	435.037***	1010.991***
	[3.455, 5.068]	[365.607, 504.467]	[850.348, 1171.635]
	s.e. = 0.410	s.e. = 35.380	s.e. = 81.753
	t = 10.400	t = 12.296	t = 12.366
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	**0.069****	-2.906	**-35.115*****
	[0.023, 0.114]	[-7.828, 2.016]	[-45.735, -24.495]
	s.e. = 0.023	s.e. = 2.508	s.e. = 5.405
	t = 2.945	t = -1.158	t = -6.497
	p = 0.003	p = 0.247	p = 0.000
Recording2021-03-05-00-00-04	0.171	**-161.927****	**-791.919*****
	[-0.671, 1.014]	[-282.852, -41.001]	[-978.466, -605.372]
	s.e. = 0.428	s.e. = 61.621	s.e. = 94.935
	t = 0.400	t = -2.628	t = -8.342
	p = 0.690	p = 0.009	p = 0.000
Recording2021-03-17-07-10-42	**1.103***	-115.229	**-934.772*****
	[0.211, 1.994]	[-297.028, 66.571]	[-1140.528, -729.015]
	s.e. = 0.453	s.e. = 92.641	s.e. = 104.711
	t = 2.435	t = -1.244	t = -8.927
	p = 0.015	p = 0.214	p = 0.000
Recording2021-03-25-08-00-05	0.570	109.370	**-714.874*****
	[-0.284, 1.424]	[-32.858, 251.597]	[-890.520, -539.229]
	s.e. = 0.434	s.e. = 72.476	s.e. = 89.387
	t = 1.314	t = 1.509	t = -7.997
	p = 0.190	p = 0.132	p = 0.000
Recording2021-03-30-09-00-04	**1.275****	71.149	**-397.758*****
	[0.374, 2.176]	[-29.651, 171.949]	[-566.926, -228.591]
	s.e. = 0.458	s.e. = 51.365	s.e. = 86.091
	t = 2.784	t = 1.385	t = -4.620
	p = 0.006	p = 0.166	p = 0.000
RecordingCS20_20200210_000404_634	1.695***	18.477	
	[0.748, 2.642]	[-322.044, 358.998]	
	s.e. = 0.481	s.e. = 173.522	
	t = 3.522	t = 0.106	
	p = 0.000	p = 0.915	
RecordingCS20_20200216_174516_791	**2.125*****	**-134.257***	**-633.094*****
	[1.189, 3.060]	[-239.619, -28.894]	[-969.834, -296.353]
	s.e. = 0.475	s.e. = 53.691	s.e. = 171.370
	t = 4.471	t = -2.501	t = -3.694
	p = 0.000	p = 0.013	p = 0.000
RecordingCS20_20200305_182937_338	**1.850*****	20.342	**1283.695*****
	[0.989, 2.711]	[-114.447, 155.130]	[644.076, 1923.314]

	s.e. = 0.437	s.e. = 68.686	s.e. = 325.507
	t = 4.230	t = 0.296	t = 3.944
	p = 0.000	p = 0.767	p = 0.000
Time5__s_ × Recording2021-03-05-00-00-04	**-0.076****	**7.580+**	**31.030*****
	[-0.124, -0.027]	[-0.607, 15.768]	[18.742, 43.317]
	s.e. = 0.025	s.e. = 4.172	s.e. = 6.253
	t = -3.067	t = 1.817	t = 4.962
	p = 0.002	p = 0.070	p = 0.000
Time5__s_ × Recording2021-03-17-07-10-42	**-0.059+**	**16.425***	**63.011*****
	[-0.125, 0.007]	[0.382, 32.468]	[42.444, 83.578]
	s.e. = 0.034	s.e. = 8.175	s.e. = 10.467
	t = -1.750	t = 2.009	t = 6.020
	p = 0.081	p = 0.045	p = 0.000
Time5__s_ × Recording2021-03-25-08-00-05	-0.021	-4.818	**41.298*****
	[-0.073, 0.031]	[-15.184, 5.549]	[29.290, 53.306]
	s.e. = 0.026	s.e. = 5.283	s.e. = 6.111
	t = -0.798	t = -0.912	t = 6.758
	p = 0.426	p = 0.362	p = 0.000
Time5__s_ × Recording2021-03-30-09-00-04	**-0.079****	-0.344	**21.932*****
	[-0.131, -0.027]	[-7.328, 6.640]	[10.648, 33.216]
	s.e. = 0.026	s.e. = 3.559	s.e. = 5.742
	t = -2.999	t = -0.097	t = 3.819
	p = 0.003	p = 0.923	p = 0.000
Time5__s_ × RecordingCS20_20200210_000404_634	**-0.077****	-8.876	
	[-0.132, -0.022]	[-28.065, 10.313]	
	s.e. = 0.028	s.e. = 9.778	
	t = -2.762	t = -0.908	
	p = 0.006	p = 0.364	
Time5__s_ × RecordingCS20_20200216_174516_791	**-0.090****	0.797	**50.112*****
	[-0.144, -0.035]	[-6.742, 8.336]	[30.304, 69.919]
	s.e. = 0.028	s.e. = 3.842	s.e. = 10.080
	t = -3.240	t = 0.208	t = 4.971
	p = 0.001	p = 0.836	p = 0.000
Time5__s_ × RecordingCS20_20200305_182937_338	**-0.095*****	-4.318	**-27.073+**
	[-0.149, -0.040]	[-11.968, 3.332]	[-54.775, 0.629]
	s.e. = 0.028	s.e. = 3.898	s.e. = 14.098
	t = -3.429	t = -1.108	t = -1.920
	p = 0.001	p = 0.268	p = 0.055
Num.Obs.	310	990	487
R2	0.546	0.089	0.460

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Duration within recording

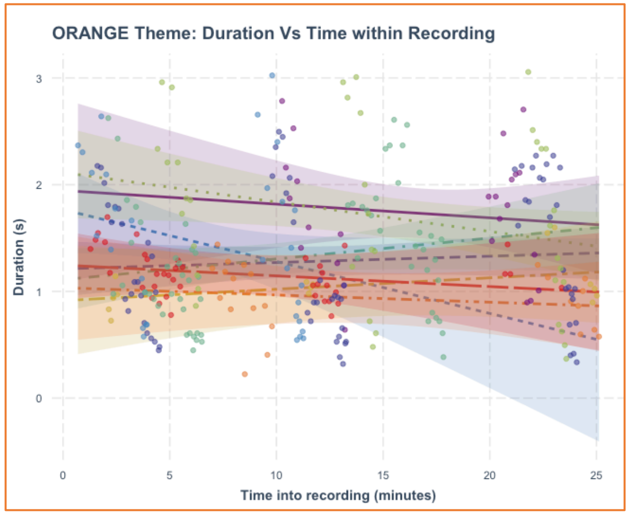


Figure A4.68: All individuals showed no significant change in the duration of the moan unit over their song sessions in the orange theme.

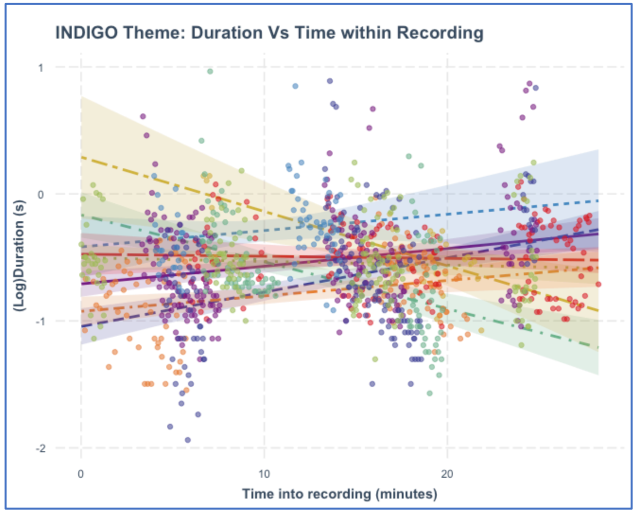


Figure A4.69: There was variation across individuals as most individuals displayed a slight increase in duration over their song sessions while two individuals showed a decrease, and two individuals showed no significant change.

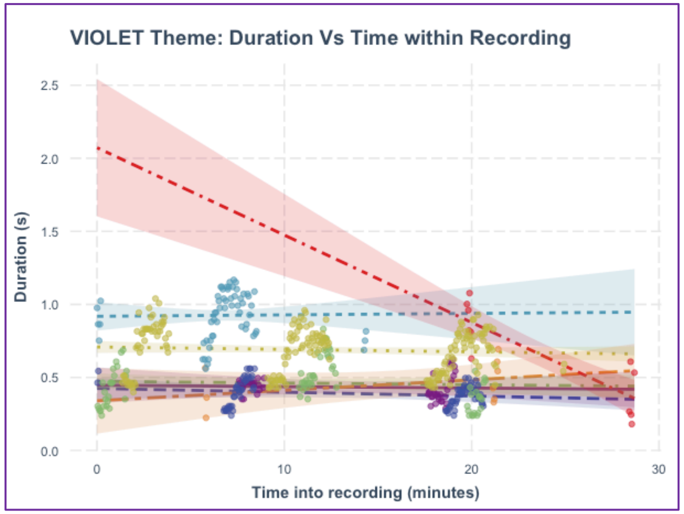


Figure A4.70: All individuals showed no significant change in duration of their moans except ID 050320 which decreased duration of moans over their song session.

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	Increase	NSC	yes
050321	NSC	Increase	NSC	yes
170321	NSC	Increase	NSC	yes
250321	NSC	Decrease	NSC	yes
300321	NSC	NSC	NSC	no
100220	NSC	Decrease	ND	yes
160220	NSC	Increase	NSC	yes
050320	NSC	NSC	Decrease	yes

Duration Within Recording Across Individuals

	ORANGE	INDIGO	VIOLET
(Intercept)	1.946***	-0.709***	0.447***
	[1.091, 2.801]	[-0.809, -0.608]	[0.325, 0.569]
	s.e. = 0.434	s.e. = 0.051	s.e. = 0.062
	t = 4.478	t = -13.857	t = 7.213
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	-0.013	**0.014*** **	-0.001
	[-0.061, 0.036]	[0.007, 0.021]	[-0.009, 0.007]
	s.e. = 0.025	s.e. = 0.004	s.e. = 0.004
	t = -0.519	t = 3.842	t = -0.238
	p = 0.604	p = 0.000	p = 0.812
Recording2021-03-05-00-00-04	-0.734	**-0.335*** **	-0.022
	[-1.628, 0.159]	[-0.510, -0.161]	[-0.163, 0.120]
	s.e. = 0.454	s.e. = 0.089	s.e. = 0.072
	t = -1.618	t = -3.764	t = -0.303
	p = 0.107	p = 0.000	p = 0.762
Recording2021-03-17-07-10-42	-0.180	**0.292***	**0.471*** **
	[-1.124, 0.765]	[0.029, 0.555]	[0.315, 0.627]
	s.e. = 0.480	s.e. = 0.134	s.e. = 0.079
	t = -0.374	t = 2.178	t = 5.935
	p = 0.709	p = 0.030	p = 0.000
Recording2021-03-25-08-00-05	**-0.837+**	**0.544*** **	0.027
	[-1.742, 0.068]	[0.338, 0.749]	[-0.107, 0.160]
	s.e. = 0.460	s.e. = 0.105	s.e. = 0.068
	t = -1.819	t = 5.190	t = 0.392
	p = 0.070	p = 0.000	p = 0.695
Recording2021-03-30-09-00-04	0.169	**0.206** **	**0.262*** **
	[-0.787, 1.124]	[0.061, 0.352]	[0.133, 0.390]
	s.e. = 0.485	s.e. = 0.074	s.e. = 0.065
	t = 0.347	t = 2.777	t = 4.006
	p = 0.729	p = 0.006	p = 0.000
RecordingCS20_20200210_000404_634	**-1.032***	**0.998*** **	
	[-2.036, -0.028]	[0.506, 1.491]	
	s.e. = 0.510	s.e. = 0.251	
	t = -2.023	t = 3.980	
	p = 0.044	p = 0.000	
RecordingCS20_20200216_174516_791	**-0.912+**	**-0.216** **	-0.106
	[-1.903, 0.080]	[-0.368, -0.064]	[-0.362, 0.149]
	s.e. = 0.504	s.e. = 0.078	s.e. = 0.130
	t = -1.810	t = -2.784	t = -0.819
	p = 0.071	p = 0.005	p = 0.413
RecordingCS20_20200305_182937_338	-0.699	**0.234***	**1.625*** **
	[-1.612, 0.213]	[0.039, 0.429]	[1.140, 2.110]
	s.e. = 0.464	s.e. = 0.099	s.e. = 0.247

	t = -1.508	t = 2.356	t = 6.583
	p = 0.133	p = 0.019	p = 0.000
Time5__s_ × Recording2021-03-05-00-00-04	0.019	**0.013***	-0.002
	[-0.033, 0.070]	[0.001, 0.025]	[-0.011, 0.008]
	s.e. = 0.026	s.e. = 0.006	s.e. = 0.005
	t = 0.717	t = 2.170	t = -0.343
	p = 0.474	p = 0.030	p = 0.732
Time5__s_ × Recording2021-03-17-07-10-42	-0.036	-0.001	0.002
	[-0.106, 0.034]	[-0.024, 0.022]	[-0.014, 0.018]
	s.e. = 0.036	s.e. = 0.012	s.e. = 0.008
	t = -1.004	t = -0.093	t = 0.247
	p = 0.316	p = 0.926	p = 0.805
Time5__s_ × Recording2021-03-25-08-00-05	0.032	**-0.051*****	0.000
	[-0.023, 0.087]	[-0.066, -0.036]	[-0.009, 0.009]
	s.e. = 0.028	s.e. = 0.008	s.e. = 0.005
	t = 1.158	t = -6.666	t = -0.041
	p = 0.248	p = 0.000	p = 0.968
Time5__s_ × Recording2021-03-30-09-00-04	-0.015	**-0.017****	-0.001
	[-0.070, 0.040]	[-0.027, -0.007]	[-0.009, 0.008]
	s.e. = 0.028	s.e. = 0.005	s.e. = 0.004
	t = -0.530	t = -3.271	t = -0.156
	p = 0.596	p = 0.001	p = 0.876
Time5__s_ × RecordingCS20_20200210_000404_634	0.023	**-0.057*****	
	[-0.035, 0.082]	[-0.084, -0.029]	
	s.e. = 0.030	s.e. = 0.014	
	t = 0.796	t = -4.013	
	p = 0.427	p = 0.000	
Time5__s_ × RecordingCS20_20200216_174516_791	0.006	-0.002	0.008
	[-0.052, 0.064]	[-0.013, 0.009]	[-0.007, 0.023]
	s.e. = 0.029	s.e. = 0.006	s.e. = 0.008
	t = 0.206	t = -0.318	t = 1.064
	p = 0.837	p = 0.750	p = 0.288
Time5__s_ × RecordingCS20_20200305_182937_338	0.003	**-0.016****	**-0.059*****
	[-0.055, 0.060]	[-0.027, -0.005]	[-0.080, -0.038]
	s.e. = 0.029	s.e. = 0.006	s.e. = 0.011
	t = 0.094	t = -2.765	t = -5.501
	p = 0.925	p = 0.006	p = 0.000
Num.Obs.	310	990	487
R2	0.163	0.178	0.623

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Start Frequency within recording

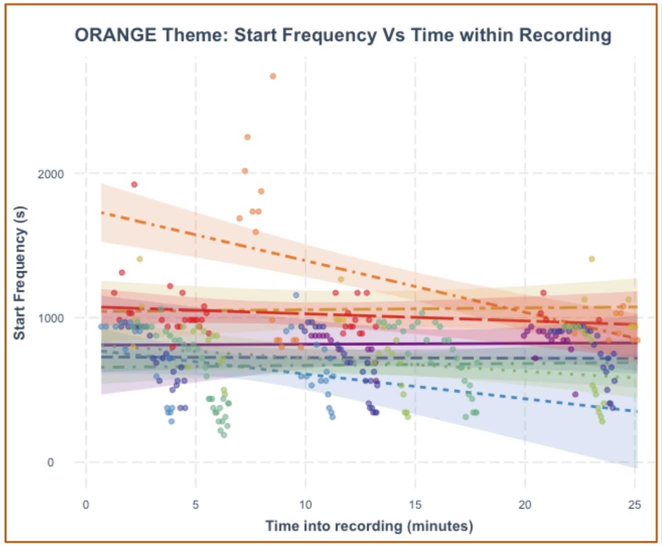


Figure A4.71: All individuals showed no significant change in start frequency except ID 160220 who displayed a decrease. Similarly, to Frequency 5, this individual started producing this unit with a significantly higher start frequency than the other individuals, so the decrease over the song session brought the individual closer to the start frequency of other individuals.

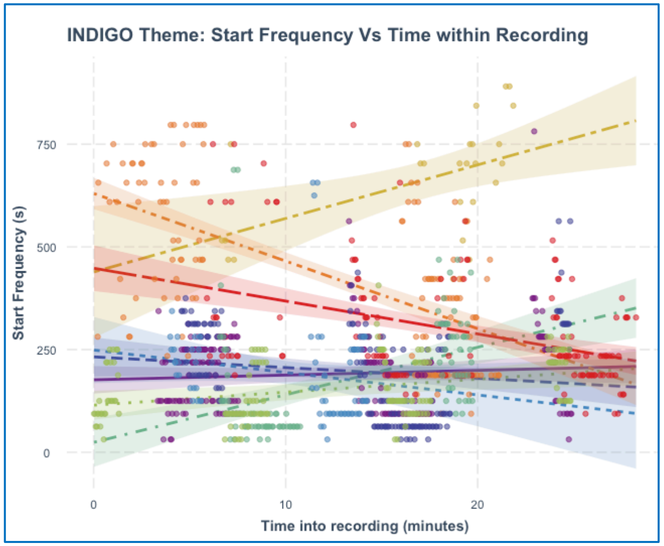


Figure A4.72: There was variation across individuals. Most individuals (4) decreased the start frequency of their units while two individuals increased and two individuals remained the same. All of the individuals displaying songs in the Caribbean started with a higher start frequency but interestingly only ID 100220 continued to increase the start frequency of their moan unit making it even more different from the other individuals displaying the moan unit in this theme.

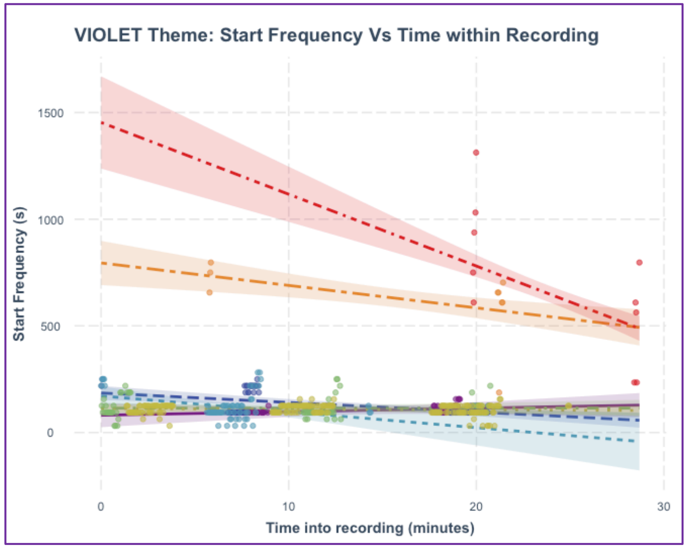
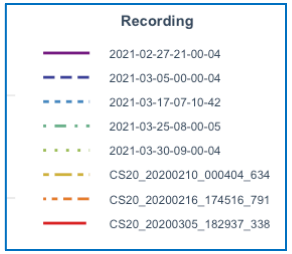


Figure A4.73: Individuals either showed no significant change in start frequency or a decrease over their song sessions. Interestingly again, individuals from the Caribbean in 2020 displayed significantly higher start frequencies than those displayed in Scotland in 2021.



ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	NSC	NSC	no
050321	NSC	Decrease	Decrease	yes
170321	NSC	Decrease	Decrease	yes
250321	NSC	Increase	NSC	yes
300321	NSC	NSC	NSC	no
100220	NSC	Increase	ND	yes
160220	Decrease	Decrease	Decrease	no
050320	NSC	Decrease	Decrease	yes

Start Frequency Within Recording Across Individuals

	ORANGE	**INDIGO**	**VIOLET**
(Intercept)	809.427***	176.387***	81.067**
	[453.375, 1165.479]	[143.054, 209.720]	[25.015, 137.119]
	s.e. = 180.915	s.e. = 16.986	s.e. = 28.525
	t = 4.474	t = 10.384	t = 2.842
	p = 0.000	p = 0.000	p = 0.005
Time5__s_	0.624	1.147	1.635
	[-19.603, 20.851]	[-1.216, 3.511]	[-2.071, 5.340]
	s.e. = 10.278	s.e. = 1.204	s.e. = 1.886
	t = 0.061	t = 0.953	t = 0.867
	p = 0.952	p = 0.341	p = 0.387
Recording2021-03-05-00-00-04	-81.938	**55.866+**	**104.161****
	[-453.915, 290.039]	[-2.190, 113.922]	[39.070, 169.251]
	s.e. = 189.007	s.e. = 29.584	s.e. = 33.125
	t = -0.434	t = 1.888	t = 3.144
	p = 0.665	p = 0.059	p = 0.002
Recording2021-03-17-07-10-42	-28.621	72.425	**90.258***
	[-422.071, 364.830]	[-14.856, 159.707]	[18.464, 162.051]
	s.e. = 199.917	s.e. = 44.477	s.e. = 36.536
	t = -0.143	t = 1.628	t = 2.470
	p = 0.886	p = 0.104	p = 0.014
Recording2021-03-25-08-00-05	-153.910	**-152.264*****	32.986
	[-530.836, 223.015]	[-220.547, -83.981]	[-28.301, 94.272]
	s.e. = 191.521	s.e. = 34.796	s.e. = 31.189
	t = -0.804	t = -4.376	t = 1.058
	p = 0.422	p = 0.000	p = 0.291
Recording2021-03-30-09-00-04	1.958	**-61.747***	31.488
	[-395.922, 399.838]	[-110.140, -13.353]	[-27.538, 90.515]
	s.e. = 202.168	s.e. = 24.660	s.e. = 30.039
	t = 0.010	t = -2.504	t = 1.048
	p = 0.992	p = 0.012	p = 0.295
RecordingCS20_20200210_000404_634	232.915	**262.495****	
	[-185.239, 651.070]	[99.012, 425.977]	
	s.e. = 212.470	s.e. = 83.307	
	t = 1.096	t = 3.151	
	p = 0.274	p = 0.002	
RecordingCS20_20200216_174516_791	**942.986*****	**453.664*****	**713.763*****
	[530.130, 1355.843]	[403.080, 504.248]	[596.266, 831.259]
	s.e. = 209.778	s.e. = 25.777	s.e. = 59.795
	t = 4.495	t = 17.600	t = 11.937
	p = 0.000	p = 0.000	p = 0.000
RecordingCS20_20200305_182937_338	266.716	**271.659*****	**1372.610*****
	[-113.317, 646.749]	[206.948, 336.371]	[1149.432, 1595.789]

	s.e. = 193.100	s.e. = 32.976	s.e. = 113.577
	t = 1.381	t = 8.238	t = 12.085
	p = 0.168	p = 0.000	p = 0.000
Time5__s_ × Recording2021-03-05-00-00-04	-1.063	-3.750+	-6.092**
	[-22.477, 20.351]	[-7.681, 0.181]	[-10.380, -1.805]
	s.e. = 10.881	s.e. = 2.003	s.e. = 2.182
	t = -0.098	t = -1.872	t = -2.792
	p = 0.922	p = 0.061	p = 0.005
Time5__s_ × Recording2021-03-17-07-10-42	-17.755	-6.611+	-9.071*
	[-46.988, 11.479]	[-14.313, 1.091]	[-16.247, -1.895]
	s.e. = 14.854	s.e. = 3.925	s.e. = 3.652
	t = -1.195	t = -1.684	t = -2.484
	p = 0.233	p = 0.092	p = 0.013
Time5__s_ × Recording2021-03-25-08-00-05	0.732	10.429***	-1.636
	[-22.152, 23.616]	[5.452, 15.406]	[-5.825, 2.554]
	s.e. = 11.628	s.e. = 2.536	s.e. = 2.132
	t = 0.063	t = 4.112	t = -0.767
	p = 0.950	p = 0.000	p = 0.443
Time5__s_ × Recording2021-03-30-09-00-04	-9.778	2.015	-1.957
	[-32.687, 13.132]	[-1.338, 5.368]	[-5.894, 1.980]
	s.e. = 11.641	s.e. = 1.709	s.e. = 2.004
	t = -0.840	t = 1.179	t = -0.977
	p = 0.402	p = 0.239	p = 0.329
Time5__s_ × RecordingCS20_20200210_000404_634	0.633	11.893*	
	[-23.571, 24.837]	[2.680, 21.105]	
	s.e. = 12.298	s.e. = 4.694	
	t = 0.051	t = 2.533	
	p = 0.959	p = 0.011	
Time5__s_ × RecordingCS20_20200216_174516_791	-36.401**	-17.609***	-12.164***
	[-60.422, -12.379]	[-21.229, -13.990]	[-19.075, -5.252]
	s.e. = 12.206	s.e. = 1.844	s.e. = 3.517
	t = -2.982	t = -9.547	t = -3.458
	p = 0.003	p = 0.000	p = 0.001
Time5__s_ × RecordingCS20_20200305_182937_338	-5.566	-9.145***	-35.303***
	[-29.591, 18.458]	[-12.818, -5.472]	[-44.969, -25.637]
	s.e. = 12.207	s.e. = 1.872	s.e. = 4.919
	t = -0.456	t = -4.886	t = -7.177
	p = 0.649	p = 0.000	p = 0.000
Num.Obs.	310	990	487
R2	0.418	0.536	0.741

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

End Frequency within recording

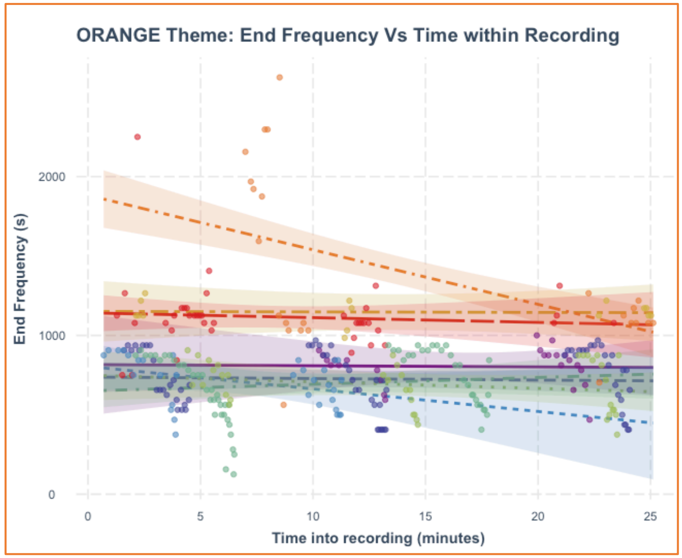


Figure A4.74: All individuals showed no significant change in the end frequency of their moans except ID 160220 who started significantly higher than the others then decreased over the song session. This was a similar finding to both Start frequency and Frequency 95.

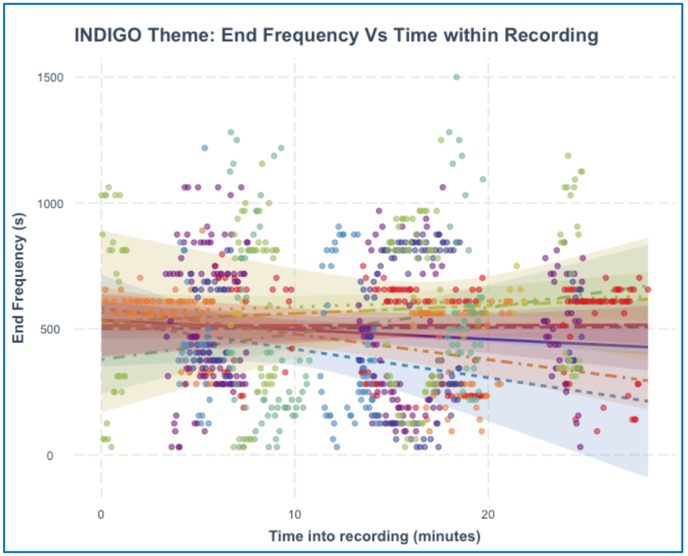


Figure A4.75: Most individuals showed no significant change in the end frequency of their moans in the Indigo theme except ID 250321 who displayed a slight increase over their song session.

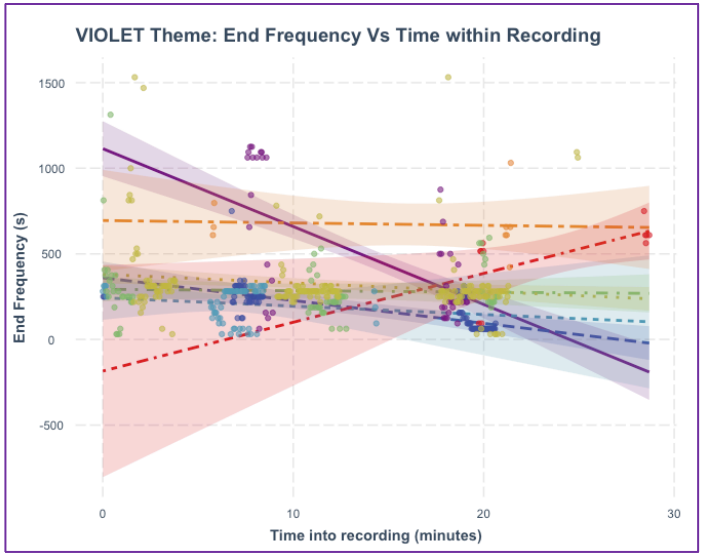


Figure A4.76: There was variation in end frequency trend across individuals as most individuals decreased the end frequency of their moans (4), two stayed the same and one individual increased end frequency.

End Frequency within recording

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	NSC	Decrease	yes
050321	NSC	NSC	Decrease	yes
170321	NSC	NSC	Decrease	yes
250321	NSC	Increase	NSC	yes
300321	NSC	NSC	Decrease	yes
100220	NSC	NSC	ND	no
160220	Decrease	NSC	NSC	yes
050320	NSC	NSC	Increase	yes

End Frequency Within Recording Across Individuals

	ORANGE	INDIGO	VIOLET
(Intercept)	815.916***	535.040***	1114.186***
	[496.327, 1135.506]	[459.759, 610.321]	[953.569, 1274.804]
	s.e. = 162.388	s.e. = 38.361	s.e. = 81.739
	t = 5.024	t = 13.947	t = 13.631
	p = 0.000	p = 0.000	p = 0.000
Time5__s_	-0.718	-3.784	**-45.469*** **
	[-18.874, 17.437]	[-9.121, 1.554]	[-56.088, -34.851]
	s.e. = 9.225	s.e. = 2.720	s.e. = 5.404
	t = -0.078	t = -1.391	t = -8.414
	p = 0.938	p = 0.164	p = 0.000
Recording2021-03-05-00-00-04	-78.343	-34.557	**-753.847*** **
	[-412.227, 255.541]	[-165.673, 96.559]	[-940.364, -567.330]
	s.e. = 169.651	s.e. = 66.814	s.e. = 94.920
	t = -0.462	t = -0.517	t = -7.942
	p = 0.645	p = 0.605	p = 0.000
Recording2021-03-17-07-10-42	-11.166	-2.058	**-870.597*** **
	[-364.324, 341.992]	[-199.177, 195.062]	[-1076.320, -664.873]
	s.e. = 179.444	s.e. = 100.448	s.e. = 104.694
	t = -0.062	t = -0.020	t = -8.316
	p = 0.950	p = 0.984	p = 0.000
Recording2021-03-25-08-00-05	-166.160	**-156.903***	**-821.127*** **
	[-504.485, 172.166]	[-311.116, -2.690]	[-996.744, -645.510]
	s.e. = 171.908	s.e. = 78.584	s.e. = 89.373
	t = -0.967	t = -1.997	t = -9.188
	p = 0.335	p = 0.046	p = 0.000
Recording2021-03-30-09-00-04	-66.892	29.447	**-734.028*** **
	[-424.027, 290.242]	[-79.847, 138.741]	[-903.168, -564.888]
	s.e. = 181.465	s.e. = 55.694	s.e. = 86.077
	t = -0.369	t = 0.529	t = -8.528
	p = 0.713	p = 0.597	p = 0.000
RecordingCS20_20200210_000404_634	335.349+	-5.002	
	[-39.983, 710.681]	[-374.218, 364.214]	
	s.e. = 190.711	s.e. = 188.145	
	t = 1.758	t = -0.027	
	p = 0.080	p = 0.979	
RecordingCS20_20200216_174516_791	**1066.712*** **	47.271	**-419.539***
	[696.135, 1437.289]	[-66.970, 161.512]	[-756.225, -82.853]
	s.e. = 188.295	s.e. = 58.215	s.e. = 171.342
	t = 5.665	t = 0.812	t = -2.449
	p = 0.000	p = 0.417	p = 0.015
RecordingCS20_20200305_182937_338	**326.006+**	-22.685	**-1298.825*** **
	[-15.109, 667.121]	[-168.833, 123.462]	[-1938.340, -659.309]
	s.e. = 173.325	s.e. = 74.474	s.e. = 325.455

	t = 1.881	t = -0.305	t = -3.991
	p = 0.061	p = 0.761	p = 0.000
Time5__s_ × Recording2021-03-05-00-00-04	-0.230	4.076	**32.174*** **
	[-19.451, 18.991]	[-4.802, 12.953]	[19.889, 44.459]
	s.e. = 9.766	s.e. = 4.524	s.e. = 6.252
	t = -0.024	t = 0.901	t = 5.146
	p = 0.981	p = 0.368	p = 0.000
Time5__s_ × Recording2021-03-17-07-10-42	-13.477	-7.541	**40.583*** **
	[-39.717, 12.762]	[-24.936, 9.854]	[20.020, 61.147]
	s.e. = 13.333	s.e. = 8.864	s.e. = 10.465
	t = -1.011	t = -0.851	t = 3.878
	p = 0.313	p = 0.395	p = 0.000
Time5__s_ × Recording2021-03-25-08-00-05	4.967	**14.141* **	**44.635*** **
	[-15.573, 25.508]	[2.901, 25.381]	[32.629, 56.641]
	s.e. = 10.437	s.e. = 5.728	s.e. = 6.110
	t = 0.476	t = 2.469	t = 7.305
	p = 0.634	p = 0.014	p = 0.000
Time5__s_ × Recording2021-03-30-09-00-04	-3.425	6.102	**40.496*** **
	[-23.989, 17.138]	[-1.471, 13.674]	[29.215, 51.778]
	s.e. = 10.449	s.e. = 3.859	s.e. = 5.741
	t = -0.328	t = 1.581	t = 7.053
	p = 0.743	p = 0.114	p = 0.000
Time5__s_ × RecordingCS20_20200210_000404_634	0.394	6.925	
	[-21.331, 22.119]	[-13.881, 27.731]	
	s.e. = 11.039	s.e. = 10.602	
	t = 0.036	t = 0.653	
	p = 0.972	p = 0.514	
Time5__s_ × RecordingCS20_20200216_174516_791	**-33.638** **	-6.410	**44.058*** **
	[-55.200, -12.077]	[-14.585, 1.764]	[24.254, 63.861]
	s.e. = 10.956	s.e. = 4.166	s.e. = 10.078
	t = -3.070	t = -1.539	t = 4.372
	p = 0.002	p = 0.124	p = 0.000
Time5__s_ × RecordingCS20_20200305_182937_338	-2.283	3.907	**73.984*** **
	[-23.847, 19.281]	[-4.388, 12.202]	[46.286, 101.681]
	s.e. = 10.957	s.e. = 4.227	s.e. = 14.095
	t = -0.208	t = 0.924	t = 5.249
	p = 0.835	p = 0.356	p = 0.000
Num.Obs.	310	990	487
R2	0.549	0.049	0.339

+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001

Frequency Ratio within recording

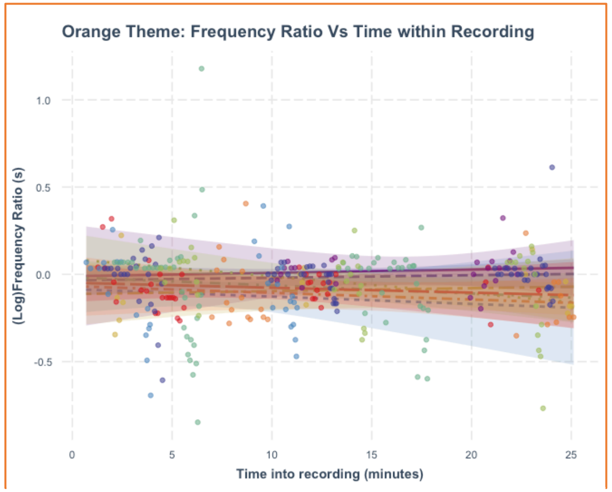


Figure A4.77: All individuals did not show any change in the frequency trend of their moan units in the orange theme across their song sessions.

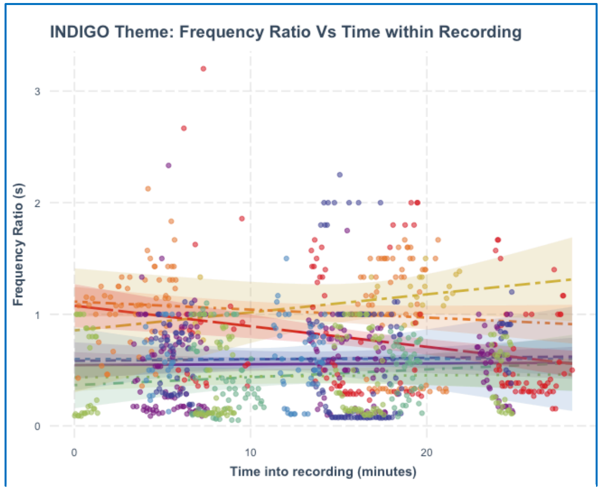


Figure A4.78: All individuals except ID 050320 showed no significant change in the frequency ratio of their moan unit in the indigo theme. ID 050320 displayed a decrease in frequency ratio.

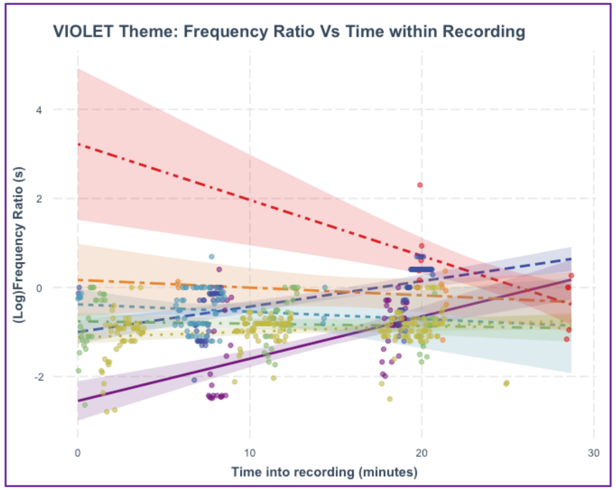


Figure A4.79: There was variation in frequency trend change across individuals. Two individuals increased frequency ratio while two individuals decreased frequency ratio, the remaining individuals showed no significant change in frequency ratio.

ID	ORANGE	INDIGO	VIOLET	Individual across theme change
270221	NSC	NSC	Increase	Yes
050321	NSC	NSC	Increase	Yes
170321	NSC	NSC	Decrease	Yes
250321	NSC	NSC	NSC	No
300321	NSC	NSC	NSC	No
100220	NSC	NSC	ND	No
160220	NSC	NSC	NSC	No
050320	NSC	Decrease	Decrease	Yes

Frequency Trend Within Recording Across Individuals

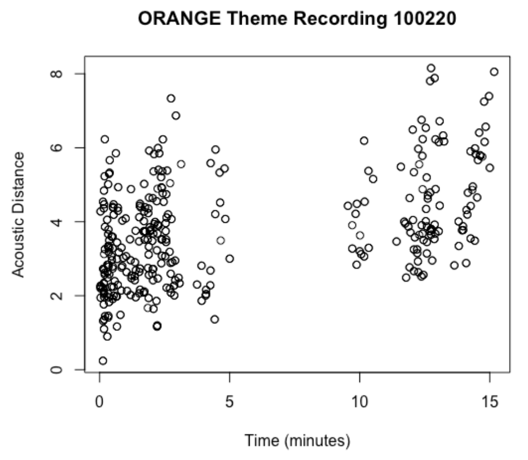
	ORANGE	INDIGO	VIOLET
(Intercept)	-0.011	0.545***	-2.549***
	[-0.305, 0.284]	[0.429, 0.661]	[-2.990, -2.107]
	s.e. = 0.149	s.e. = 0.059	s.e. = 0.225
	t = -0.071	t = 9.238	t = -11.346
	p = 0.943	p = 0.000	p = 0.000
Time5__s_	0.002	0.001	**0.095*** **
	[-0.015, 0.019]	[-0.007, 0.009]	[0.066, 0.124]
	s.e. = 0.008	s.e. = 0.004	s.e. = 0.015
	t = 0.225	t = 0.170	t = 6.393
	p = 0.822	p = 0.865	p = 0.000
Recording2021-03-05-00-00-04	-0.023	0.039	**1.547*** **
	[-0.331, 0.284]	[-0.163, 0.240]	[1.035, 2.060]
	s.e. = 0.156	s.e. = 0.103	s.e. = 0.261
	t = -0.150	t = 0.376	t = 5.930
	p = 0.881	p = 0.707	p = 0.000
Recording2021-03-17-07-10-42	-0.074	0.054	**2.170*** **
	[-0.399, 0.251]	[-0.249, 0.357]	[1.604, 2.735]
	s.e. = 0.165	s.e. = 0.155	s.e. = 0.288
	t = -0.449	t = 0.348	t = 7.540
	p = 0.654	p = 0.728	p = 0.000
Recording2021-03-25-08-00-05	-0.006	-0.180	**1.789*** **
	[-0.317, 0.305]	[-0.417, 0.058]	[1.306, 2.271]
	s.e. = 0.158	s.e. = 0.121	s.e. = 0.246
	t = -0.038	t = -1.486	t = 7.281
	p = 0.970	p = 0.138	p = 0.000
Recording2021-03-30-09-00-04	0.098	-0.111	**1.426*** **
	[-0.231, 0.426]	[-0.279, 0.057]	[0.962, 1.891]
	s.e. = 0.167	s.e. = 0.086	s.e. = 0.237
	t = 0.584	t = -1.294	t = 6.029
	p = 0.560	p = 0.196	p = 0.000
RecordingCS20_20200210_000404_634	-0.102	0.310	
	[-0.447, 0.244]	[-0.258, 0.878]	
	s.e. = 0.176	s.e. = 0.289	
	t = -0.580	t = 1.072	
	p = 0.562	p = 0.284	
RecordingCS20_20200216_174516_791	-0.057	**0.568*** **	**2.718*** **
	[-0.398, 0.285]	[0.392, 0.744]	[1.792, 3.643]
	s.e. = 0.173	s.e. = 0.090	s.e. = 0.471
	t = -0.326	t = 6.345	t = 5.771
	p = 0.744	p = 0.000	p = 0.000
RecordingCS20_20200305_182937_338	-0.037	**0.531*** **	**5.771*** **
	[-0.351, 0.277]	[0.307, 0.756]	[4.013, 7.529]

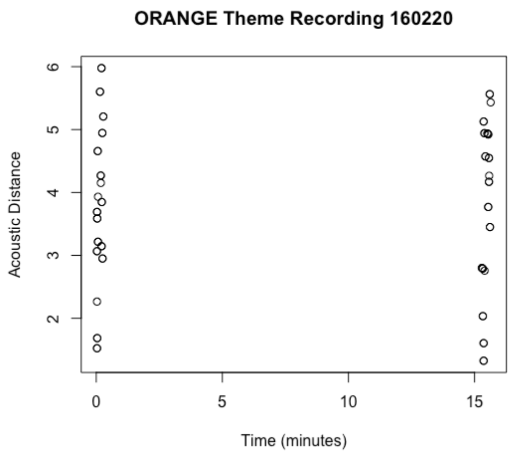
	s.e. = 0.160	s.e. = 0.115	s.e. = 0.895
	t = -0.234	t = 4.638	t = 6.451
	p = 0.815	p = 0.000	p = 0.000
Time5__s_ × Recording2021-03-05-00-00-04	0.000	0.001	**-0.038***
	[-0.018, 0.017]	[-0.013, 0.014]	[-0.071, -0.004]
	s.e. = 0.009	s.e. = 0.007	s.e. = 0.017
	t = -0.052	t = 0.082	t = -2.194
	p = 0.958	p = 0.935	p = 0.029
Time5__s_ × Recording2021-03-17-07-10-42	-0.006	-0.001	**-0.112*****
	[-0.030, 0.018]	[-0.027, 0.026]	[-0.168, -0.055]
	s.e. = 0.012	s.e. = 0.014	s.e. = 0.029
	t = -0.500	t = -0.046	t = -3.878
	p = 0.617	p = 0.963	p = 0.000
Time5__s_ × Recording2021-03-25-08-00-05	-0.007	0.006	**-0.100*****
	[-0.025, 0.012]	[-0.011, 0.024]	[-0.133, -0.067]
	s.e. = 0.010	s.e. = 0.009	s.e. = 0.017
	t = -0.683	t = 0.716	t = -5.971
	p = 0.495	p = 0.474	p = 0.000
Time5__s_ × Recording2021-03-30-09-00-04	-0.012	0.000	**-0.082*****
	[-0.031, 0.007]	[-0.011, 0.012]	[-0.113, -0.051]
	s.e. = 0.010	s.e. = 0.006	s.e. = 0.016
	t = -1.218	t = 0.036	t = -5.201
	p = 0.224	p = 0.971	p = 0.000
Time5__s_ × RecordingCS20_20200210_000404_634	0.000	0.015	
	[-0.020, 0.020]	[-0.017, 0.047]	
	s.e. = 0.010	s.e. = 0.016	
	t = -0.023	t = 0.948	
	p = 0.981	p = 0.343	
Time5__s_ × RecordingCS20_20200216_174516_791	-0.006	-0.008	**-0.112*****
	[-0.026, 0.014]	[-0.020, 0.005]	[-0.167, -0.058]
	s.e. = 0.010	s.e. = 0.006	s.e. = 0.028
	t = -0.570	t = -1.225	t = -4.050
	p = 0.569	p = 0.221	p = 0.000
Time5__s_ × RecordingCS20_20200305_182937_338	-0.005	**-0.019****	**-0.221*****
	[-0.025, 0.015]	[-0.032, -0.006]	[-0.297, -0.144]
	s.e. = 0.010	s.e. = 0.007	s.e. = 0.039
	t = -0.471	t = -2.939	t = -5.694
	p = 0.638	p = 0.003	p = 0.000
Num.Obs.	310	990	487
R2	0.062	0.201	0.423
+ p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001			

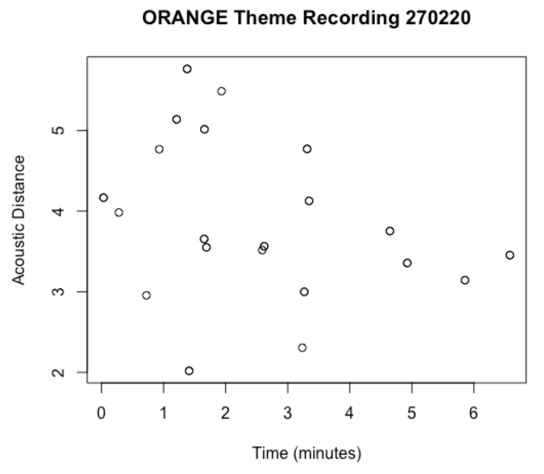
Appendix 4.12 – Euclidean Distance – Individual and Theme split

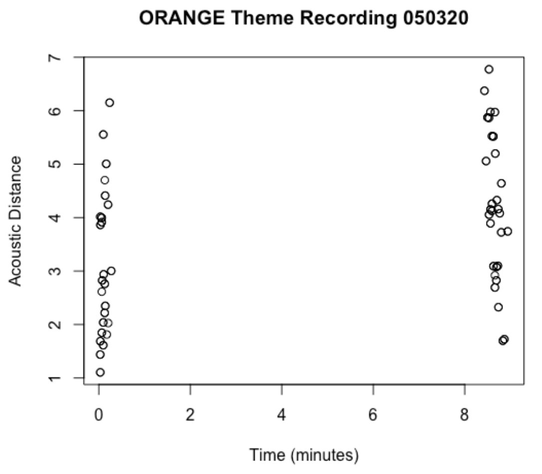
	Mantel	Sig	Mantel	Sig	Mantel	Sig
	Orange		Indigo		Violet	
100220	**-0.01448**	0.576	**0.4498**	0.001	**ND**	ND
160220	0.06115	0.1	**0.2692**	0.001	0.01332	0.419
270220	**0.9552**	0.008	-0.3103	0.984	ND	ND
050320	**0.01929**	0.21	**0.1637**	0.001	**0.3639**	0.001
270221	0.06475	0.046	**0.0877**	0.001	**0.3508**	0.001
050321	0.0157	0.152	**0.07661**	0.001	**0.5722**	0.001
170321	0.08763	0.006	**-0.09126**	1	**0.431**	0.001
250321	0.009236	0.263	**0.1987**	0.001	**0.08174**	0.001
300321	0.04357	0.05	**0.07896**	0.001	**0.2031**	0.001

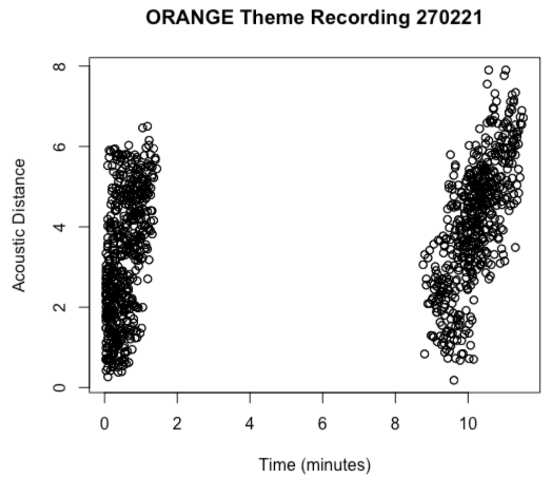
Appendix 4.13 – Individual Mantel Tests Plots

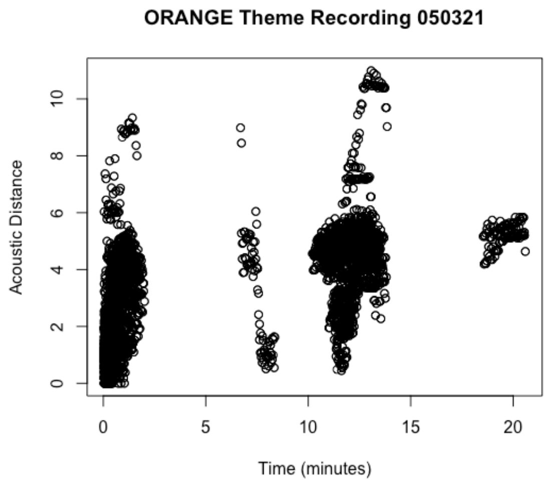

ORANGE Theme Recording 100220

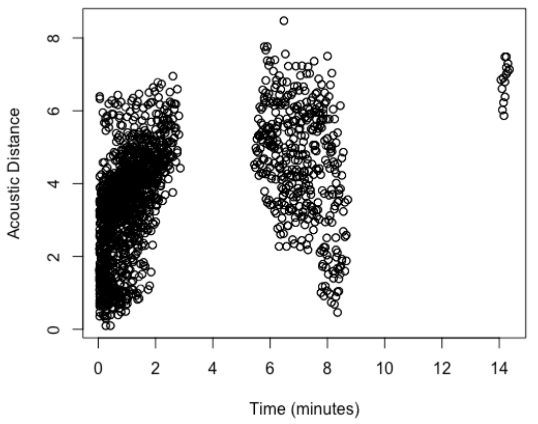

ORANGE Theme Recording 160220

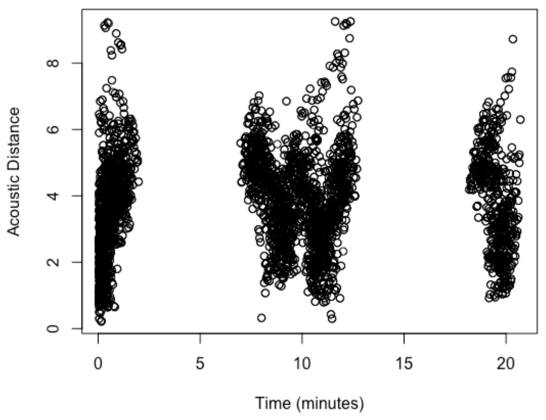

ORANGE Theme Recording 270220

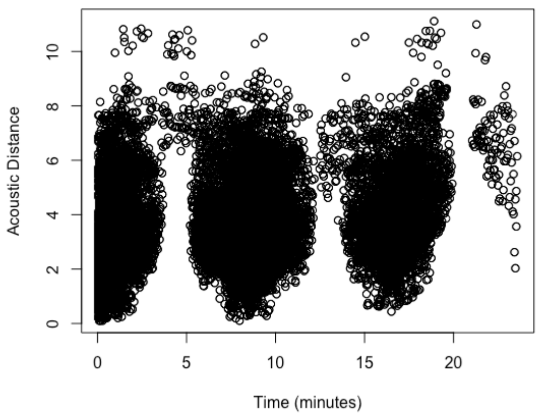

ORANGE Theme Recording 050320

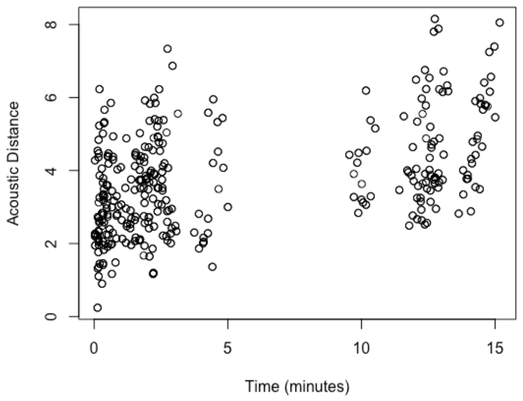

ORANGE Theme Recording 270221

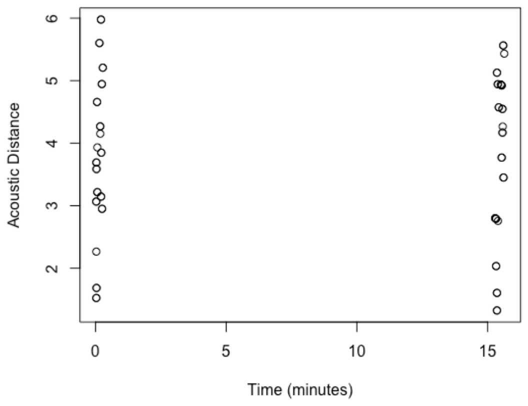

ORANGE Theme Recording 050321

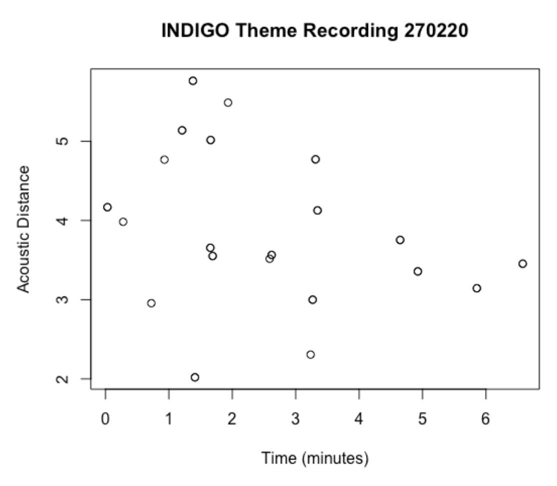

ORANGE Theme Recording 170321

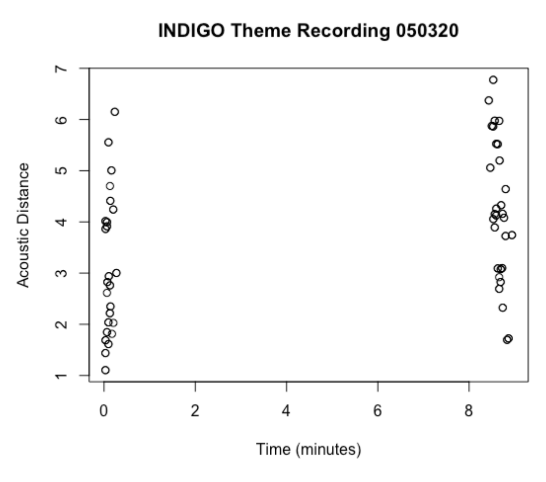

ORANGE Theme Recording 250321

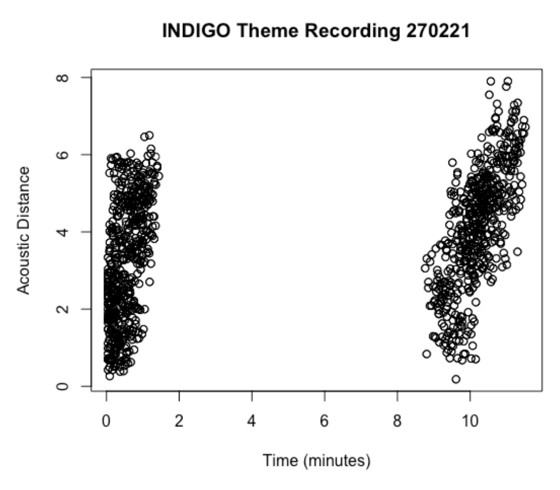

ORANGE Theme Recording 300321

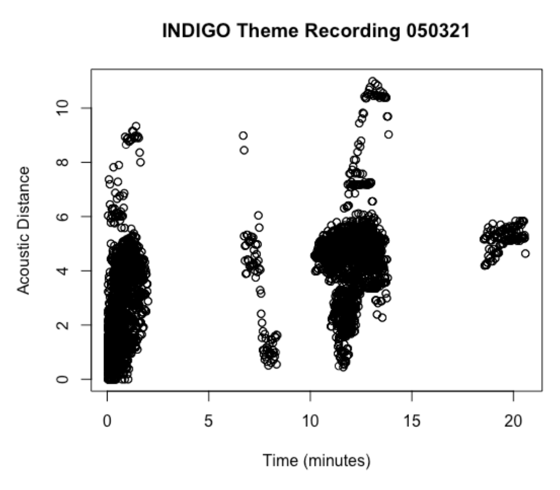

INDIGO Theme Recording 100220

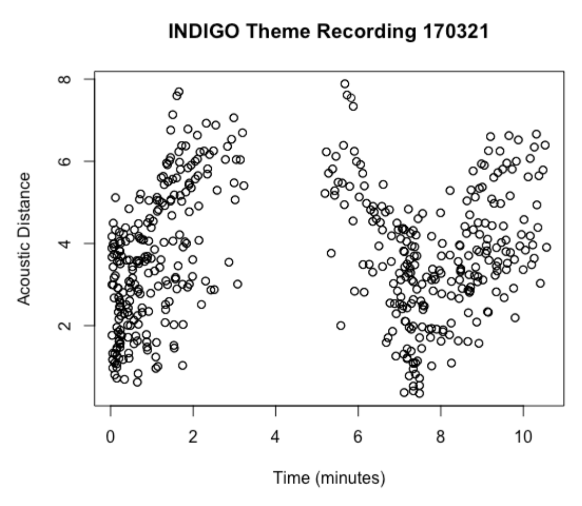

INDIGO Theme Recording 160220


INDIGO Theme Recording 270220


INDIGO Theme Recording 050320


INDIGO Theme Recording 270221


INDIGO Theme Recording 050321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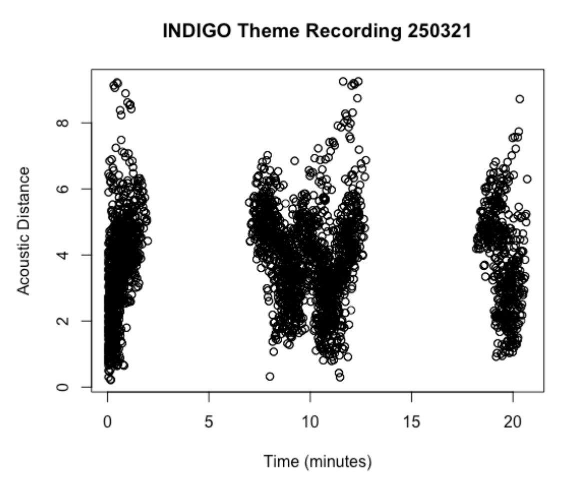
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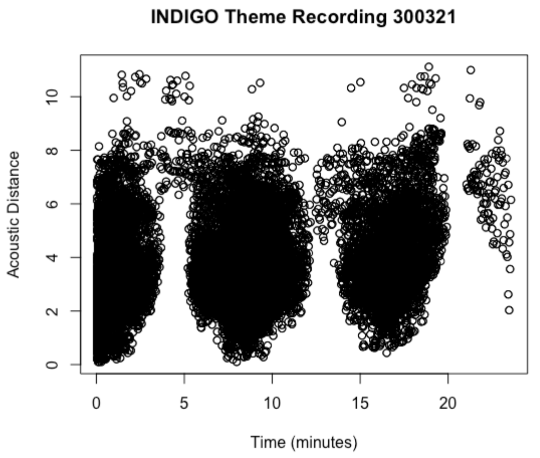

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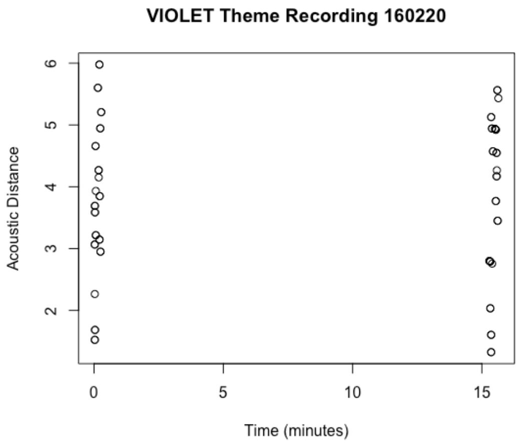

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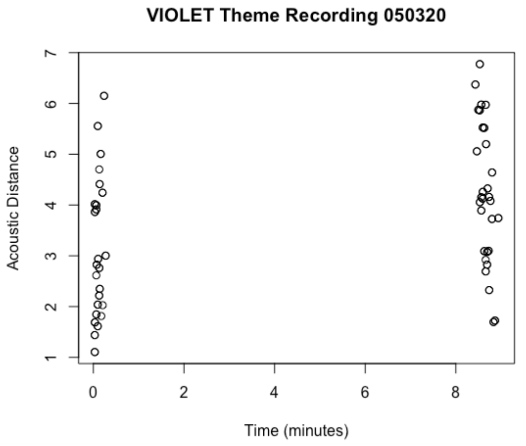

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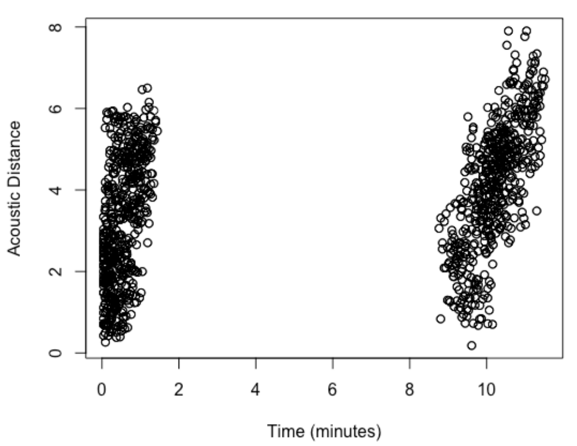

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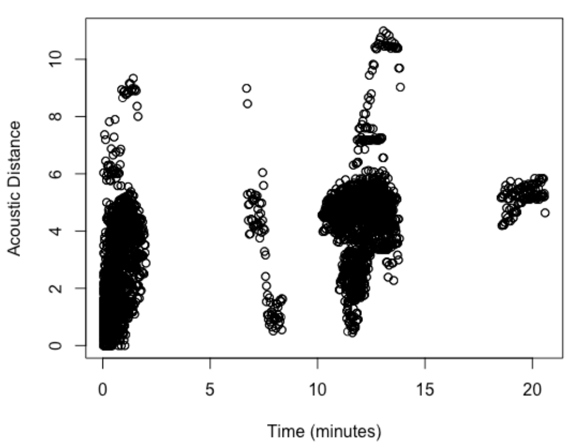

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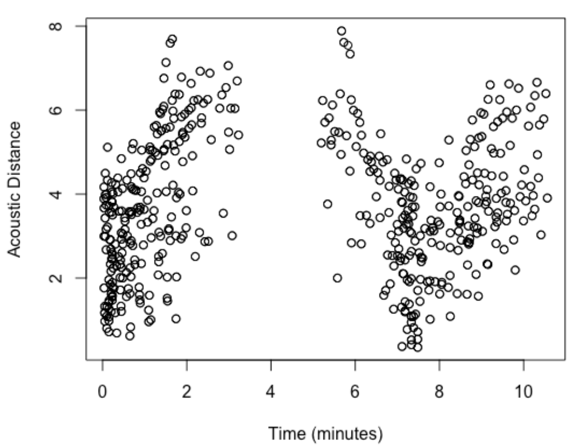

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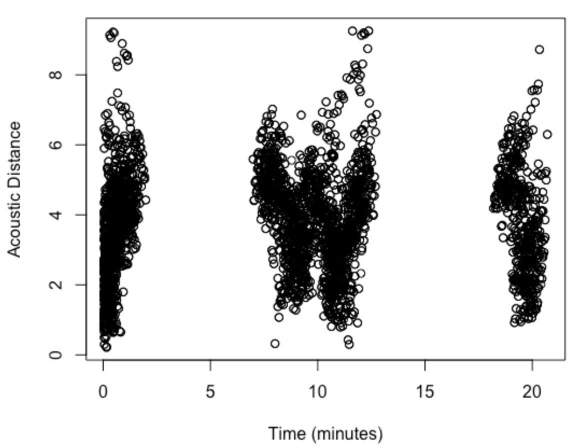

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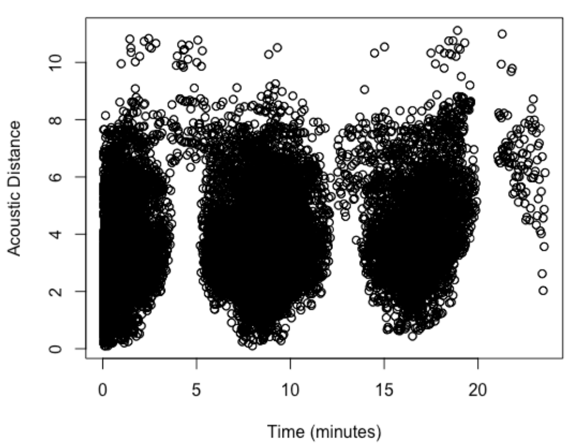

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Appendix 4.14a – Summary measurements (Freq 95, Peak Freq, Freq 5, BW90) of original units

Unit	N	Freq 95 (Hz)		Peak Frequency (Hz)		Freq5 (Hz)		BW90	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd
am	11	485.80	56.53	369.32	45.97	306.82	41.50	178.98	31.53
asqb	2	703.12	22.10	656.25	0.00	593.75	44.19	109.38	22.10
ba	48	2729.49	910.55	1361.33	825.54	594.73	299.78	2134.77	702.62
bA	282	442.93	260.83	238.09	95.65	141.73	47.09	301.20	254.64
bC	116	1774.52	775.98	548.90	529.54	256.20	184.89	1518.32	676.82
bD	205	609.91	205.44	247.26	115.38	122.41	46.57	487.50	198.15
cr	27	3942.71	873.70	2380.21	519.60	980.90	399.22	2961.81	762.85
d	106	4747.64	1139.85	2747.94	1002.61	1056.01	420.47	3691.63	830.65
dws	34	3253.22	798.71	2291.36	488.11	1883.27	480.23	1369.94	753.17
h-bC	162	1011.00	656.92	348.48	300.30	199.85	64.30	811.15	644.79
m	378	389.14	110.20	307.33	96.01	245.78	79.00	143.35	73.87
mm	4	531.25	36.08	453.12	31.25	382.81	15.62	148.44	29.92
mod-sqb	5	718.75	79.67	650.00	80.89	606.25	71.94	112.50	41.93
modws	284	3881.44	1124.14	2839.57	1032.84	2082.31	857.77	1799.13	1088.94
n-ws	1	3468.75		3281.25		3046.88		421.88	
sqb	305	994.93	362.17	866.60	314.70	734.32	269.94	260.60	188.46
sqb-sqb	3	666.67	18.04	541.67	18.04	510.42	18.04	156.25	31.25
t	595	768.88	166.41	469.51	223.80	229.18	134.78	539.71	218.56
t-sp	10	703.12	51.56	356.25	180.54	234.38	149.69	468.75	190.94
tsp	4	742.19	15.62	562.50	292.04	203.12	90.21	539.06	100.05
tt	1	656.25		609.38		375.00		281.25	

u-ws	4	2832.03	1782.50	2414.06	1409.69	2082.03	1254.12	750.00	697.37
usqb	12	679.69	147.26	528.65	149.85	466.15	160.71	213.54	47.74
uws	403	2288.07	1391.52	1752.25	916.18	1487.05	775.41	801.02	782.49
vws	1	1375.00		1312.50		1187.50		187.50	
ws	11	1781.25	792.79	1600.85	675.95	1521.31	670.47	259.94	170.77

Appendix 4.14b – Summary measurements (Duration90, Start Frequency, End Frequency, Freq Trend) of original units

Unit	N	Duration90 (s)		Start Frequency (Hz)		End Frequency (Hz)		Frequency Trend	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd
am	11	0.71	0.21	298.30	47.11	443.18	73.71	0.68	0.09
asqb	2	0.42	0.15	578.12	66.29	687.50	44.19	0.84	0.04
ba	48	0.72	0.15	1381.84	725.54	1443.36	910.38	1.30	1.13
bA	282	0.72	0.21	145.22	137.79	237.31	120.09	0.74	0.70
bC	116	0.38	0.25	705.68	695.49	541.35	584.85	1.81	1.92
bD	205	0.43	0.13	120.88	106.43	383.99	298.42	0.42	0.25
cr	27	1.37	0.30	2453.12	755.28	2032.99	813.16	2.08	3.06
d	106	0.78	0.11	1802.48	764.51	2070.02	882.99	1.20	1.84
dws	34	0.48	0.23	2420.04	697.56	2303.77	659.38	1.08	0.26
h-bC	162	0.47	0.17	583.91	557.71	270.64	227.97	2.65	3.01
m	378	0.68	0.24	257.48	113.00	286.09	124.60	0.96	0.35
mm	4	1.34	0.15	382.81	15.62	492.19	29.92	0.78	0.05
mod-sqb	5	0.41	0.07	637.50	71.94	700.00	92.70	0.91	0.07
modws	284	0.79	0.39	2623.95	1032.01	2504.13	1063.01	1.14	0.52
n-ws	1	0.25		3000.00		3046.88		0.98	
sqb	305	1.38	0.61	829.71	306.34	861.32	314.95	0.97	0.16
sqb-sqb	3	1.26	0.24	614.58	47.74	531.25	0.00	1.16	0.09
t	595	0.53	0.17	236.95	216.00	649.82	256.03	0.45	0.43
t-sp	10	2.04	0.52	221.88	166.31	515.62	176.93	0.52	0.40

tsp	4	1.95	0.33	187.50	119.68	515.62	31.25	0.37	0.26
tt	1	0.25		656.25		609.38		1.08	
u-ws	4	0.29	0.06	2355.47	1496.27	2667.97	1865.75	0.93	0.22
usqb	12	0.65	0.14	471.35	164.53	617.19	169.67	0.75	0.08
uws	403	0.33	0.17	1634.46	922.51	1978.06	1236.12	0.86	0.23
vws	1	0.34		1312.50		1312.50		1.00	
ws	11	0.32	0.22	1671.88	763.07	1632.10	770.40	1.04	0.12

Appendix 4.15

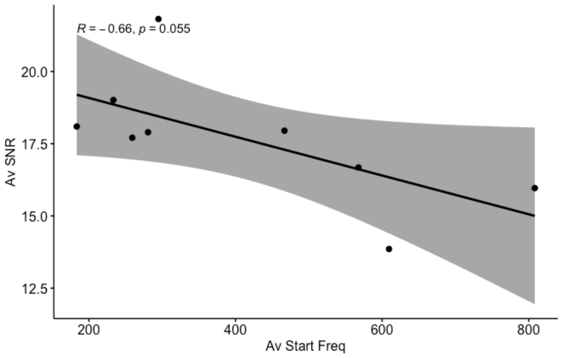


Figure A4.80: Average Start Frequency and average SNR per recording. R = -0.66, p = 0.055. No significant relationship between Start frequency and SNR.

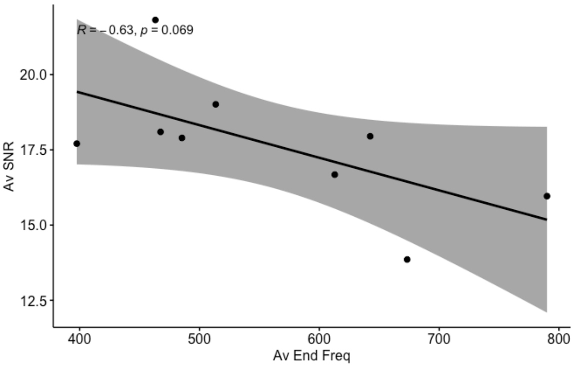


Figure A4.81: Average End Frequency and average SNR per recording. R = -0.63, p = 0.069. No Significant relationship between End Frequency and SNR.

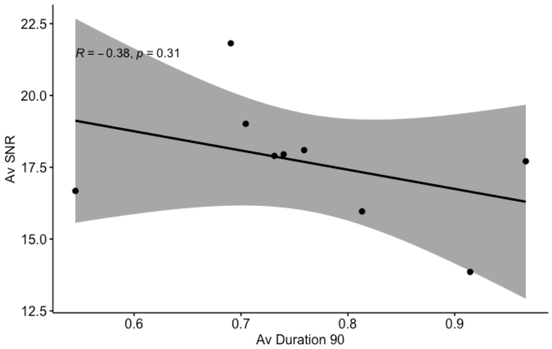


Figure A4.82: Average 'Duration 90' and average SNR per recording. R = -0.38, p = 0.31. No Significant relationship between robust measurement 'Duration 90' and SNR.

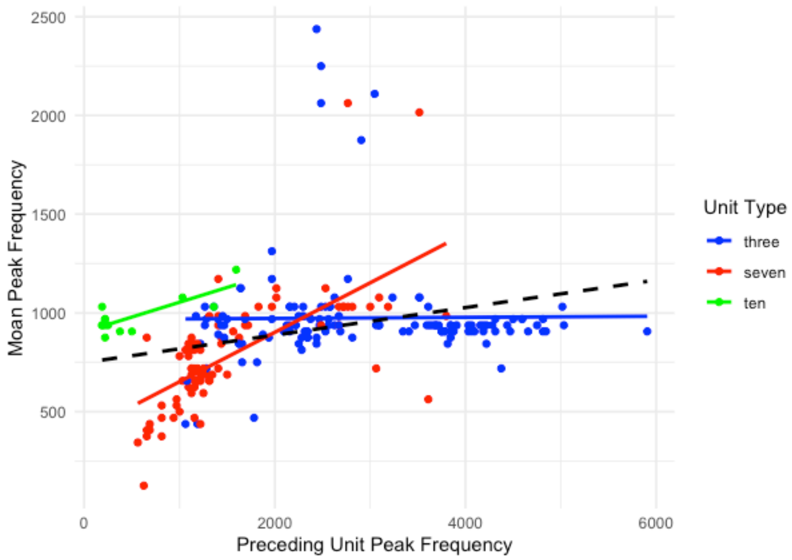


Figure A4.83: To examine potential coarticulation effects, a linear regression model incorporating interactions was employed to explore the association between preceding unit type, preceding peak frequency, and the peak frequency of moan units. The analysis yielded a highly significant model (F-statistic = 16.87, p < 0.001), explaining 27.81% of the variance in moan peak frequency. Notably, the preceding unit 'seven' exhibited a significant positive effect on PeakFreq_Hz (p < 0.001), while the preceding unit 'ten' had no significant impact (p = 0.588). Significant interaction effects between preceding peak frequency and unit types (seven and ten compared to three) were observed, indicating that the relationship between preceding peak frequency and moan peak frequency varies depending on the preceding unit type. However, the relationship between preceding peak frequency alone and moan peak frequency was not statistically significant (p = 0.887).

Model Summary Table:

Term	Estimate	Std.Error	Statistic	P-Value
(Intercept)	972.82353	24.6941876	39.3948383	2.29E-101
preceding_peak_frequency	0.00272499	0.01922421	0.14174803	0.88740934
preceding_unit_typeseven	-5.7922053	44.0924936	-0.1313649	0.89560727
preceding_unit_typeten	270.11527	260.879633	1.03540191	0.3016232
preceding_peak_frequency:preceding_unit_typeseven	0.24778202	0.03969109	6.24276139	2.20E-09
preceding_peak_frequency:preceding_unit_typeten	0.14723104	0.14407807	1.02188374	0.30796342

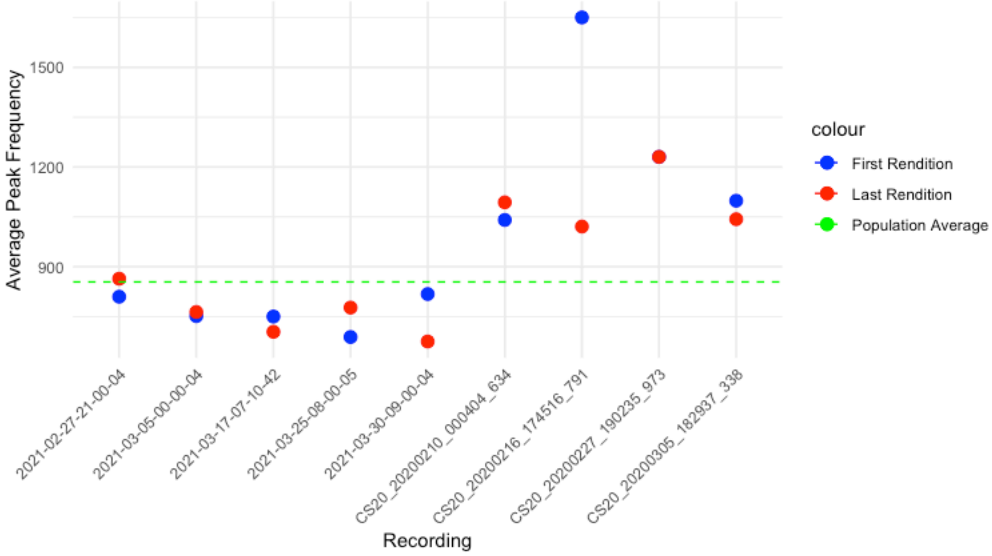


Figure A4.84: In the paired t-test conducted to investigate possible exhaustion effects on the differences between the "First Rendition" and "Last Rendition" values and the "Overall Population Average," a t-statistic of 0.86681 with 8 degrees of freedom was obtained. The resulting p-value was 0.4113, indicating that there is no significant difference in means between these two sets of differences. The 95 percent confidence interval (-106.7641, 235.3702) further supports this conclusion. Therefore, there is not sufficient evidence to reject the null hypothesis, suggesting that the true difference in means is not significantly different from zero. The sample estimates indicate a mean difference of 64.Hz, which is consistent with the findings of no significant difference.

5 Chapter 5: Bridging the Gap: Utilising Science Centre Exhibitions for Public Engagement in Low Science Capital Communities

Abstract:

In a world faced with complex challenges, such as climate change and public health crises, the importance of delivering impactful science has gained recognition in the United Kingdom. The ability to translate intricate scientific knowledge into tangible outcomes that benefit society is now considered a cornerstone of modern scientific endeavours. To this end, science centres and exhibitions have emerged as dynamic and interactive channels for public engagement with science. These centres offer hands-on, interactive experiences that bridge the gap between the scientific community and the public. This chapter explores a public engagement case study that focuses on utilising science centre exhibitions to communicate scientific research to the public, with a particular emphasis on individuals from low science capital locations. The case study examines the development, implementation, and impact of the exhibition "Sea Symphonies: Whale Songs of the South Pacific" at Dundee Science Centre. The exhibition aimed to engage the public with humpback whale research through interactive exhibits. The Sea Symphonies exhibition achieved most of the original objectives during the design and implementation phases and received highly positive visitor feedback. The study documented short-term changes in participants' learning. Many visitor responses indicated references to 'song' or 'sound,' and a majority of participants grasped the learning outcome that "whales sing songs," with even more understanding that "whales make sounds." The study also highlighted the importance of adaptable approaches and the role of evaluation in public engagement initiatives. It underscored the need to continuously assess the impact and outcomes of such initiatives to better serve the diverse needs and interests of the audience. In summary, the Sea Symphonies exhibition provides valuable insights into equitable science communication and public engagement, emphasising the significance of adaptability and short-term impacts in these endeavours.

5.1 Introduction

In the United Kingdom, there is a growing recognition of the importance of delivering impactful science (Illingworth *et al*., 2015). As the world faces complex challenges, ranging from the urgent need to address climate change to the management of public health crises, the need for scientific advancements and their effective communication becomes increasingly crucial. The ability to translate intricate scientific knowledge into tangible outcomes that benefit society is now a cornerstone of modern scientific endeavours. This realisation has spurred a heightened emphasis on the significance of science communication and public engagement in driving meaningful impact (Illingworth *et al*., 2015).

Science communication practitioners regularly use the terms 'science communication' and 'public engagement' interchangeably, as well as the terms 'informal science learning' and 'education outreach' (Illingworth *et al*., 2015). Traditionally, science communication was seen as a way of educating those who were deemed to 'not know something' (Illingworth *et al*., 2015). This is now called the 'deficit model' in which individuals outside of the academic sphere were deemed to be (Illingworth *et al*., 2015). Science communication was viewed as a one-way process in which information is disseminated, such as in documentaries, books, magazines, or traditional public lectures in which information is packaged in a top-down format. Now, there is better understanding that public engagement with science should be a two-way process with all parties benefiting from the process (NCCPE, 2020). The National Coordinating Centre for Public Engagement (NCCPE) defines public engagement as "the myriad of ways in which the activity and benefits of higher education and research can be shared with the public. Engagement is by definition a two-way process, involving interaction and listening, with the goal of generating mutual benefit" (NCCPE, 2020).

Public engagement with science is important both for those aiming to communicate their science and those members of the public they hope to engage. Within the academic environment, the National Coordinating Centre for Public Engagement lists five main arguments for why public engagement is important to universities. These are accountability, values and purpose, trust, relevance and responsiveness (NCCPE, 2020). A key extrinsic motivator driver in researchers participating in public engagement are requirements from international funding and policy bodies (Palmer & Schibeci, 2014). This is particularly relevant as most universities are publicly funded and therefore scientists have a responsibility to share their results with the public. However, research has shown that, while participation in public engagement is often seen as rewarding by scientists, there are also profound challenges to participation by different academic groups (Davies *et al*., 2013). Many scientists view these events as voluntary work which is additional to their main academic responsibilities (Bauer & Jensen, 2011). On the other hand, many researchers cite a moral responsibility attached to public engagement (TNS, 2015).

Another crucial reason is that science and innovation are at the forefront of economic growth in the UK (House of Commons, 2018). The Scottish Government cite their main reason for funding science engagement opportunities is to encourage more people to pursue careers in science (Government, 2023). For example, the Scottish Government invested over £3 million into delivering public engagement experiences for more than one million people in 2021 - 2022 with the aim of encouraging more people in Scotland to study and pursue careers in STEM (Government, 2023). Most of this money goes to science centres across the country with smaller amounts going to science festivals and directly to school initiatives. Furthermore, recruitment to science professions is a current concern as the impact of leaving the European Union may make the UK more sensitive to changes in the availability of STEM skills (National Audit Office, 2018; Parliament, 2017; Osborne and Dillon 2008).

In this context, science centres and exhibitions have taken centre stage as dynamic and interactive channels for public engagement with science. These centres offer a unique platform where science comes to life, and exhibitions play a pivotal role in this endeavour. Science exhibitions provide hands-on, interactive experiences that engage visitors in ways that traditional science communication formats often cannot. The design and implementation of these exhibitions are crucial to bridge the gap between the scientific community and the public.

As described above, public engagement activities in science are motivated by key objectives in their audience such as improvement of scientific literacy and need to be evaluated accordingly. In our pursuit of enhancing science accessibility for everyone, it is essential to acknowledge the concept of science capital, which encompasses an individual's science-related knowledge, experiences, family influence, attitudes, and behaviours (Canovan, 2019). Recognising science capital as a measure becomes imperative as we work towards making science an inclusive domain for all individuals. It is important that any impact of science engagement activities are captured, from knowledge gain to behaviour change as a result of the event (Spicer, 2017). This is particularly important in science relating to biodiversity and the natural world as the world seeks to have more active community members to help combat the climate crisis (Carleton-Hug & Hug, 2010). Aligning with the generic learning outcomes outlined by Arts Council England can provide a structured framework for evaluating the broader impacts of these science engagement activities, encompassing knowledge and understanding alongside attitudes, enjoyment, skills, and behaviour (Figure 5.1).

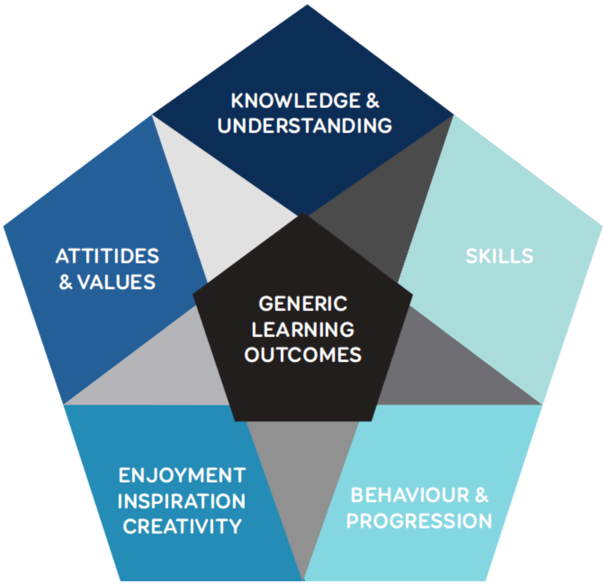


Figure 5.1: Generic Learning Outcomes from Arts Council England. The Generic Learning Outcomes model (GLOs) was developed as a tool for museums, libraries and archives to demonstrate the outcomes and impact of users' learning experiences

5.1.1 Aims

This chapter presents a public engagement case study with a specific focus on utilising science centre exhibitions as a means to communicate scientific research to the public. The central objective of this case study exhibit was to engage participants in informal science learning by transforming existing materials within science centres and embedding evaluation within the design. The audience for this particular case study consists of individuals from low science capital locations, who typically have limited access to science learning opportunities in informal settings. The chapter will provide an in-depth examination of the science centre exhibition case study, starting from its development and proceeding through to its impact, before culminating in a discussion of the findings.

The exhibition “Sea Symphonies: Whale Songs of the South Pacific” at Dundee Science Centre (DSC) was designed to engage people from Dundee and neighbouring areas with whale research that was being conducted at the University of St Andrews. Dundee Science Centre annually engages over 65,000 people from communities within Dundee and Fife. Dundee Science Centre has a range of interactive science exhibits over several floors and provides live workshops and events to a diversity of public groups including residents from across Dundee, Fife, Angus and Perth & Kinross, plus tourists visiting from further afield. DSC work with individuals and community groups living in areas of high socio-economic deprivation, out of employment/education or at risk of exclusion, and/or with assisted needs. As well as tailored programmes, they also offer subsidised visits and transport to help reduce financial barriers to the centre. This made DSC an ideal place to engage people from a diversity of backgrounds. Furthermore, Dundee has a long history with whales which began with whaling in the 1700’s and continued until just before the First World War. At the peak of the whaling industry nearly 20 whaling ships sailed from Dundee. At the time, whale oil was needed for many things, including Dundee’s jute factories. Today, both the Universities of Dundee and nearby St Andrews produce world renowned research into the lives of whales. This exhibition provides the perfect opportunity to update Dundee’s connection with whales through research into humpback whales.

The overall aims of Sea Symphonies were to engage the public with humpback whale research, including song, individual identification, and evolutionary history through a series of interactive exhibits housed within the Dundee Science Centre and more specifically to:

- Reach children of primary school age in Dundee and beyond including those living in low SES locations
- Engage school age children in humpback whale song research
- Create an interface for members of the community to connect with scientists
- Repurpose equipment within the Dundee Science Centre space to communicate whale song research
- Share knowledge about humpback whale research including about humpback whale song, identification, and evolution
- Facilitate a fun and interactive learning experience

The key indicators of these aims can be found in section 5.2.2. Evaluation.

5.2 Sea Symphonies Exhibition: Development and Outputs

I was part of a team that delivered a major science engagement exhibition with associated activities, about research on humpback whale song, in the Dundee Science Centre (DSC) opening September 28 2019 named ‘Sea Symphonies: Whale songs of the South Pacific’. A complete logic model for this exhibition can be found at Table 5.2.1. The exhibition comprised eight stations spread out in one large (approx. 60 m^2) corner on the ground floor of Dundee Science Centre (Figure 5.2.1). On arrival at the exhibition space, participants were given a ‘Whale Passport’ (Figure 5.2.2) which opened to reveal a map (Figure 5.2.3) to allow navigation between the eight stations. I designed this in conjunction with University of St Andrews graphic designer, Steve Smart. The Whale Passport conveyed the appearance of a travel passport and opened to reveal an idealised map of the exhibition space including each of the eight exhibit stations. The exhibit stations on the map appeared as stamps on the ‘Whale Passport’. The passport encouraged participants to attend each of the eight stations (Table 5.2.2) and once each stamp was completed (with ticks added by pens and pencils available around the exhibition space) to hand back to DSC staff at reception to receive the incentive, which was a Sea Symphonies badge to take home (Figure 5.2.4). I designed the Sea Symphonies badges alongside graphic designer Steve Smart. There were four full colour badges to choose from each. Each variation had a different colour and whale song unit type which mirrored the whale song unit graphics at the ‘Copy’ mini exhibit (detailed at Figure 5.2.12). The badge was a small incentive to encourage the participant to complete all eight of the mini exhibits, which included the two evaluation stations as part of the overall exhibition.

Table 5.2.1: Logic model for Sea Symphonies – includes Stages of evaluation planning for the case study Sea Symphonies

Activity/Project	**Sea Symphonies: Whale Songs of the South Pacific (Dundee Science Centre Exhibition)**
Aims & Objectives	• To share knowledge of whales to public audiences outside of St Andrews • Create a user-led interactive exhibition housed within Dundee Science Centre. • Engage visitors to respond to the exhibit via free text postcards • Engage visitors to respond with a posted question on luggage tags • Launch to coincide with University of St Andrews 'Explorathon' 2019 (28th September)
Audiences	• Families (parents and children) attending the Dundee Science Centre • Guides/Boys brigade groups • School classes and teachers (focus on less advantaged schools) • Weekend young adults/adults • Disabled groups • Funders – University, Royal Society • Festival audiences
Inputs (what is required to achieve aims/objectives)	• Funding - University of St Andrews KE - Royal Society – 10 K • Time - Natalie Sinclair – Evaluation lead – Liaison between organisations and people and supporting project manager - Luke Rendell – Project support and obtaining funding - Ellen Garland – Project support and obtaining funding - Steve Smart – Graphic designer - St Andrews PER Team – Evaluation support - Additional PhD students • Organisations - Dundee Science Centre – provision of space and existing exhibits - BIOME – Whale song game creation

		- Ken Boyd/FifeX – Project manager of exhibit revamp and installation - Independent artist - Design of Jigsaw pictures
Activities (what the project does with the resources)		• Creation of eight user-led exhibits within Dundee Science Centre • Creation of clear instructions for each exhibit • Creation of a cohesive exhibition within Dundee Science Centre combining eight exhibits focused on whale research • Revamp existing exhibits to suit whale research focus • Create cohesive signage and branding for the exhibition space • Create evaluation materials (postcards, luggage tags) and corresponding evaluation exhibits integrated into the experience • Create a ‘whale passport’ which guides the participants around the exhibition space and provides an incentive for completing the evaluation stations • Create an incentive for completion – small pin badges with sea symphonies branding
Outputs		• Eight exhibits related to whale research (Research, Evolve, Identify, Play, Innovate, Copy, Communicate, Respond) • Twitter account dedicated Postcards: Questions to a whale scientist
Short-term Outcomes (0-6 months)		• Enjoyable and fun interaction with experiences and information based on whale song • Participants learning that whales sing songs and have their own cultures • Training opportunities (Royal Society public engagement day)
Longer-term Outcomes (6 months +)		• Inclusion of evaluation as chapter in PhD thesis • Evidence of outreach to funders • Increasing of whale culture in research in very broad audiences • Increased awareness and desire for marine conservation • University/School profile raising • Strengthened network for outreach activities across School of Biology
Measurement	Evaluation Questions	• What did participants learn about whales from their experience of the exhibition

	Data collection techniques	• Capture the number and demographics of the public attending the Dundee Science Centre during the exhibition’s lifetime. • Collate exhibition focused data from two main methods: - A ‘whale-spout’ tag wall to record answers to the prompt ‘what did you learn about whales today?’ - A whale post box in which participants could ask a whale scientist a question and document their favourite parts of the exhibition
	Analysis & Interpretation of data	• Group and analyse the tag comments from the respond station – identify key topics and learning outcomes • Group and analyse the questions from the postcards • Analyse the number of DSC visitors and level of engagement with the exhibit via tag and postcard numbers • Draw out key learning points and recommendations for next steps
	Reporting	• Update for funders • Update for Dundee Science Centre • PhD thesis chapter case study
Assumptions		• DSC visitors want to engage with the exhibition • Participants use the Whale Passport and engage with the evaluation materials • A project manager is obtained • The budg*et al*located covers the expenses of the exhibit and associated organisations

5.2.1 Sea Symphonies Exhibits

The eight exhibitions were named as verbs, actions that whales can carry out themselves: Identify, Research, Evolve, Innovate, Play, Copy, Communicate, Respond. Each of the stations within the exhibition are described below.

Table 5.2.2: The eight stations within the Sea Symphonies exhibition space

Sea Symphonies: Songs of the South Pacific		
Exhibit Name	**Description**	**Rationale and learning outcome**
Research	Hear, see and learn about whale song sounds	The format that researchers analyse sounds using visuals too
Evolve	Four-stage body-part jigsaw	How whales evolved from land mammals
Identify	Photographic Identification tutorial	How researchers in the field know humpback individuals
Play	Whale song game developed by BIOME	Cognitive skills to put sequences together
Innovate	Light beam activated sounds	Process of creativity in whale song evolution
Copy	Floor piano with 'whale song sheet music'	Being able to reproduce sequences and conform
Communicate	Send a postcard to a whale scientist with a question	Whales send communication signals to other whales
Respond	Answer a question on a tag and add to the whale spout wall	Whales make sounds in response to another whale's sound

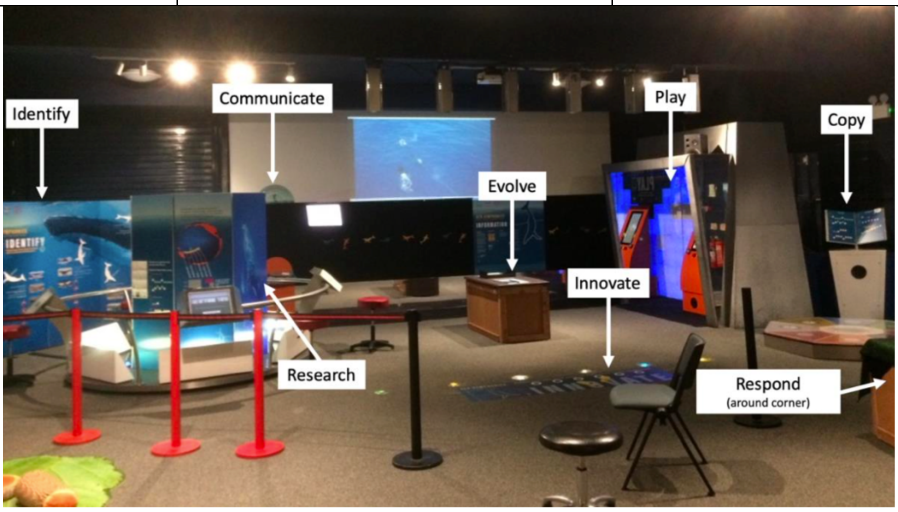


Figure 5.2.1 The Sea Symphonies exhibition space with each of the stations complete and installed. Each of the eight stations are labelled.

Figure 5.2.2: Final version of the 'Whale Passport' outside view. The instructions read: "Complete all stamps and show to staff at the main desk to receive your Sea Symphonies badge!". My preliminary drawings for the whale passport can be found in Appendix 5.1.

Figure 5.2.3 Inside of the final version of the 'Whale Passport' – Participants were given this passport when the entered the DSC and encouraged to return the passport having ticked off each of the whale stamps to collect their whale song stamp.

Figure 5.2.4 Each of the four Sea Symphonies badges that participants could collect on completion of all of the mini exhibitions in the Sea Symphonies exhibition space. Each badge has a different stylised whale song unit visualisation.

Identify

The **Identify** exhibit allowed participants to play a matching game in which photographs of humpback whale tail flukes were matched to one of eight identified individuals (Figures 5.2.5 and 5.2.6). This corner of the exhibit also provided information the life histories of each of the eight individuals. This form of photo-identification is typically used in scientific field research by whale biologists and a great way to let participants experience doing something that scientists would do in the field.

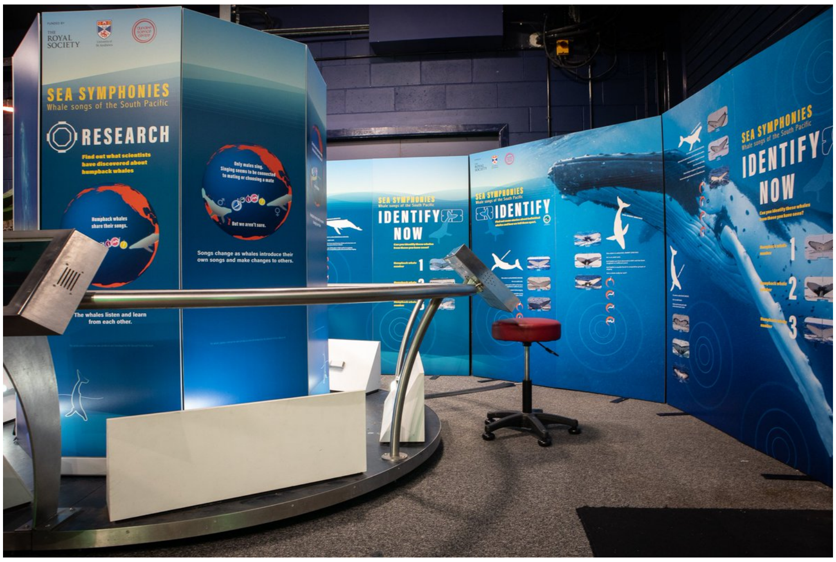


Figure 5.2.5 The Identify station (and part of the Research station). The Identify station included humpback whale tail photographs to show how humpback whales can be identified by their unique markings using photographic identification (Photo ID). This was the original storytelling corner of Dundee Science Centre.

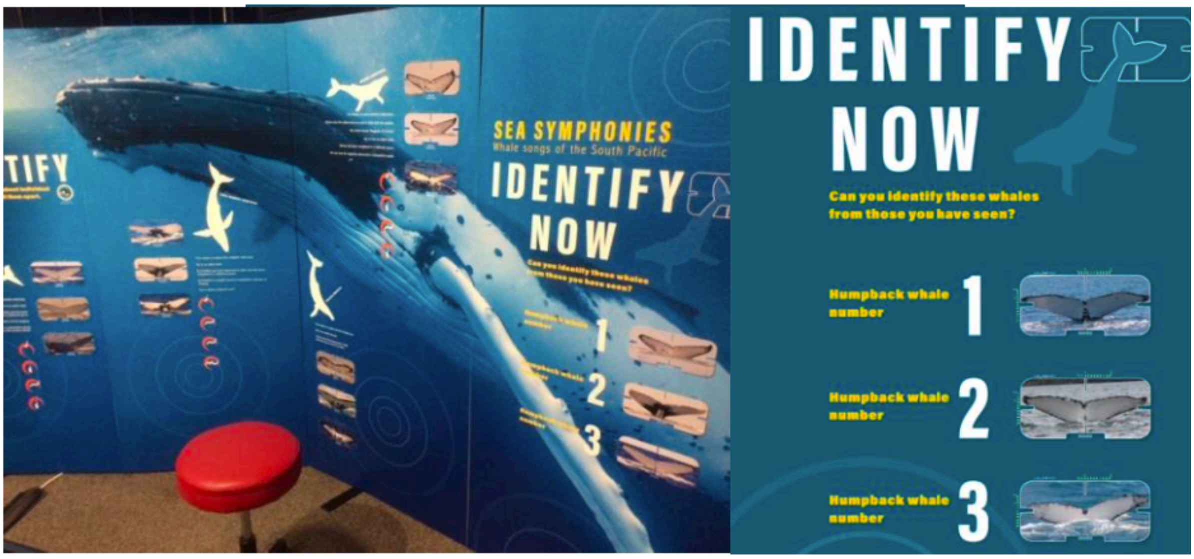


Figure 5.2.6 A close-up of the Identify station. After learning about humpback whale individuals that have been tracked by Photo ID, the participant was asked to identify the correct individual based on three photographs.

Research

The **Research** station repurposed an existing large octagon display with information about whale song research from the South Pacific (Figure 5.2.7: A, B). Four touch screens were also placed around the octagon display which allowed participants to learn more about particular sounds (Figure 5.2.7: C, D).

Figure 5.2.7: Components of the Research station. (A): Information signs showing whale song spectrograms from across the South Pacific (including how these relate to the 'Copy' station). (B): A participant sits at the 'Humpback whale Juke Box'' interactive screen. (C): The interactive touch screen (D): An example of one of the pages within the touchscreen catalogue

Evolve

The **Evolve** Station allowed participants to learn about the evolution of whales, from land mammals to obligate sea mammals, in a four-part jigsaw (Figure 5.2.8). Each of the four stages of evolution was split into four pieces so that the participant could track the development of different body parts such as the head or tail regions. The jigsaw images were painted by Cornelia Oedekoven.

Figure 5.2.8: Photos of the Evolve station in various levels of completion. A: The bottom Pakicetus layer. B: The jigsaw pieces before completion. C: The Basilosaurus layer in process.

Innovate

The **Innovate** station repurposed an existing light beam activated sound game. The light beams were already present within Dundee Science Centre. We simply had to supply high quality sound files to produce the humpback whale song unit sound. Each of the six light beams corresponded to a different whale song unit (Figure 5.2.9). When the light beam was broken but a hand or foot a sound was activated. Participants were invited to create their own song from the six whale song units (Figure 5.2.9).

Figure 5.2.9: The Innovate station installed within the exhibition space.

Play

The ‘Play’ station was video game developed in conjunction with the BIOME Collective (A creative games studio based in Dundee) (Figure 5.2.10: B). The game required players to press the correct coloured buttons when requested on the screen. Each colour denoted a different whale song unit and when correctly matched the player created a whale song and collected points. As the player progressed between levels they were presented with information screens conveying facts about whale songs. As the game was developed, I met with BIOME in Dundee and then carried out two short pilot studies of an early version of the game (Figure 5.2.10: A) in which a class of nine-year olds played the game and provided feedback at Canongate Primary school and at St Andrews University science festival. This feedback was used to enhance the game before the final version in Figure 5.2.10: B was created.

Figure 5.2.10: (A) The prototype version of the BIOME whale song game when being trialled at Explorathon 2019. The 4 buttons reflected different whale song units and the silver dial could manipulate the speed of the game. At this stage the game was called ‘lovely whale song game’. (B) The final version of the BIOME whale song game installed in Dundee Science Centre.

Copy

The **Copy** station repurposed an existing floor piano that was already present in the exhibition space (Figure 5.2.11, and before adaptation photos can be found in Appendix 5.1; Figure A5.3). This provided an excellent opportunity for whale song research. I designed a musical score in which eight whale song units were ascribed to 8 notes on a standard treble clef sheet music. I then chose specific whale song phrases from whale songs collected in French Polynesia and added these to sheet music as if they were notes. I then worked with graphic designer, Steve Smart, to create the final version for use in the exhibit. I supplied the graphic designer with spectrograms of the eight whale song units so that he could create idealised symbols of each whale song unit (Figure 5.2.12). These were used at the **Copy** and **Innovate** stations, as well as on the badges. I used my knowledge of piano music theory to create the sheet music. I chose eight whale song units (gt, ba, am, mm, t, w, aws, ahq) based on their frequency characteristics to pair with eight notes on the treble clef. I then isolated recordings of each of these whale song units from data I was analysing from French Polynesia. Each isolated whale song unit recording was cleaned of background noise, increased in amplitude and soft start and end was applied before passing to the Dundee Science Centre team to be included in the **Copy** station.

Figure 5.2.11: The final version of the floor piano now as the Copy Station within the Sea Symphonies exhibition space. In the image you can see each of the floor piano notes now has a stylised whale song unit on each 'note', the new whale song sheet music is installed and the Copy sign with instructions and logo is present. I am playing some whale song.

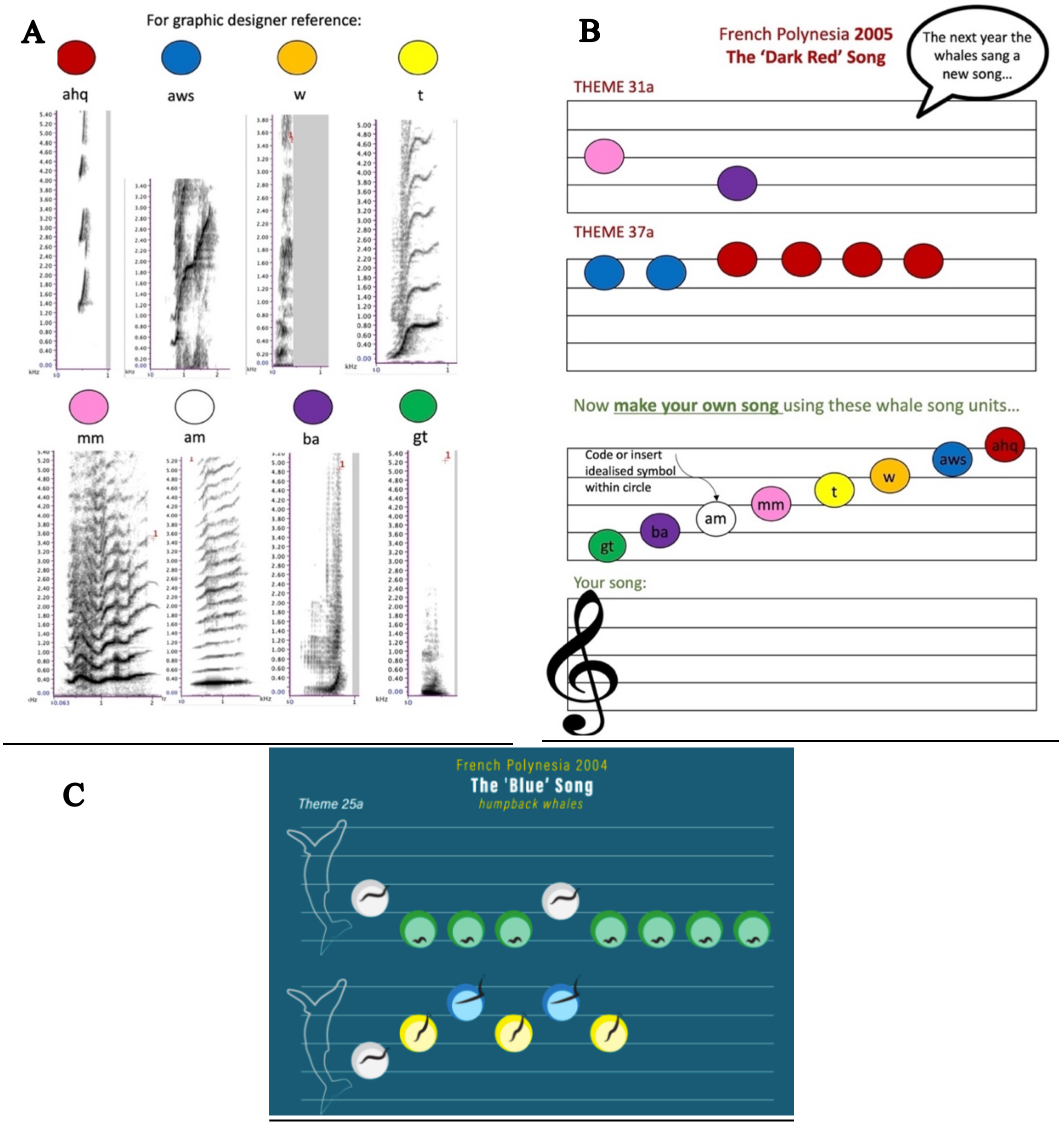


Figure 5.2.12: (A) The whale song unit spectrograms and codes for each of the eight floor piano 'keys' and each of the colours the units were paired with. The unit spectrograms were used by the graphic designer to create stylised units Copy, Innovate and to create the Sea Symphonies badge designs. (B) Page 1 of the original 'whale song sheet music' for the Copy Station. This version was passed to the Graphic designer Steve Smart for editing before the final print. (C) The final verson of the whale song sheet music after updates from the graphic designer to add the whale song unit stylised symbols and add a special humpback music clef and blue background to match the exhibition signage.

5.2.2 Sea Symphonies Evaluation

A full ethics approval application was made to and granted from the University Teaching and Research Ethics Committee (UTREC) to enable evaluation of data collected during this project. The full application can be viewed here. The objectives and indicators for the evaluation of the Sea Symphonies exhibition can be viewed in Table 5.2.3.

Table 5.2.3 Specific objectives and evaluation indicators for Sea Symphonies

Objectives	Indicator
Reach children of primary school age in Dundee and beyond including those living in low SES locations	1. Number of people entering the Dundee Science Centre
Engage school age children in humpback whale song research	1. School age children responding to the Respond and Communicate stations 2. School age children showing evidence of learning that whales make songs (song) and that whales create sounds (sounds)
Sharing knowledge about humpback whale research including about humpback whale song, identification, and evolution	1. Number of people responding to the 'Respond' station question and 'Communicate' station 2. Specific answers to 'what did you learn about whales today?' (Respond) 3. Analysis of the questions asked to scientists (Communicate)
Create an interface for members of the community to connect with scientists	1. Postcards sent at the communicate station 2. Questions answered on the dedicated Twitter page
For the audience to enjoy a fun and interactive learning experience	1. Responding to favourite station 2. Analysing postcard and tags comments for indications of enjoyability 3. Colouring in the whale stamp
Repurpose equipment within the Dundee Science Centre space	1. Floor piano updated 2. Optima units updated 3. Information panels updated 4. Information computer pads updated

Communicate

At the **Communicate** station (Figure 5.2.13) each participant was invited to send a postcard to a scientist. Double sided postcards were supplied (Figure 5.2.14). On side one the participant was asked to write their questions and on side two the participant was asked to tick which exhibit they enjoyed the most. I worked with graphic designer Steve Smart and project manager Ken Boyd to create a Whale post box for the postcards to be posted through. The opening to the post box was in a laser cut shape of a whale (which matched the signage on each of the exhibits). Photographs of whale researchers in the field were displayed above the whale post box so the participants had an image of the scientists they were asking their questions of. I set up a Twitter account with the handle @DundeeSciWhales at which questions asked on the postcards could be publicly answered by whale scientists. Again, I worked with graphic designer, Steve Smart to create a Twitter logo and banner for this account.

All data was anonymised. I collected date, age, gender along with a written answer. The handwritten responses on the postcards were photographed and then transcribed. Photographs and postcards were then destroyed. There was a disclaimer on the postcards that responses may be used within my thesis and other outputs. I collected data on the impact and reach of the Dundee Science Centre whale song exhibition in 4 ways: 1. Answers to a question (e.g. "What did you find out about whales today?"), were handwritten by respondents on small tags which are then attached by magnets to a large whale spout, along with age and gender data. 2. Postcards were provided to allow attendees to send a question to whale scientists, in a whale postbox within the exhibit, along with age and gender data, 3. Answers to postcard questions and engagement were given and monitored on a dedicated Twitter page. 4. Daily entrant data from Dundee Science Centre. The data was anonymised – I collected information on date, age and gender (in the format of Male- checkbox, Female- checkbox, Other (with space to provide any answer), Rather not say – checkbox) along with a written answer. All data was anonymised. The handwritten responses on the postcards were photographed and then transcribed. Photographs and postcards were then destroyed. There was a disclaimer on the postcards that responses may be used within my thesis and other outputs.

The written answers were subject to simple textual analysis. I firstly 'cleaned' each of the raw evaluation answers i.e. I removed any additional words (find correct words for this) to leave core words. I also assigned each answer to a topic – or multiple topics based on my own understanding as a biologist. I input the core words to a word cloud generator (e.g. https://www.wordclouds.co.uk). I noticed that both Communication and Song emerged as topics i.e. that many people answered that they found out whales make ‘noises’ or ‘sounds’ but didn’t say that they ‘sing’. I was interested as to whether the core learning outcome of ‘whales sing’ could be age related and so I ran an analysis.

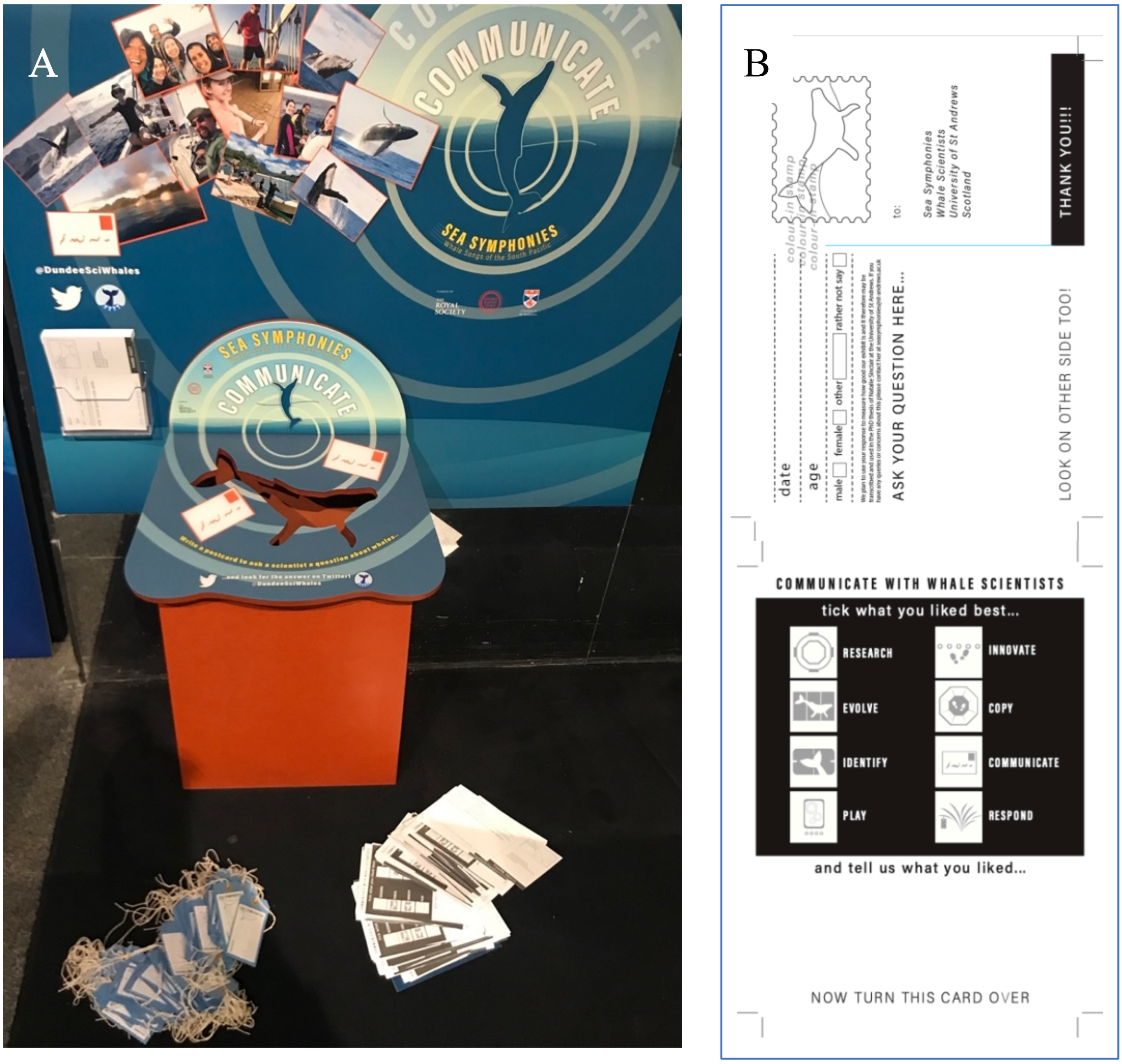
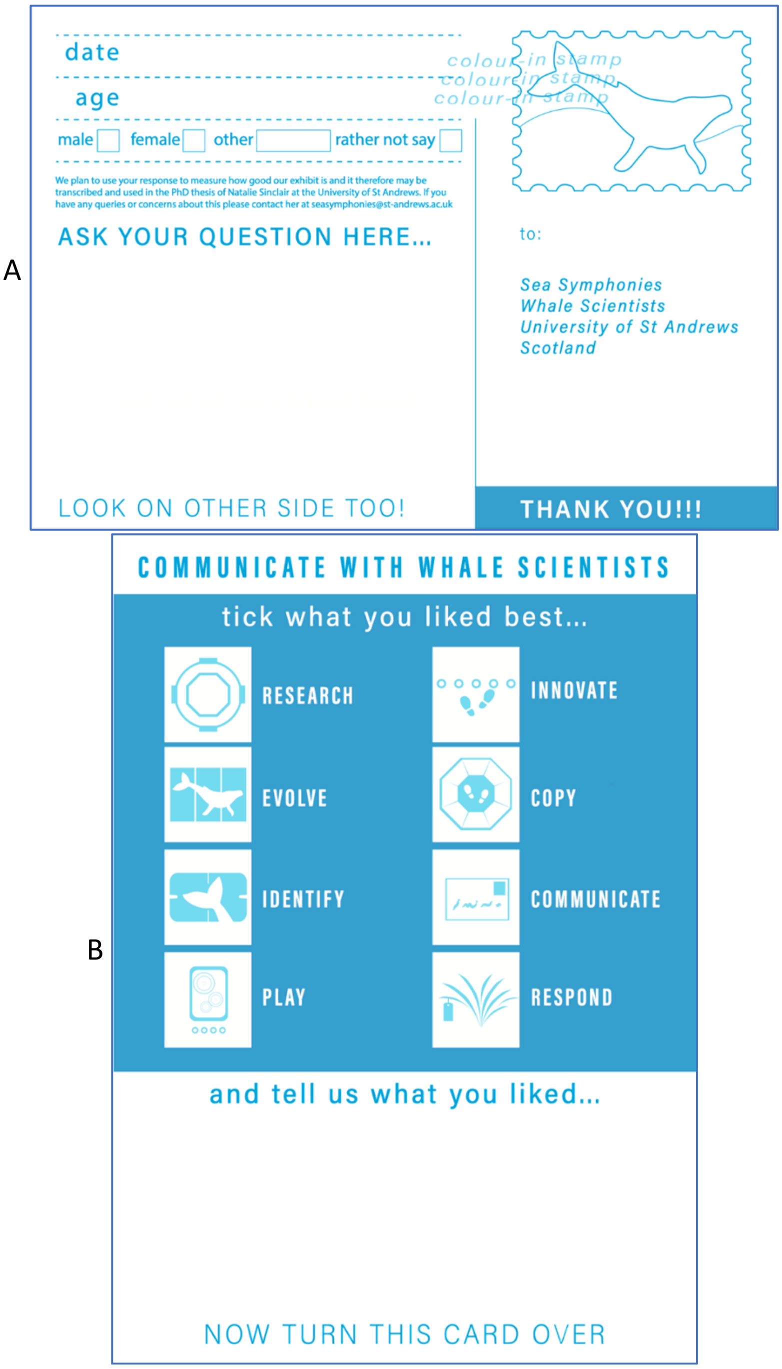


Figure 5.2.13: (A) The Communicate station with the ‘postcard to a scientist’ whale postbox. A lazer cut humpback whale served as the postbox entry point. The wall behind the postbox included photos of whale scientists in the field (including those from the Sea Symphonies team). On the floor you can see the first collection of postcards collected from the Communicate station. (B)The front and back of the postcard in the final black and white version.



A

date

age

male ☐ female ☐ other ☐ rather not say ☐

We plan to use your response to measure how good our exhibit is and it therefore may be transcribed and used in the PhD thesis of Natalie Sinclair at the University of St Andrews. If you have any queries or concerns about this please contact her at seasymphonies@st-andrews.ac.uk

ASK YOUR QUESTION HERE...

LOOK ON OTHER SIDE TOO!

colour-in stamp
colour-in stamp
colour-in stamp

to:

Sea Symphonies
Whale Scientists
University of St Andrews
Scotland

THANK YOU!!!

B

COMMUNICATE WITH WHALE SCIENTISTS

tick what you liked best...

RESEARCH

INNOVATE

EVOLVE

COPY

IDENTIFY

COMMUNICATE

PLAY

RESPOND

and tell us what you liked...

NOW TURN THIS CARD OVER

Figure 5.2.14 (A) The front side of the 'postcard to a whale scientist' at the Communicate station. The postcard included the text to enable me to include the evaluation responses within this thesis. "We plan to use your response to measure how good our exhibit is, and it therefore may be transcribed and used in the PhD thesis of Natalie Sinclair at the University of St Andrews. If you have any queries or concerns about this, please contact her at seasymphonies@st-andrews.ac.uk". Each postcard asked for date, age and gender information and included a Sea Symphonies logo stamp that could be coloured in. (B) The second side of the postcard at the Communicate station. This included an option to tick what station of the Sea symphonies exhibition the participant liked best (it was possible to tick more than one station). There was also a space to 'tell us what you liked'. This allowed us to capture more information about participants experience of the exhibition.

Respond

The **Respond** station asked a question (in a light box) to which each participant could answer on a luggage tag label while also providing information on date of arrival, age and gender (Figure 5.2.15). The light box was utilised to allow me to change the question over time and to be a clear prompt for participants before they left the exhibition space. The whale tag wall included the silhouette of a whale at the sea surface. An array of small metal hangers was attached to the wall above the whale silhouette. This meant that as participants added each of their blue tags, the appearance of a whale blow was created on the wall. The first question posed to participants was designed to be open ended and specific to the event 'What did you learn about whales today?'.

Your answer:

age:
date:
male ☐ female ☐ other ☐ rather not say ☐

We plan to use your response to measure how good our exhibit is and it therefore may be transcribed and used in the PhD thesis of Natalie Sinclair at the University of St Andrews. If you have any queries or concerns about this please contact her at seasymphonies@st-andrews.ac.uk

90 x 53mm

Figure 5.2.15: (A) The final version of the Respond station. Participants were asked to answer the question "what did you find out about whales today?". Participants wrote their answer alongside information on date, age and gender and then attached their tag to the whale blow. The blue tags created the spectacle of water droplets from the whale blow. (B) A close up of the Respond station tag. As this information would be used for my thesis the disclaimer "We plan to use your response to measure how good our exhibit is, and it therefore may be transcribed and used in the PhD thesis of Natalie Sinclair at the University of St Andrews. If you have any queries or concerns about this please contact her at seasymphonies@st-andrews.ac.uk."

Cook island workshop

The Cook Island Whale Workshop followed a methodology that combined informative presentations, interactive games, and facilitated connections between Scottish and Cook Island pupils. The workshop commenced with a short presentation introducing various whale species and their distinct sounds, imparting knowledge about these remarkable creatures. Subsequently, the session transitioned to a series of interactive games centred around whale sounds. One of these engaging activities involved participants creating a unique phrase or coda to communicate with their partner while keeping their eyes closed, encouraging them to rely solely on auditory cues. Additionally, as part of fostering connections, all students were provided with updated versions of the "Postcards to a Whale Scientist." These postcards served as a means of communication, allowing students to exchange thoughts and questions, facilitating interactions between Scottish and Cook Island pupils. This methodology ensured an immersive learning experience while promoting cross-cultural connections and enhancing the overall impact of the workshop.

5.3 Sea Symphonies Exhibition: Impact

The "Sea symphonies" launched on 28th September 2019 during an 'Explorathon' day in which scientists were present at the exhibits with additional workshops. The 'Sea Symphonies' exhibition was accessible until 11 am on the 18th of March – the day Dundee Science Centre closed to the public due to the Covid-19 pandemic. Excluding closed days over the 2019 – 2020 Christmas period (4 days closed) this meant the exhibition was open for 169 days. The evaluation material (tags and postcards) were picked up in batches from Dundee Science Centre (Figure 5.2.16). The first pick up from Dundee Science Centre was longer (28 days) than the rest of the pickups (7 days). In total 31,399 people accessed Dundee Science Centre in the time when the Sea Symphonies exhibition was active and therefore had the potential to interact with the exhibition. 983 pieces of evaluation material were submitted by participants within the "Sea Symphonies: Whale songs of the South Pacific" exhibition space across both the 'Communicate' and 'Respond' evaluation stations (Figure 5.2.17).

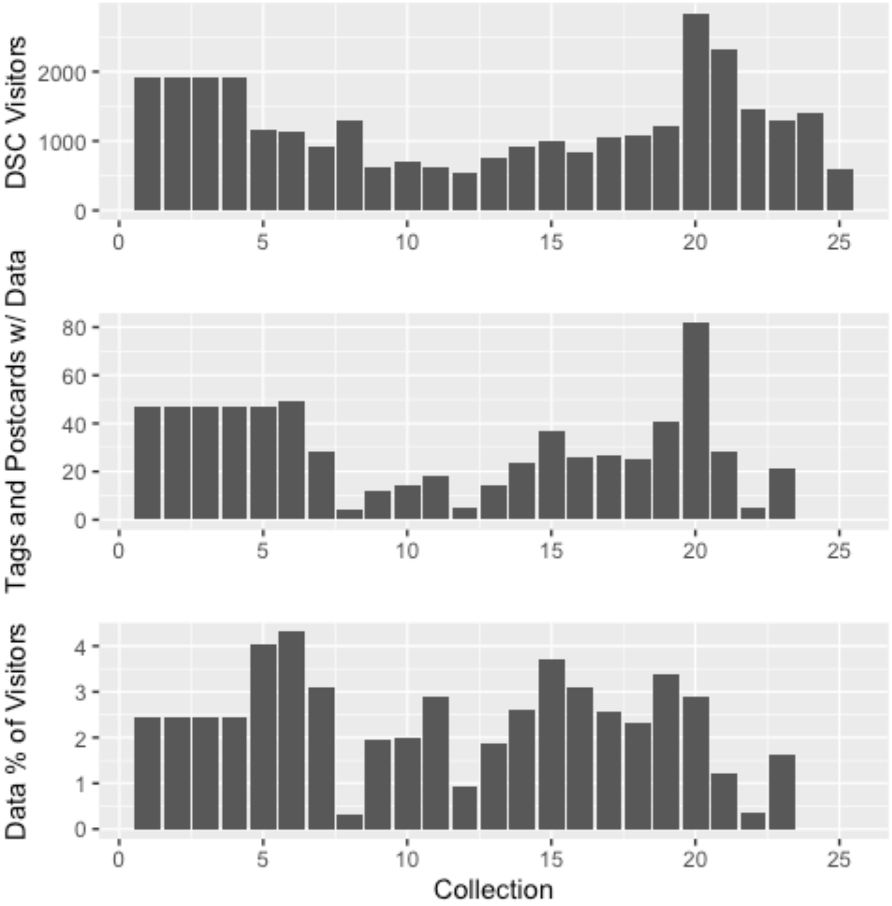


Figure 5.2.16: Number of visitors and data collected over each collection period. All collection periods were 7 days in duration with exception of the first collection which was 28 days and this was divided in four to match the rest of the data collection periods. The top graph shows total number of Dundee Science Centre visitors over each collection period in which the Sea Symphonies exhibition was available. The middle graph shows the number of tags and postcards with data that were collected in each collection period and the bottom graph shows the percentage people that filled in evaluation material from Sea Symphonies as a proportion of total number of DSC visitors.

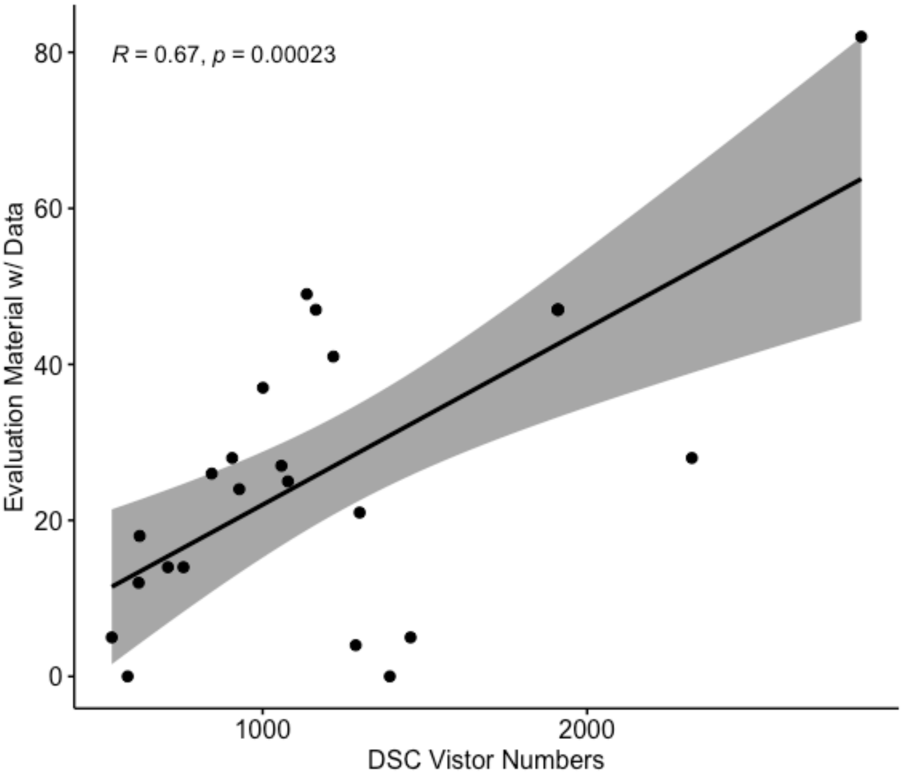


Figure 5.2.17: Correlation test of DSC visitors and evaluation material collected in each collection period. A Pearson correlation coefficient was computed to assess the linear relationship between Dundee Science Centre visitor numbers and number of tag and postcard data. There was a positive correlation between the two variables, Rr(20) = .67, p < 0.001).

<u>Tags – Respond Station</u>

In total 632 tags were collected at the whale spout – 'Respond' – station. A total of 18 tags were completely blank but were put up on the whale spout wall by a participant. Not all of the tags were fully filled in with all required data. 309 tags had indicated gender data. Of these 202 respondents indicated female, 87 male, 10 rather not say and 10 indicated other.

320 tags indicated age data. Two tags were removed as they indicated an age of 100 when they were evidently filled in by children. The maximum age was 63 and minimum age was 1. The mean age of the tag respondent was 10.2 and the median age was 8. In response to the question "What did you learn about whales today?" at the 'Respond' station 84 answers referenced the word "sing" and a further 34 mentioned "song". 62 respondents mentioned "sounds" but not "song" (Figure 5.2.18: A). Each of the 145 different words were assigned to 40 different topics of which the topic 'songs' was the most common (124) followed by 'sounds' (77), 'size' (21) and 'evolution' (15) (Figure 5.2.18: B).

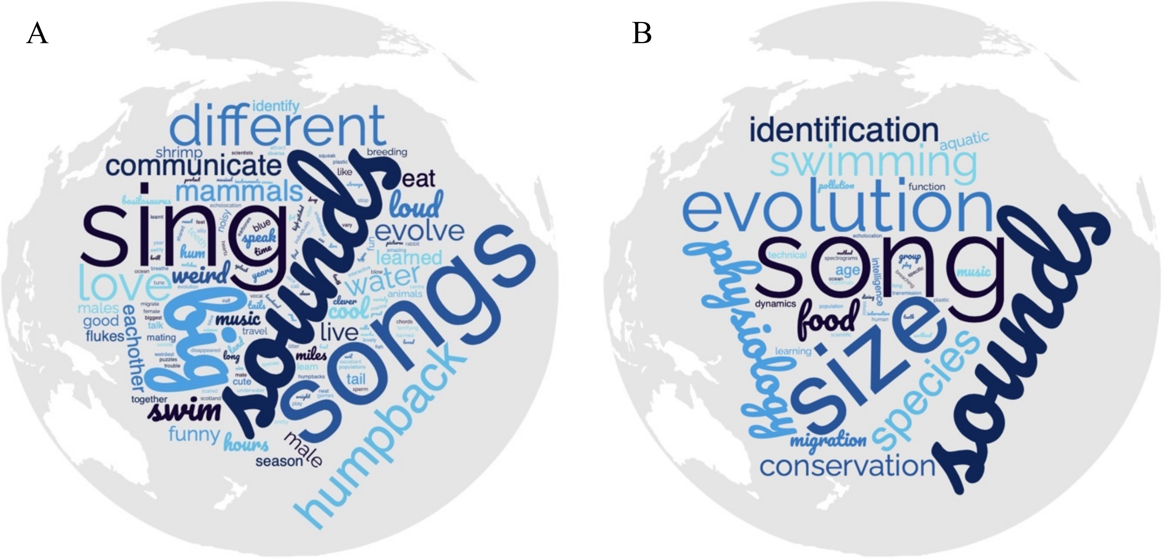


Figure 5.2.18: (A)Tags all words: In response to "What did you learn about whales today?" the most popular answer included reference to singing "sing" = 89 or "sounds" = 62, followed by "songs" (34), "different" (28), "big" (18) and "humpback" (10). 145 different words were identified. (B): Tags – Topics: In response to "What did you learn about whales today?" the most popular topic focused on song = 124 then "sounds" = 77 , followed by "size" (21), "evolution" (15), "physiology" (10) and "species" and swimming (9 each). 40 different topics were identified.

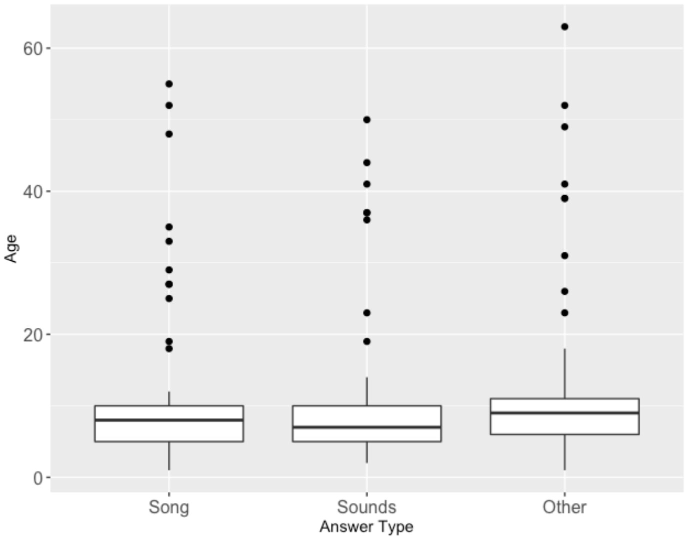


Figure 5.2.19: Model of age and answer type (Song or Sounds) A simple linear regression was used to test if age significantly predicted answer type, i.e. whether a participant was more likely to report the key learning outcome that whales sing. The fitted regression model was: lm(formula = Age ~ AnswerType, data = alldata1). The overall regression was statistically insignificant ($R^2 = 0.006879$. $F(2, 222) = 0.77$ $p = 0.4648$). It was found that age did not predict answer type

Postcards – Communicate Station

351 postcards were received in the whale post box. Of these 120 were filled in with some sort of data (including only the whale stamp being filled in). Total postcards with gender data was 96 (55 female, 38 male, 2 rather not say and 1 as 'other'). 91 postcards contained age data. The maximum age was 52 and the minimum age was 2, the mean age was 9.2 and the median age was 7 years old. The votes for favourite station were as follows Research: 12, Evolve: 13, Identify: 12, Play: 37, Innovate: 11, Copy: 25, Communicate: 12, Respond: 7. Some participants indicated multiple stations as their favourite.

The participants were asked to write a question to a whale scientist. Most questions indicated reference to 'big' and 'eat' (8 questions each) followed by sing (6 questions) (Figure 5.2.10: A). Sorting the question topics into topics – 35 different topics were identified with the most popular questions relating to 'physiology' (17 questions) and 'size' (12 questions) (Figure 5.2.20: B). The postcard also included a separate space to 'Tell us what you liked (about the exhibition)' in which 25 different words were identified and the most popular was 'Sounds' (7), 'play' (6) and 'song' (4).

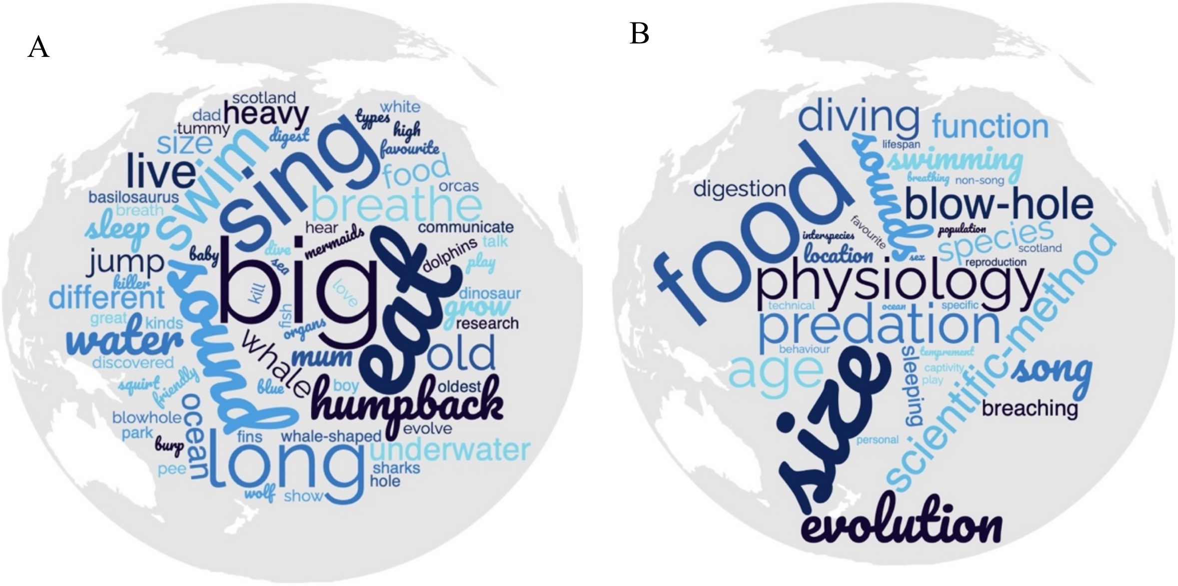


Figure 5.2.20: A: Postcard Questions - Cleaned questions - ALL PARTICIPANTS – Prevalence of words in all postcard questions collected at the whale post box at the Sea Symphonies exhibit during the complete opening times. The top 6 words were as follows: Most questions mentioned the word 'big' and 'eat' (8 questions each) followed by 'sing' (6), 'long' (5), 'sound' (5), 'swim' (4). There were a total number of 68 words in the cleaned questions. Similar words were combined. B: Postcard questions topics: Most questions related to physiology (17) and size (12). Other popular questions focused on food (10) and predation (10), sounds (9), scientific-method (8), age (5) and evolution (5). 35 different topics were identified.

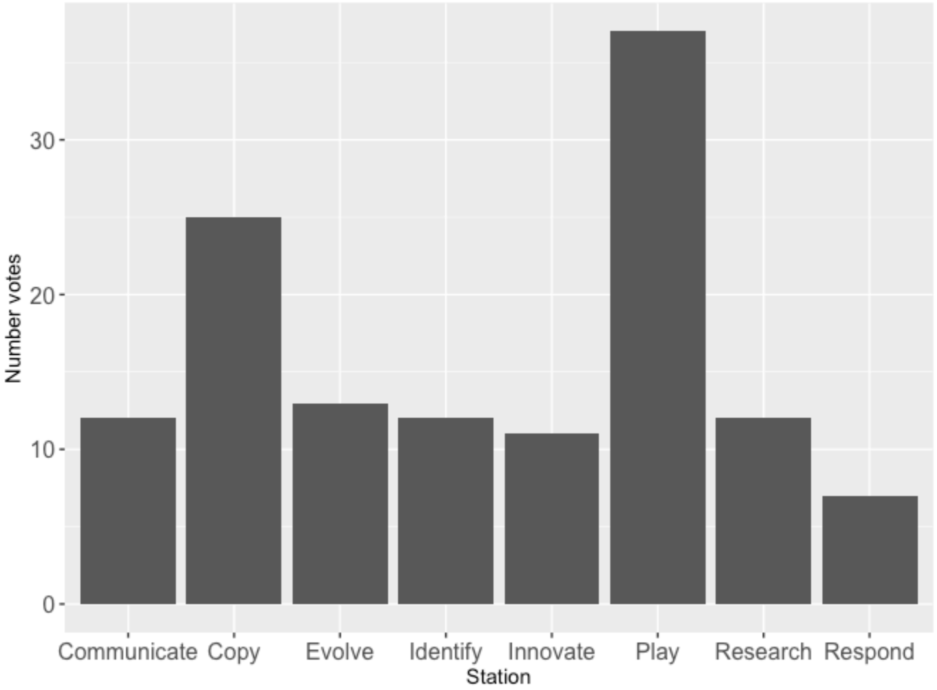


Figure 5.2.21: Favourite Part of Exhibition: Respondents could tick multiple stations. The graph shows the total number of votes for each station as indicated on the postcards. The votes for favourite station were as follows Research: 12, Evolve: 13, Identify: 12, Play: 37, Innovate: 11, Copy: 25, Communicate: 12, Respond: 7.

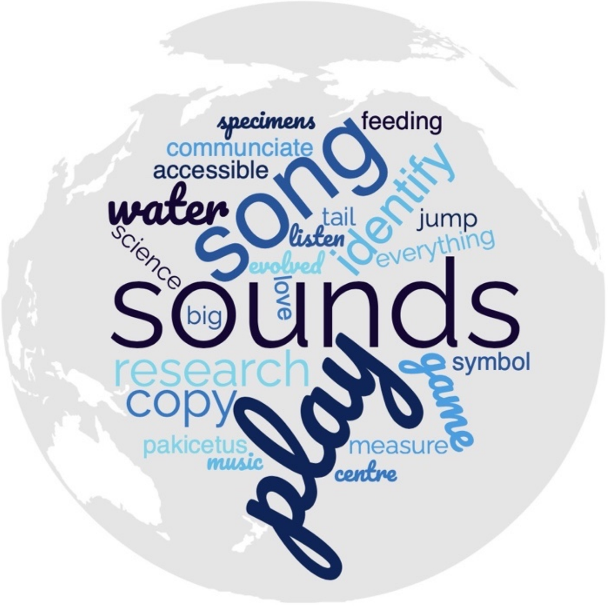


Figure 5.2.21: Tell us what you liked – on the postcard. 25 different words. Sounds (7); Play (6); Song (4); Copy, Game, Identify, Research, Water (2). 25 different words were identified.

Cook Islands whale song workshop

Eighteen 9 – 10-year-old children from one primary school class participated in the Cook Island whale workshop (Figure 5.2.22). Fifteen children filled in a modified postcard (see Figure 5.2.24) with an even gender split (7 girls and 6 boys). The most popular word was "song" and topic was 'species' (Figure 5.2.23). All but one of the children created a drawing on their postcard (see example in Figure 5.2.24). These mostly included drawings of a variety of species of whale, as well as ecosystems, sharks and a megalodon. Thirteen of the 15 children coloured in their whale stamp.

Figure 5.2.22: The class with teacher after the Whale song workshop. Taken with permission. August 2019, St Joseph's Catholic School, Rarotonga, The Cook Islands.

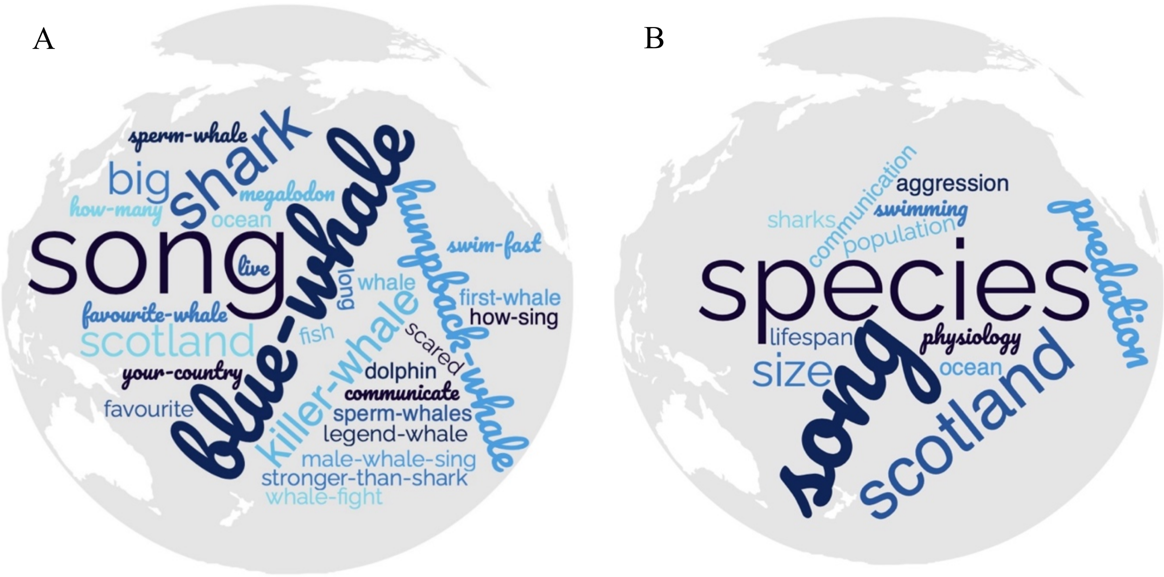
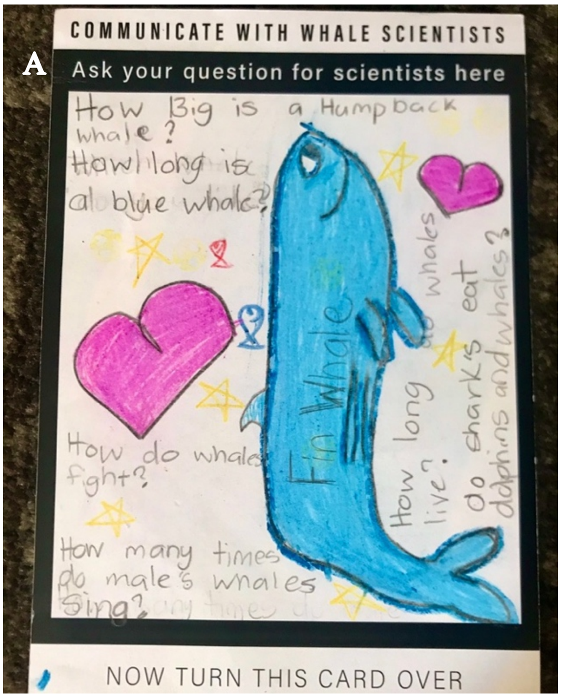


Figure 5.2.23: (A) 'Ask your question of scientists here' – on the postcard. 29 different words. Song (7); Blue whale (4); Shark (3); Big, humpback whale, killer whale, Scotland, (2). The complete list of words and weighting can be found in Appendix. (B): Cook Island Workshop Postcard questions topics: Most questions related to species (8) and song (6). Other popular questions focused on Scotland (3) and predation (2), size (2). 13 different topics were identified.



COMMUNICATE WITH WHALE SCIENTISTS

Ask your question for scientists here

How Big is a Humpback whale?

How long is a blue whale?

How do whales fight?

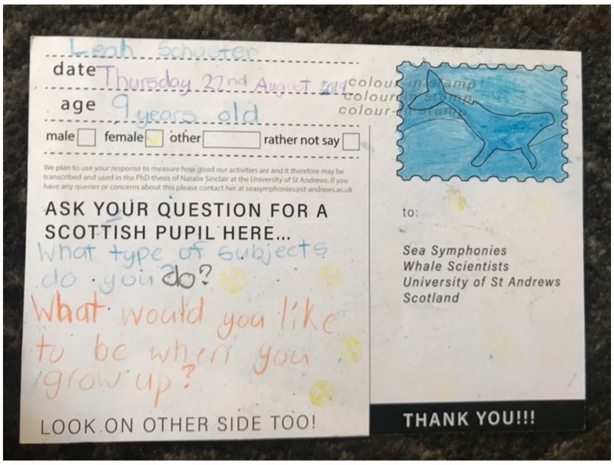
How many times do male's whales sing?

How long do whales live?

do shark's eat dolphins and whales?

NOW TURN THIS CARD OVER

B



Leah Schuster

date Thursday 22nd August 2019

age 9 years old

male ☐ female ☑ other ☐ rather not say ☐

We plan to use your response to measure how good our activities are and it therefore may be transcribed and used in the PhD thesis of Natalie Sinclair at the University of St Andrews. If you have any queries or concerns about this please contact her at seasymphonies@st-andrews.ac.uk

ASK YOUR QUESTION FOR A SCOTTISH PUPIL HERE...

What type of subjects do you do?

What would you like to be when you grow up?

LOOK ON OTHER SIDE TOO!

colour-in stamp
colour-in stamp
colour-in stamp

to:

Sea Symphonies
Whale Scientists
University of St Andrews
Scotland

THANK YOU!!!

Figure 5.2.24: (A) An example of a postcard to a whale scientist from the Cook Island class. They particularly liked drawing images of whales with lots of positive imagery. (B) The reverse side of the Cook Island postcard with questions for a Scottish pupil – to encourage the children to forge connections across the world with different cultures.

Figure 5.2.25: Long-term impacts from the Sea Symphonies exhibition. Unrealised ambitions in red (due to early closure and COVID19 pandemic restrictions).

5.3.1 COVID19 Impact Statement

The Sea Symphonies exhibition came to a close earlier than expected due to the COVID19 pandemic and resulting national lockdown restrictions. This meant that Dundee Science Centre was no longer open to the public from 19/3/23 date and I was only able to collect evaluation data for 4 months. I was also unable to change the question asked at the 'Respond' station analyse differences in responses nor was I able to perform school workshops which would have followed longer term impacts of the exhibition (Figure 5.2.25). The pandemic also found me moving back to my hometown to be with my family. Due to these reasons I decided to investigate a different format for reaching out to this particular audience, participants from low SES and low science capital backgrounds. Being at home was the perfect opportunity to do this. I applied for funding from National Geographic to create a community BioBlitz event and accompanying videos. I was awarded $2000 to get started and is public engagement event is explored in Chapter 6.

Discussion

Some of the original Sea Symphonies targets were not met due to the early closure of the exhibit caused by the complete shutdown of the Dundee Science Centre as a result of the Covid-19 pandemic and the accompanying restrictions. The 'Respond' station was intended to facilitate changing questions to monitor responses over time, but we did not have the opportunity to modify the question as planned. Furthermore, the early closure of the DSC and the Covid-19 pandemic prevented me from conducting any school workshops or additional follow-up questionnaires to assess the medium to long-term impacts of the Sea Symphonies exhibition. Instead, I embarked on the Wild Bannockburn project, partly in response to the Covid-19 restrictions that compelled me to relocate to Bannockburn and recognise the necessity for such a project in my area. The Wild Bannockburn project was also designed as an open-air event, making it less susceptible to changing Covid-19 restrictions and is explored in Chapter 6.

The Sea Symphonies achieved most of the original objectives during the design and implementation phases in engaging school age children in humpback whale song research and reaching people in low SES areas through targeting Dundee. Utilising and repurposing the existing equipment within Dundee science centre was successful evident in the positive feedback. The exhibition received highly positive feedback from both the 'Respond' and 'Communicate' stations aligning with my aim to create an enjoyable and fun interactive learning experience. Although I couldn't modify the question at the 'Respond' station over time, I recognise the significance of documenting any changes in attitudes over time. However, I did obtain evidence of a shift in attitude based on the specific question I devised for the 'Respond' station: "What did you learn about whales today?" Therefore, I can assume that we have captured at least a short-term change in participants' learning.

Many tag responses indicated references to 'song' or 'sound,' and I am confident that the majority of participants grasped the learning outcome that "whales sing songs," with even more participants understanding that "whales make sounds", which aligns with my aim to share knowledge about humpback whale research. There was no notable difference in the age ranges of those who responded in either way, suggesting that understanding the learning outcome about whale songs was not solely related to the participant's age. However, this analysis may be biased since it is likely that many tags for younger participants were completed by adults, and it remains unknown whether these parents accurately transcribed their children's responses or provided their own answers. To ensure that the tags accurately reflect the responses of children rather than their parents, it is recommended to implement a clear and explicit instruction for adults to record the answers verbatim as provided by their children. This instruction should emphasise the importance of capturing the authentic thoughts and perspectives of the young participants. Additionally, providing a designated space for parents or guardians to note their own responses separately, if they wish to contribute, can help distinguish between the two sources of information. Regular reminders and clear signage can reinforce these guidelines and encourage adherence to the intended data collection approach.

The response rate to our evaluation prompts was found to be consistent with other methodologies, especially considering that the exhibits and evaluation stands were designed to be user-led, with minimal encouragement from DSC staff or Sea Symphonies project members to fill out evaluation forms. The only exception to this was during the opening day when several team members and additional volunteers were present. On the opening day (September 28th), we observed a significant increase in the number of filled-in postcards and tags, which can be attributed to the higher visitor turnout at DSC for the ‘Explorathon’ day and the active encouragement from project members for participants to engage with the materials. The Play station with the custom video game was identified as the most popular station in the exhibition, this was evident in the postcard feedback section, specifically in the "tell us what you liked" category, where the word "Play" emerged as the most commonly mentioned term. Following Play, the Copy station ranked as the second most popular. This finding is supported by the feedback section, where words like "sounds," "song," and "copy" were frequently mentioned. Both Play and Copy stations provided clear instructions for participants to follow, whereas the Innovate station, which offered more freedom in the activity, proved to be less popular. The Innovate station required additional input from staff or volunteers to prevent it from going off track. Moreover, the Play and Copy exhibits accommodated only one person at a time, ensuring their proper usage and enhancing enjoyment. Conversely, the Innovate exhibit could be used by multiple people simultaneously and was located between other exhibitions, potentially leading to its unintended use.

The Respond station received the fewest votes (7), as expected, since it serves as one of the two evaluation stands. However, it is noteworthy that the Communicate stand was less utilised (with fewer postcards filled in), yet it received more votes as a favourite. This discrepancy could be attributed to participants being prompted to answer a question at the Communicate stand, making it more salient in their minds. Alternatively, individuals may have enjoyed the interaction of posing a question to a scientist, or they might have visited the Communicate stand before the Respond station.

To assess the feedback received from tags and postcards collected within the exhibition I employed basic text analysis tools. This involved manually cleaning and stemming each comment before inputting them into a word cloud generator. In the context of text analysis, "stemming" refers to the process of reducing words to their base or root form to aid in analysis and grouping similar words together. While developing my simple methodology for the relatively small dataset I had (allowing for manual labelling and stemming), I researched text analysis techniques. I discovered that this approach would be highly valuable for larger datasets and could enable tracking of customised hashtags across social media platforms for exhibitions or projects running over an extended period. Text analysis methodologies possess the capability to analyse substantial amounts of text, which could also facilitate conducting interviews with participants of the exhibition. These interviews could be recorded and transcribed, enabling a broader range of participants to share their perspectives on the events taking place in their community. One potential drawback of conducting interviews during the event is that it may distract participants and detract from their overall experience, as it requires their time and attention. However, the interview questions could be kept concise, and people generally speak faster than they write. Alternatively, an online Qualtrics form with preformed answers could be used, although its effectiveness compared to interviews remains to be determined.

In conclusion, the Sea Symphonies exhibition has provided valuable insights into the dynamics of public engagement and the importance of adaptability in the face of unforeseen challenges. These findings contribute to the ongoing dialogue on equitable science communication and public engagement, emphasizing the importance of adaptable approaches and long-term impact. Importantly, this experience underscores the indispensable role of evaluation in the Sea Symphonies exhibition, showcasing how it can be effectively embedded into the exhibition experience. By continuously assessing the impact and outcomes of such initiatives, we can refine and tailor them to better serve the diverse needs and interests of our audience, ultimately advancing the broader goals of science communication and public engagement.

Chapter 5 Appendices

Appendix 5.1 Developmental drawings and additional figures of engagement outputs

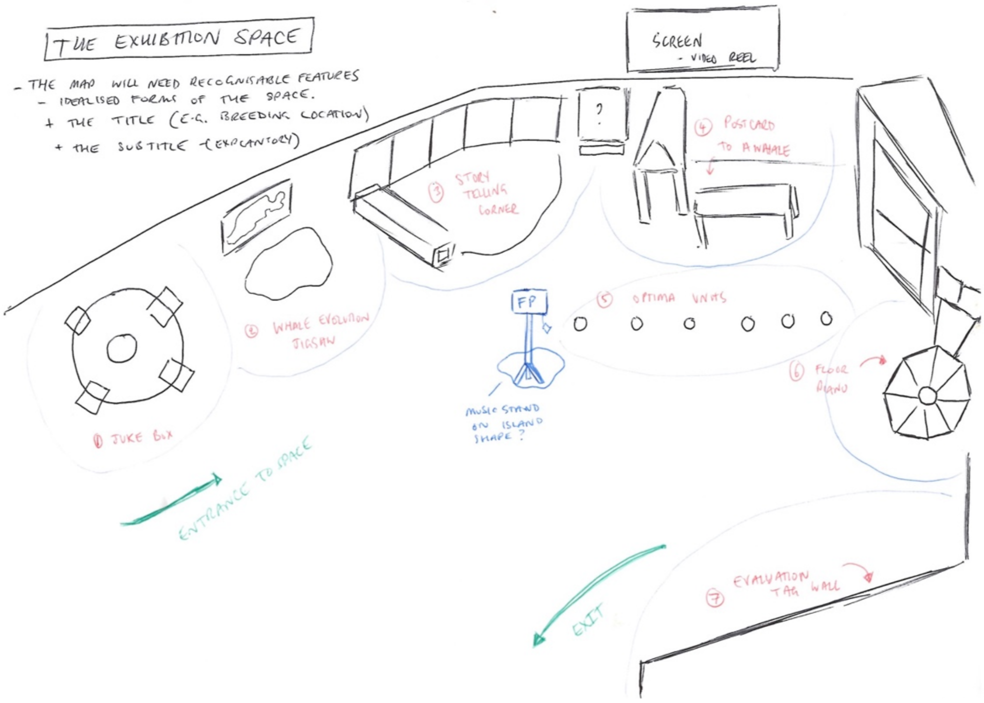


Figure A5.1: Drawing of the exhibition space prior to modifications

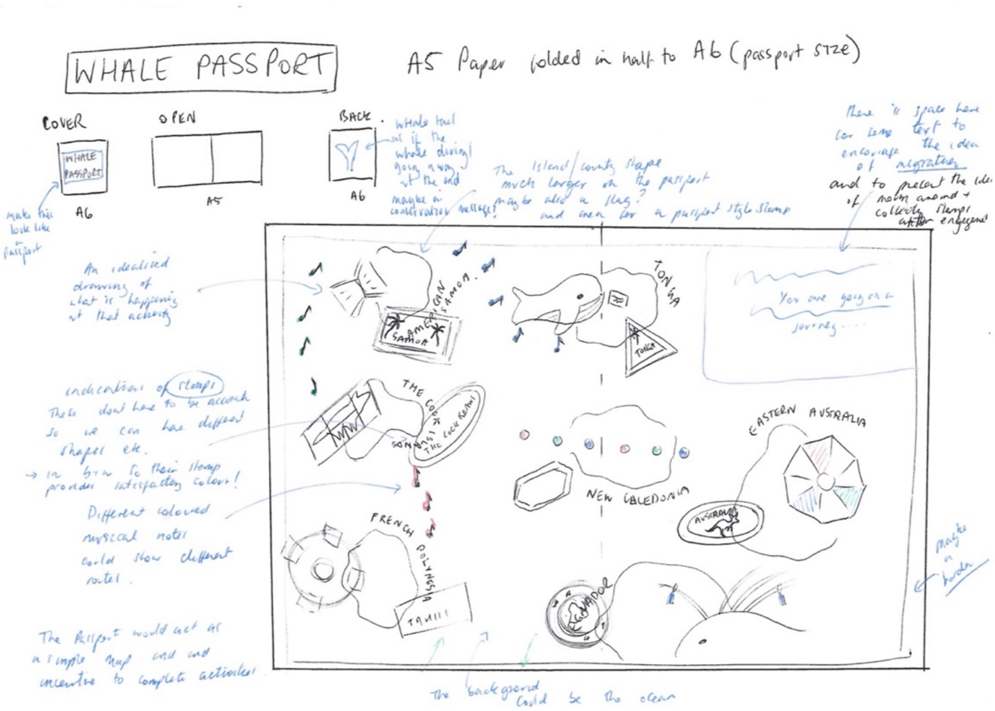


Figure A5.2: Preliminary drawings of the Whale Passport before passing to graphic designer

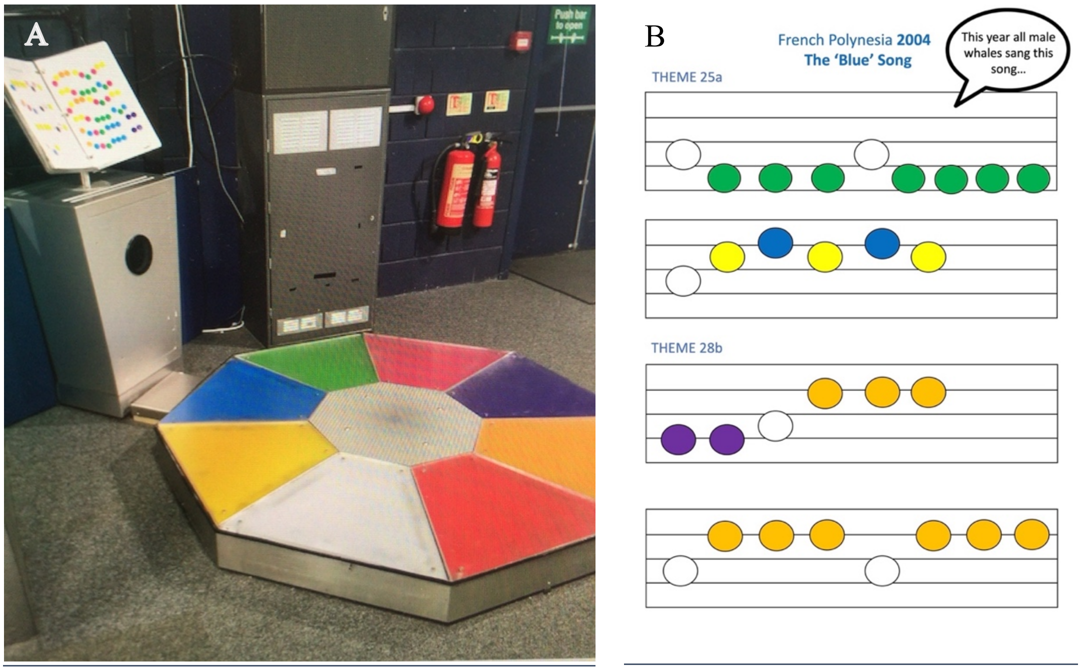


Figure A5.3 (A) The original 'floor piano' within the Dundee Science Centre before repurposing for the Sea Symphonies exhibition. (B) Page 2 of the 'whale song sheet music' (original version). The 'whale song sheet music' shows two themes (25a) and (28b) from the 'Blue' song present in French Polynesia in 2004. Each page of the 'whale song sheet music' shows a different song sang in the same location in different years delivering the learning outcome that humpback whale populations change their songs. Again, this original version was passed to the graphic designer for editing before the final print.

A

B

Figure A5.4 (A) The sign at the Innovate station was placed on the floor (partly because this station was in the middle of the exhibition space) however this served the purpose well as participants were asked to step on the light beam to create a whale song sound. The sound was activated by breaking the light beam. Six whale song units were chosen for the Innovate station. Each whale song unit sound recording was isolated from a French Polynesian dataset. (B) The signage at the Play station including affiliation from BIOME.

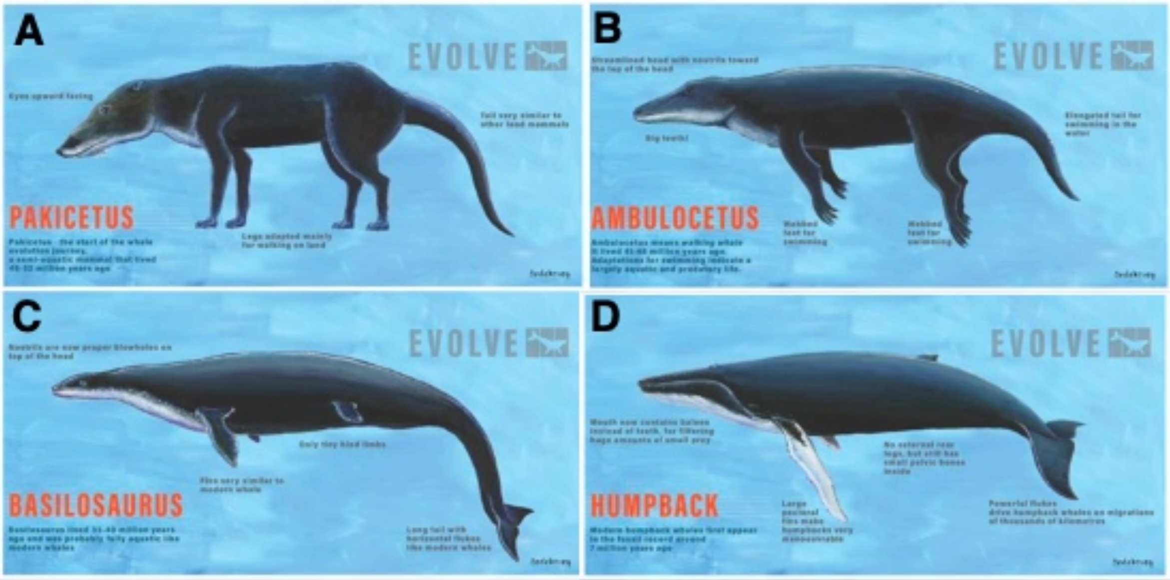


Figure A5.5 The graphics of each layer of the 'Evolution' station puzzle. The puzzle took the participant through four stages of marine mammal evolution from Pakicetus (A), Ambulocetus (B), Basilosaurus (C) and finally a humpback whale (D). The puzzle layers were commissioned by painter Cornelia Oedekoven. Information about each of the changes of evolution are highlighted in text on the puzzle layer.

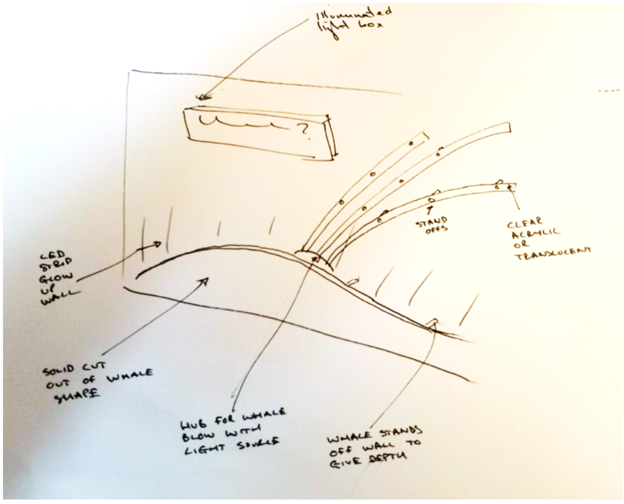


Figure A5.6 The original drawing of the Respond station visualising the question location, whale, and whale spout for answers.

6 Chapter 6: Implementing Live Open-Air Science Events in Low Science Capital Communities: A Two-Year Case Study

Abstract:

This chapter presents a two-year case study focused on the implementation of live open-air science events in a community with low science capital. The events, collectively referred to as the Bannockburn BioBlitz, aimed to engage the local community with their natural environment and informal science learning. The chapter highlights key short-term and long-term impacts of these events and shares insights gained during the process. In 2021 and 2022, the Bannockburn BioBlitz events centred around community-driven wildlife activities. These events encouraged participants to discover and identify as many local species as possible within a specified timeframe. To organise and manage these events effectively, a team was formed, collaborations with local charities and businesses were established, and a range of engaging workshops were offered. Short-term impacts included an increase in community engagement, with a significant rise in attendance from the first year to the second year. Participants expressed their intent to make behavioural changes and actively contribute to the well-being of the local environment. Furthermore, the creation of community art projects, such as the "WILD Bannockburn sign" and the "Bannockburn banner," provided participants with opportunities for hands-on involvement and creative expression. Long-term impacts of the Bannockburn BioBlitz extended to the global stage, with the project gaining recognition and support, including participation in the prestigious COP26 Concert for the Climate. On a local level, the event has become an anticipated annual occurrence within the community. It has also inspired the formation of a local "river guardians" group, showcasing the lasting legacy of the initiative. Small grants and the pursuit of charity registration are expected to ensure the project's sustainability, preserving its commitment to environmental conservation and education. Overall, this case study demonstrates the potential for science events to have a profound and lasting impact on communities, especially those with low science capital. It underscores the value of community engagement, creative expression, and collaborative efforts in fostering a sense of ownership and responsibility for local environments.

6.1 Introduction

While the importance of a two-way process of science engagement and its role in effective science communication is undeniable (Illingworth *et al.*, 2015), there is another facet of this landscape that deserves our attention—the role of science capital in shaping participation across diverse socio-economic groups. As we strive to make science accessible to all, we must recognise that science capital, as a measure of an individual's science-related knowledge, experiences, family influence, attitudes, and behaviours (Canovan, 2019), is not evenly distributed across our society. The link between a student's socio-economic status (SES) and their performance and participation in science learning has been well-established (Archer et al., 2015). Higher SES students tend to perform better in science examinations and are more likely to pursue careers in science. However, the impact of SES is not limited to academic achievement; it also influences a student's decision to study science beyond compulsory education.

Addressing this inequality in science participation is a longstanding policy objective. It is clear that representations from low SES backgrounds remain disproportionately low, as even at an early age, many working-class children face disadvantages and are at risk of falling out of the 'leaky pipeline' that leads to a science career, despite their interest in the subject (Archer, DeWitt, Osborne et al., 2012).

Having a population that understands science and can discuss important science topics is the foundation for democracy as individuals are able to make more informed decisions that affect their lives, especially when considering important issues such as the climate and biodiversity crisis and the recent pandemic (Osborne & Dillon, 2008). During the recent pandemic it was clear how important it was for scientists and politicians to successfully communicate their findings and predictions to the public, and how better public engagement could allow for better outcomes for everyone (Terezinha Nunes, 2017). Understanding the barriers faced by individuals from low SES and/or low science capital backgrounds is crucial. These barriers can range from limited free time, caring responsibilities or difficulty accessing transport (Godec & Watson, 2021). Bridging these gaps and creating inclusive opportunities for low-income and/or low science capital communities is essential.

While public engagement in science can coincide with other forms of science communication, such as from books and documentaries that can be accessed at any time, many public engagement initiatives focus on live events in which a participant participates in live workshops, live talks, or can have a hands-on experience in a science centre with props and facilities or at a science festival (Fogg-Rogers *et al*., 2015). Live, in person events engage the public with science in a social context which adds to their power of providing informal learning opportunities (Durant *et al*., 2016). This can be extremely beneficial to building public understanding of science and evidence shows that public science events that bring scientists and the public together can build long-term, trusting relationships with new audiences (Durant *et al*., 2016). Informal learning opportunities such as live science events, outside of formal education institutions, have been found to be intrinsic to long-term outcomes for citizens going on to pursue science post-16 (Archer *et al*., 2015). For example, DeWitt, Archer and Mau (2016) suggests that, while the formal school environment has a part to play, post-16 science participation is heavily influenced by family perceptions of science as well as out-of-school experiences. However, due to direct participation in science events having a larger financial barrier, access to live science events is not even across socio-economic demographics (DeWitt *et al*., 2016).

One approach is to offer free-to-attend live science events within low science capital communities. These initiatives have the potential to foster greater participation among groups that have historically been underrepresented. Furthermore, environmental education has proven to be an effective low-barrier method for engaging low-participation communities. Environmental education aligns with the free access to outdoor natural laboratories, such as natural habitats (Christie et al., 2015), and the growing comfort people have with open-air activities, particularly in the wake of the recent pandemic (ONS, 2021).

As I delve into this aspect of public engagement with science, I will explore the concept of science capital and its impact on participation. With this project I aimed to engage individuals from low science capital communities in science and outdoor learning and in this chapter, I evaluate to what extent this was successful. My overall aim is to contribute to the broader conversation on equity in science communication and public engagement.

In the subsequent sections of this chapter, I will delve deeper into the methodologies employed, specific research objectives, and the outcomes of my exploration. Together, I aim to address the challenges and opportunities associated with enhancing science capital and engaging low to middle income groups in meaningful science communication and public engagement efforts.

6.1.1 Aims

The format is an open-air citizen science workshop event called the Bannockburn BioBlitz. Bannockburn, Stirling is where I am currently situated (due to the pandemic) and where I grew up attending both Bannockburn Primary and Bannockburn High School and therefore, I am a long term and current community member. The town of Bannockburn includes the Bannockburn Heritage Walk which follows the Bannock Burn. This area is unfortunately spoiled by litter pollution. I obtained information from a lecturer within the School of Management at the University of St Andrews (Lawrence Laselle) who studies the transition to higher education from different parts of Scotland. This information included that the proportion of pupils progressing to HE is below the Scottish national average for Bannockburn High School. Furthermore, the percentage of pupils eligible for free school meals (FSM) is above the Scottish national average. Additionally, I obtained insights about the proportion of students from this area who go onto higher education at the University of St Andrews, which is extremely low. For these reasons the second case study takes the form of a free to participate wildlife engagement event within the heart of the Bannockburn community.

The overall aims of the Bannockburn BioBlitz were to engage the community of Bannockburn with their local environment and informal science learning through a series of workshops and a community BioBlitz and more specifically to:

- Create a free to access wildlife event to enable anyone (including low SES communities) to participate in wildlife informal learning opportunities in their own community's nature spots
- Facilitate ongoing engagement from community through creation of a hub and follow up events
- Bring together community for shared purpose through communal activities and outputs (such as art projects)
- Use community participant feedback to improve future events and community initiatives

The indicators for each of these aims can be found in section 6.2.2.

6.2 Development and Outputs

The Bannockburn BioBlitz annual event is centred around a "BioBlitz" which is a community event that focuses on finding and identifying as many species as possible in a particular area in a particular timeframe (National Geographic, 2023). I set up a group called Wild Bannockburn alongside a website and social media channels on Facebook, Instagram and Twitter. Wild Bannockburn (the group) ran the Bannockburn BioBlitz event day. Wild Bannockburn acted as a hub to recruit volunteers and create collaborations with local charities and businesses. A complete logic model for the event can be found at Table 6.2.1.

The event ran in the same format in both 2021 (Saturday 21st September) and 2022 (Saturday 18th June). This format was the general focus of the BioBlitz plus a series of interactive workshops beginning at 11 am and closing at 3 pm (Table 6.2.2). The event was totally free to participate in and open to everyone. Participants could register their interest on the Facebook event, or they could simply turn up on the day. On arrival each participant or participant group received two pieces of paper. The first was the BioBlitz Bingo card (Figure 6.2.7). This double sided A5 leaflet included guidance for the BioBlitz on one side and a series of short evaluation questions on the other side (Figure 6.2.7). BioBlitz Bingo encouraged participants to tick off as many observations as they can and encouraged them to explore different habitats of the Bannock Burn and heritage trail.

The second was a full colour A4 map of the BioBlitz area which included time and location information of the workshops (Figure 6.2.1). On the back side of the map there were step by step instructions on how to download and use the iNaturalist app. The iNaturalist app is a species identification app which allows participants to automatically add photos, with GPS and time data, directly to the BioBlitz survey. Participants were encouraged to keep their map but to hand back their filled in BioBlitz Bingo card and evaluation questions.

In year 1 the Bannockburn BioBlitz partnered with the Home River BioBlitz - a world-wide BioBlitz event taking place on the 25th and 26th of September. In year 2 the Bannockburn BioBlitz ran in in conjunction with the St Andrews BioBlitz. In both years Wild Bannockburn partnered with local charities and businesses to include a series of workshops during the event. Each workshop focused on some aspect of the natural ecosystem of the Bannock Burn. In year 1, Wild Bannockburn partnered with Froglife, Buglife, Nikki's Supply Store and Tranceform Therapies. In year 2 Wild Bannockburn partnered with Froglife, Buglife, Blaeberry River Art and Move & Nourish with Marianna.

Table 6.2.1: Logic model for The Bannockburn BioBlitz

Activity/Project	**The Bannockburn BioBlitz**
Aims & Objectives	• To create video content to enable my community to accurately identify local species for upload to iNaturalist • To break down the technological learning curve barrier for using iNaturalist • To engage my community in plant and animal species identification in our local woodland/water areas • To encourage dialogue and understanding of the ecological connections between species in the Bannock Burn and surrounding woodland ecologies • To plan, execute and evaluate the Bannockburn BackYard BioBlitz – as a way of putting the video content and community into action! • To create a trailer video of the Bannockburn BioBlitz to enthuse future participants in ongoing ecology focused workshops and the Wild Bannockburn Group
Inputs (what is required to achieve aims/objectives)	• Funding – (To create and edit videos, social media boosting and small print run for community advertising) • Funding – (To create trailer video and further print run for evaluation material) • Time - Project lead: Natalie Sinclair - Project management include filming, logistics, activity promotion and collaborative working with teachers. - St Andrews PER Team - Project guidance and support with connecting to teachers and developing classroom resources - Members of the Bannockburn community – Data collection during the BioBlitz, Participation in workshops - Members of the Bannockburn community – Volunteering – Guidance to workshops and collecting feedback forms • Organisations - National Geographic/iNaturalist Team – training in BioBlitz and iNaturalist for project leader - Froglife – Provide information stall and promotion - Buglife – Provide workshop and promotion - Freelance local artist – to create community art project at the BioBlitz event - Freelance photographer and videographer - Editorial support for video production, creation of short film for promotion - Bannockburn Primary School - To support the development of video resources into educations aids for schools

Activities (what the project does with the resources)		• Creation of user-led videos in which community members are invited step by step to identify local species in the field and then upload them to the iNaturalist app – both in the field (on iPhone and Android) and at home on the computer or tablet device • Create a Bannockburn community online on iNaturalist for users to connect with each other and share sightings • Identify local species of interest to boost for partner projects • Launch a Bannockburn BackYard BioBlitz – a one day action filled event in which the community puts the training into action for Bannockburn's first ever BioBlitz • Create a Facebook, Instagram and Twitter page to advertise the event and as a hub for video content • Create website for Wild Bannockburn • The videos will be developed as teaching resources for schools after the community focused teaching
Outputs		• Online video content created for identification instruction • YouTube channel dedicated to local species identification and iNaturalist use • Educational resources • BioBlitz offline event focused in the Bannockburn woodland area • Trailer video to encourage further engagement with Wild Bannockburn from more members of the community
Short-term Outcomes (0-6 months)		• Videos are created and uploaded to a community page for use • A community of local naturalists is brought together both through social media advertising and through approaching local established groups
Longer-term Outcomes (6 months +)		• Community members are confident in their identification skills for a set group of species and upload to iNaturalist • Community members take part in a Bannockburn BackYard Bioblitz • Videos are repurposed as a catalogue of outdoor learning materials for local schools • The trailer video is created and released for ongoing engagement
Measurement	Evaluation Questions	• Is this event something that the community wants on an annual basis? • Are community members willing to engage with their local environment? • What are community members ideas for action for our nature spots?

	Data Collection Techniques	• Capture the number and demographics of the public attending the Bannockburn BioBlitz and any additional community events • Ask participants to fill in paper and online surveys to document their ideas and opinions of the event and future actions • Capture number of people adding to the community art projects • Capture number of people engaging with online media and social media hubs • Capture number of people visiting website
	Analysis and interpretation of data	• Use postcode district maps to plot where visitors live • Plot demographic data • Group comments from evaluation questionnaires and analyse for popular answers • Analyse Likert scale questions
	Reporting	• Assess how to improve the event and make changes • Update for funders • PhD thesis chapter case study
Assumptions		• Community members want to engage with iNaturalist and local wildlife • Schools want to engage with outdoor teaching using iNaturalist • Community members who take part have access to a digital camera or smartphone • Community members who take part have access to an internet-enabled device to allow them to upload images with the associated meta data. • Community members want to engage with iNaturalist and local wildlife • Schools want to engage with outdoor teaching using iNaturalist • Community members who take part have access to a digital camera or smartphone • Community members who take part have access to an internet-enabled device to allow them to upload images with the associated meta data. • Meta data will be present on all photos (dependent on data services on digital camera or smartphone) • Funding will be secured to allow creation of good quality user- led videos, social media advertising and local print advertising • Funding will be secured to allow creation of the Bannockburn BioBlitz Trailer

Table 6.2.2: The activities of the Bannockburn BioBlitz

The Bannockburn BioBlitz			
Year 1	**Year 2**	**Description**	**Rationale**
The BioBlitz	The BioBlitz	Identification of plants and animals and upload to iNaturalist	Bring community together for shared purpose to explore local environment
Froglife Stall – Pond Doctor	Froglife Stall – Virtual Reality	Learn how to make a pond and experience the human made barriers amphibians face	Bring local charity resources to community and participants have chance to ask conservationists questions
Buglife River Dipping workshop X2	Buglife River Dipping workshop X2	Identify invertebrates from the Bannock burn	Hands on workshop to reveal the hidden animals of the Bannock burn
Buglife Pollinator	Buglife Polliniator	Identification of pollinator species on wildflower meadows	Exploring the flying invertebrates on our doorstep
Community art project with local artist	Community art project with local artist	Creation of 'WILD' leaf sign and 'Bannockburn' bunting banner	Bringing the community together to create a shared outcome
Mindfulness in nature	Yoga in nature	Connecting with nature through senses and movement	Wind down for the end of the event and to showcase local practitioners
Photography and film	Photography	Capturing candid shots of the event and a group shot at the end	Memories for participants and promotion material for ongoing funding
	Local church stall	Refreshments provided by local churches	Community support

Figure 6.2.1: The Bannockburn BioBlitz map was given to each participant or group as a guide through the day's activities. The map was a stylised version of the Bannockburn Heritage Trail created from a real map. The locations, times and collaborators of each workshop were included on the map (A4). The same for both Year 1 and Year 2.

6.2.1 Bannockburn BioBlitz activities

Froglife: Pond Doctor Stall and Virtual Reality experience

In year 1 Froglife brought their Pond Doctor Stall (Figure 6.2.2: A) which answered questions on pond creation, management and restoration while also providing preserved amphibian and reptile species for participants to view. In year 2 Froglife brought their virtual reality stall (Figure 6.2.2: B). This virtual reality experience allowed participants to experience life as a common toad when trying to cross a road and learn more about the dangers of roads to wildlife, including amphibians and reptiles. Both the Froglife Pond Doctor stall and virtual reality stall ran for the duration of the event and could be visited at the participants leisure.

Figure 6.2.2: (A) Participants of the Bannockburn BioBlitz visit the 'Pond Doctor' Stall provided by local wildlife charity Froglife in year 1. The pond doctor stall included information on how to make your own pond in your garden and also included preserved specimens of amphibian and reptile species that could be found in the area (in year 1). (B) Participants visit the virtual reality experience provided by Froglife in year 2.

Buglife Scotland: River dipping and pollinator workshops

In both years 1 and 2 Wild Bannockburn partnered with Buglife Scotland, in particular Rebecca Lewis, to conduct river-dipping and pollinator workshops. The Buglife river-dipping workshop allowed participants to observe how to take a kicksample (Figure 6.2.3: A) from the Bannock burn and then to find and identify a series of invertebrates (Figure 6.2.3: B). All materials were provided by Buglife Scotland including long handled nets, white trays and buckets, small pots/jars, plastic teaspoons and river invertebrate identification guides. This workshop ran for approximately half an hour at two defined times within each BioBlitz event.

Figure 6.2.3: (A) Rebecca Lewis from Buglife Scotland counts down the kick sample during the river dipping session at the Bannockburn BioBlitz (in year 1 and 2) (B) Participants look for invertebrates after a kick sample during the river dipping session (years 1 and 2)

The Buglife pollinator workshop ran once per event (between river dipping sessions). The pollinator workshop included a short introduction to UK pollinators and then allowed participants to find and identify pollinators in wildflower meadows near the Bannock burn (Figure 6.2.4). Butterfly nets, identification guides and plastic pots were provided by Buglife Scotland.

Figure 6.2.4: (A) Participants use ID guides to identify pollinators in a local wild flower meadow next to the Bannock burn. I am providing some guidance. (B) Rebecca Lewis from Buglife leads a workshop in pollinator identification with local participants of the Bannockburn BioBlitz

The community art projects years 1 and 2

In both years Wild Bannockburn partnered with local artists to create a community art installation during the event itself. In the first year Nikki's Supply store created bold lettering of the word 'WILD' on large MDF boards provided by Wild Bannockburn. Participants were encouraged to collect fallen leaves (in late September) to decorate the lettering over the duration of the event (Figure 6.2.5: A). The art project also served to bring people into the woodland, another habitat around the Bannock burn. This would be a visual representation of the community coming together for nature. In the second year Blaeberry River Art brought a print making workshop. Blaeberry River art created four bespoke prints of different species that could be found around the Bannock burn (e.g. kingfisher, oak leaf) (Figure 6.2.5: C). Wild Bannockburn created bunting from white cotton and on the day participants created their own lino print to add to the banner which included the name 'Bannockburn' (Figure 6.2.5: D). This project built on the previous year's project to complete the organisation's name 'Wild Bannockburn'.

Figure 6.2.5: (A) Nikki McWilliams from local business Nikki's Supplies Store helps a participant of the Bannockburn BioBlitz attach a fallen leaf onto the WILD art project board (in Year 1). (B): The complete WILD art project. Participants of the Bannockburn BioBlitz collected fallen leaves and sorted them by shape and colour to attach to the WILD boards (in reference to Wild Bannockburn – their community nature group) (in year 1). (C): Local artist Fiona McKenzie van Baardwijk of Blaeberry River art helps a participant of the Bannockburn Bioblitz create her first lino print onto a piece of bunting for the community 'Bannockburn' banner. The participant could choose from four wildlife prints of plant and animal species present around the Bannock burn (in year 2). (D): The finished community art project of year 2 Bannockburn BioBlitz – a bunting Bannockburn banner held by all the volunteers and workshop leaders who made the second year happen!

<u>Mindfulness and Yoga workshops</u>

In both years Wild Bannockburn brought local mind and body practitioners to help the kids (and adults) connect with nature and wind down from the days events. In year 1 the event finished with a mindful moment in nature with local business Tranceform Therapies, a local mindfulness practitioner (Figure 6.2.6: A). This mindfulness workshop allowed participants (both adults and children) to connect with the Bannock burn through their five senses. In year 2 the event finished with nature yoga with local business, Move with Marianna, a local yoga teacher. The yoga workshop encouraged participants to create yoga poses in reflection of the natural world, including tree poses (Figure 6.2.6: B).

Figure 6.2.6: (A) In year 1 a mindfulness workshop for kids was held by local mindfulness practictioner Louise Cullen of Tranceform Therapies. Participants were asked to tune into each of their senses while standing on the banks of the Bannock burn. (B) In year 2, local yoga teacher Marianna Doneva led a yoga class in which participants were asked to take nature themed poses.

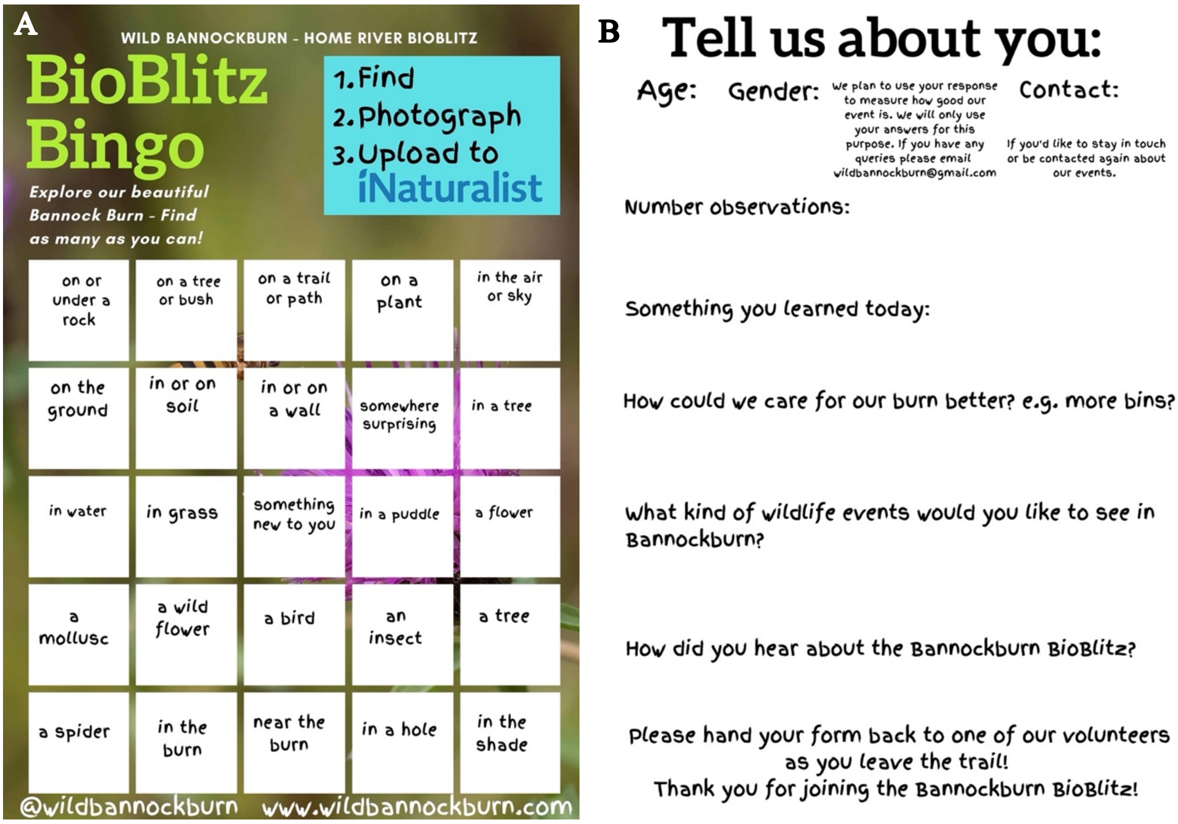
6.2.2 Bannockburn BioBlitz Evaluation

The original outreach ethics form to UTREC was amended to include the evaluation of outputs from the Bannockburn BioBlitz events. The ethical approval form amendment can be found here. The specific objectives and indicators for this project can be found in Table 5.4.3. In the first year evaluation material was collected using a small questionnaire on the back of the BioBlitz bingo card (see Figure 6.2.7:B). In the second year an online Qualtrics questionnaire was designed which could be filled in at any time point before data analysis (see Appendix 6.2).

Table 6.2.3: Specific objectives and evaluation indicators for the Bannockburn BioBlitz

Objectives	Indicators
A free to access wildlife event is created to enable anyone to participate in wildlife informal learning opportunities in their own community's nature spots	Obtaining funding and volunteers to enable free event
Bannockburn community is engaged in own natural heritage	1. Numbers attending the Bannockburn BioBlitz events and workshops

	2. Volunteers from the community helping at the events 3. Creating a website 4. Creating a Facebook page and Instagram page to keep the community connected 5. Bring local organisations to Bannockburn to perform workshops and demonstrations
Ongoing engagement from community	1. The production of a high-quality short film of the event 2. Document the The Bannockburn BioBlitz activities each year via local photographers 3. Maintain website and social media presence 4. Becky river guardians group set up by Buglife 5. Participants likely to recommend to a friend 6. People returning the event each year
Community is brought together for shared purpose	1. Producing a community art project each year based around nature and Bannockburn 2. Taking a community photo each year with the artwork 3. Analysing responses for aspects of community engagement



WILD BANNOCKBURN - HOME RIVER BIOBLITZ

BioBlitz Bingo

1. Find
2. Photograph
3. Upload to iNaturalist

Explore our beautiful Bannock Burn - Find as many as you can!

on or under a rock	on a tree or bush	on a trail or path	on a plant	in the air or sky
on the ground	in or on soil	in or on a wall	somewhere surprising	in a tree
in water	in grass	something new to you	in a puddle	a flower
a mollusc	a wild flower	a bird	an insect	a tree
a spider	in the burn	near the burn	in a hole	in the shade

@wildbannockburn www.wildbannockburn.com

Tell us about you:

Age:

Gender: We plan to use your response to measure how good our event is. We will only use your answers for this purpose. If you have any queries please email wildbannockburn@gmail.com

Contact: If you'd like to stay in touch or be contacted again about our events.

Number observations:

Something you learned today:

How could we care for our burn better? e.g. more bins?

What kind of wildlife events would you like to see in Bannockburn?

How did you hear about the Bannockburn BioBlitz?

Please hand your form back to one of our volunteers as you leave the trail!
Thank you for joining the Bannockburn BioBlitz!

Figure 6.2.7: (A) The BioBlitz bingo card (A5) encouraged participants to explore their natural surroundings and update findings to the iNaturalist app. (B): The back of the BioBlitz bingo card had a series of evaluation questions (used in year 1).

6.3 Impact

In 2021, at least 88 people participated in the Bannockburn BioBlitz and workshops (Figure 5.4.8). This included the creation of a community art project: the WILD Bannockburn sign (Figure 5.4.9: A). Under 20 years = 38; 20 – 35 years = 28 and over 35 years = 22). In 2021, 8 volunteers helped make the Bannockburn BioBlitz happen (including me as the coordinator, workshop leads and general volunteers). We collaborated with over 10 charities and businesses including Froglife and Bugllife.

Twelve evaluation forms were returned representing 18 people who participated on the day (this represented 17.6% of the total 102 participants). The evaluation forms were filled in by mainly adults and parents on behalf of their children and therefore some feedback forms represented more than one person. Of the 18 people represented on the 12 feedback forms the mean age was 12.1 years (max 34 and minimum 3) and median age was 7. Most people found out about the event via social media (5) or school (4) or ‘word-of-mouth’ (3). The average number of observations made on the day by each respondent was 11.8 (minimum = 2 and maximum 24). More than half of respondents were happy to leave a contact number or email address for future events (seven of twelve).

In 2021, responding the prompt ‘Something you learned today’ – the most popular response was ‘river’ (4) followed by ‘bugs’ (2) and ‘health’ (2) (Figure 5.4.10). A main topic was ‘animals’ appearing in 7 of the 12 responses. In 2021, responding to ‘How could we care for our burn better? E.g. more bins?’ over half of respondents (7) indicated ‘litter picks’, followed by ‘more bins’ (5) other answers included ‘bike path’, ‘no pollutants in drains’, ‘plant trees’ and ‘signs’ (Figure 2). In 2021, in response to ‘What events would you like to see in Bannockburn?’ the most popular response indicated ‘similar events’ (4) (to the one attended), followed by ‘bird watching’ (3) and ‘river dipping’ (3) (Figure 3). Other ideas included ‘bat boxes’, ‘beehives’, ‘bug hotel’, ‘nest boxes’, ‘wildlife walks’, ‘fish ladder’ and ‘river clean-ups’.

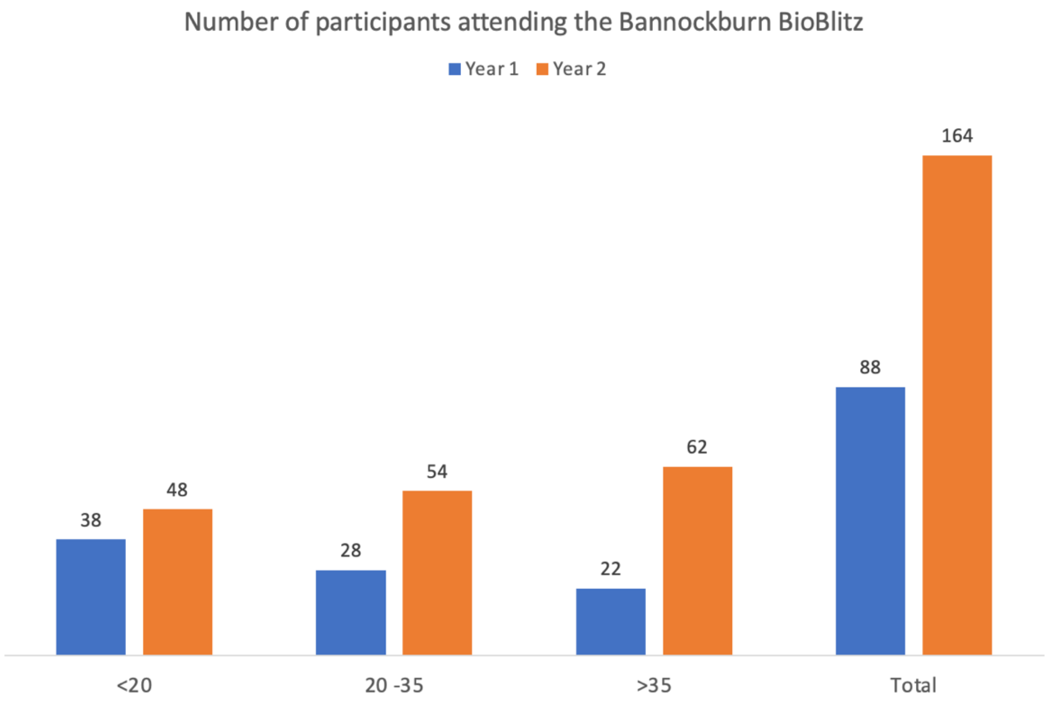


Figure 5.4.8: The number of people in each age band (by visual observation) attending the Bannockburn BioBlitz in each year (blue – Year 1 and orange year 2). The overall total almost doubled between years.

Figure 5.4.9: (A) The final group photo of some of the participants and some of the workshop leaders in year 1 of the Bannockburn BioBlitz. The community WILD art project is revealed. This photo made it into the local newspaper 'The Stirling Observer' in 2021. (B): Group photo of some participants, workshop leaders and volunteers at the end of the 2022 (year 2) Bannockburn BioBlitz with both the WILD sign from year 1 and the Bannockburn banner from 2022 spelling the group name 'Wild Bannockburn'.

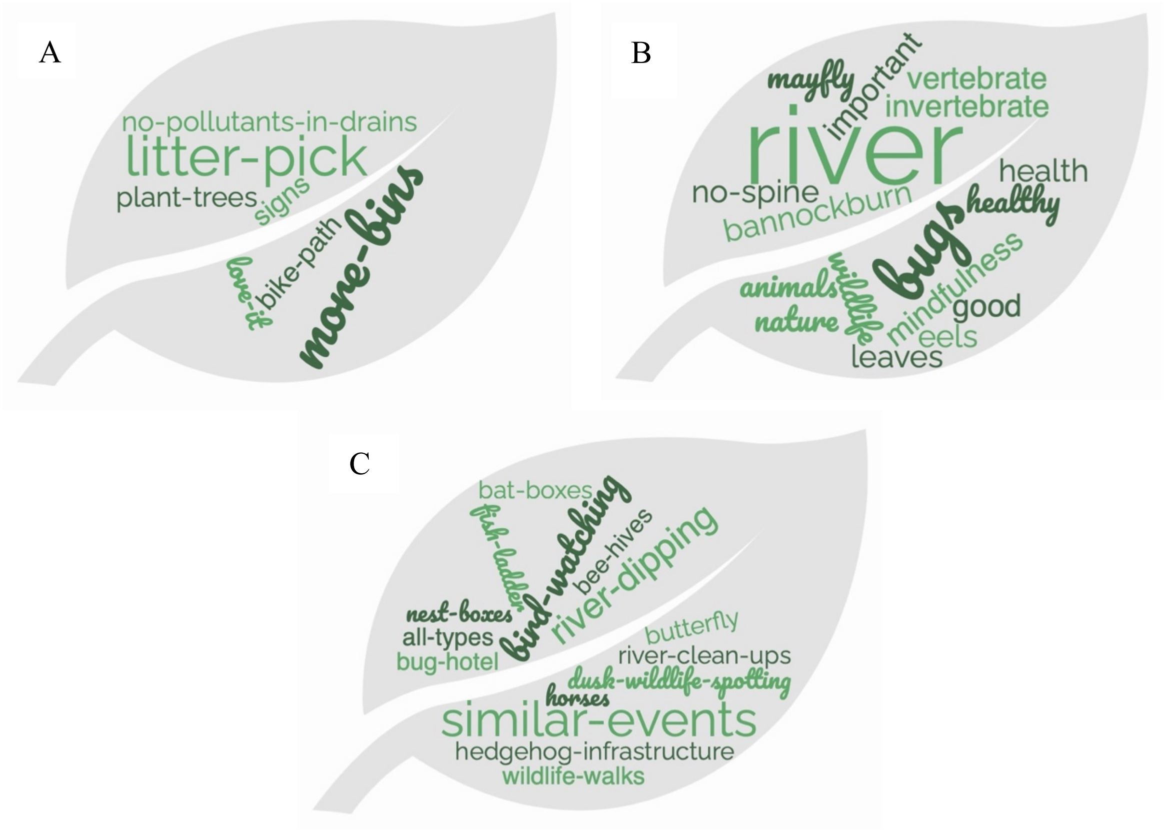


Figure 5.4.10: A: 2021 Word cloud of answers to the question 'How could we care for our burn better?' 7 = Litter-pick; 5 = 'more bins'; 1 = 'bike path'; 1 = 'love it'; 1 = 'no pollutants in drains'; 1 = 'plant trees' and 1 = 'signs'. B: 2021: Word cloud of answers to the question 'What did you learn today?' 4 = "river"; 2 = "bugs": 1 = "animals"; 1 = "Bannockburn"; 1 = "eels 1 = "good"; 2 = "health"; 1 = "important"; 1 = "invertebrate"; 1; = "leaves"; 1 = "mayfly"; 1 = "mindfulness"; 1;"nature"; 1= "no-spine";1="vertebrate"; 1 = "wildlife" C: 2021: Word cloud of answers to the question: "What events next?": 4 = "similar-events"; 3 = "bird-watching"; 3 = "river-dipping"; 1 = "all-types"; 1 = "bat-boxes"; 1 = "bee-hives"; 1 = "bug-hotel"; 1 = "butterfly"

In 2022, at least 164 people participated in the Bannockburn BioBlitz and workshops (Figure 5.4.8). This included the creation of a community art project: the WILD Bannockburn banner (Figure 5.4.9: B). Under 20 years = 48; 20 – 35 years = 54 and over 35 years = 62). In 2022, 8 volunteers helped make the Bannockburn BioBlitz happen (including me as the coordinator, workshop leads and general volunteers). We collaborated with 10 charities and businesses and additionally the local churches joined forces to bring a stand with refreshments for the participants.

In 2022, the evaluation form was circulated in an online format due to low uptake of paper evaluation forms on the event day. This allowed me to make several updates to the original form to improve the data collection process. 9 people indicated they had attended the 2022 event, 5 people the 2021 event and 1 person the litter pick event in March 2022. Eleven evaluation forms were returned representing 38 people (This represented 23% of the 164 total participants). Most groups attended the events in groups of three people (4 groups) followed by 2 and 6 people (2 groups each) (Figure 5.4.12). In response to the question 'How likely are you to make a change as a result of attending this event?' the most popular answer was 'very likely' (5 responses) followed by 'likely' and 'neutral' (3 responses each). 'Unlikely' and 'very unlikely' received no votes. In response to the question 'what actions will you take as a result of this event?' 6 of the 11 respondents provided an answer. The most popular answers indicated 'litter picking' and 'walking' as actions (3 each) followed by answers indicating more time spent by the burn (2). Other responses are indicated in Figure 5.4.13. In response to the question 'How likely are you to recommend the event to a friend?' 9 responses indicated 'very likely' and 1 'likely'. 1 response indicated 'very unlikely' but this respondent's overall answers indicated they really enjoyed the event, so it is likely this was human error. Like 2021, the 2022 evaluation form included the question 'How could we care for our burn better?' but this time included a list of options. 'Regular community litter clean ups' and 'more wildlife and conservation events' each received 11 votes each (100% of respondents voted for these). 'Information signs around the trail' obtained 9 votes and 'More bins' 8 votes and foraging workshops 7 votes (see Figure 5.4.13). In response to 'Do you think the Bannockburn Heritage trail should be considered as one of Stirling Council's new local Nature Conservation Areas 9 respondents voted 'Definitely yes' and 2 respondents 'Probably yes' (Figure 5.4.14). Postcode information was also obtained in this new updated evaluation form to map on to the SIMD index. The respondents of the 2022 survey were mostly women (8 females and 3 males). Beyond a thorough examination of the quantitative data extracted from the evaluation forms, the inclusion of individual reflections made by participants was deemed equally pivotal in the analysis. One anonymous participant, in particular, expressed their sentiments, stating: "We are grateful to have these events within our community. It brings people together in a fun way but also educates children and adults alike."

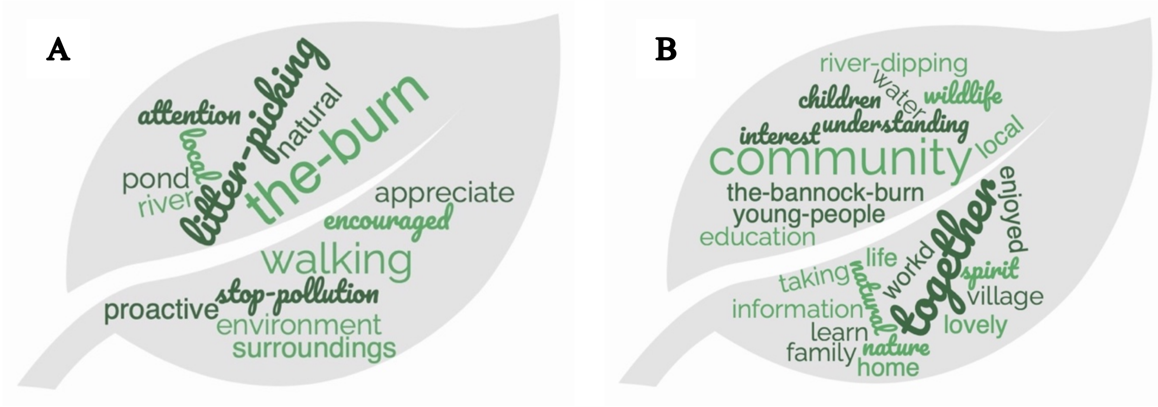


Figure 5.4.11: (A) 2022: Word cloud of answers to the question: "What actions will you take?" 3 = "litter-picking"; 3 = "walking"; 2 = "the burn"; 1 = "appreciate"; 1 = "attention"; 1 = "encouraged"; 1 = environment; 1 = "local" (B): 2022: Word cloud of answers to the question: "What did you find useful?" 4 = "community"; 2 = "together"; 1 = "children"; 1 = "education"; 1 = "enjoyed"; 1 = "family"; 1 = "home"; 1 = "information"

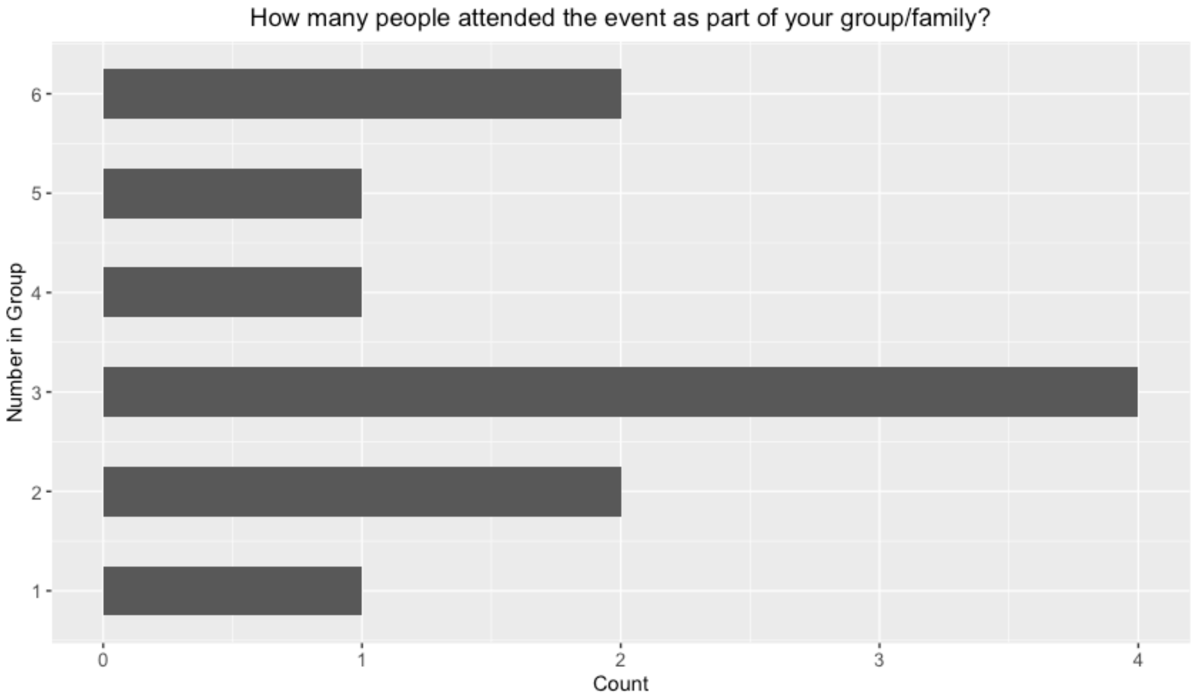


Figure 5.4.12: Group size of participants joining the Bannockburn BioBlitz

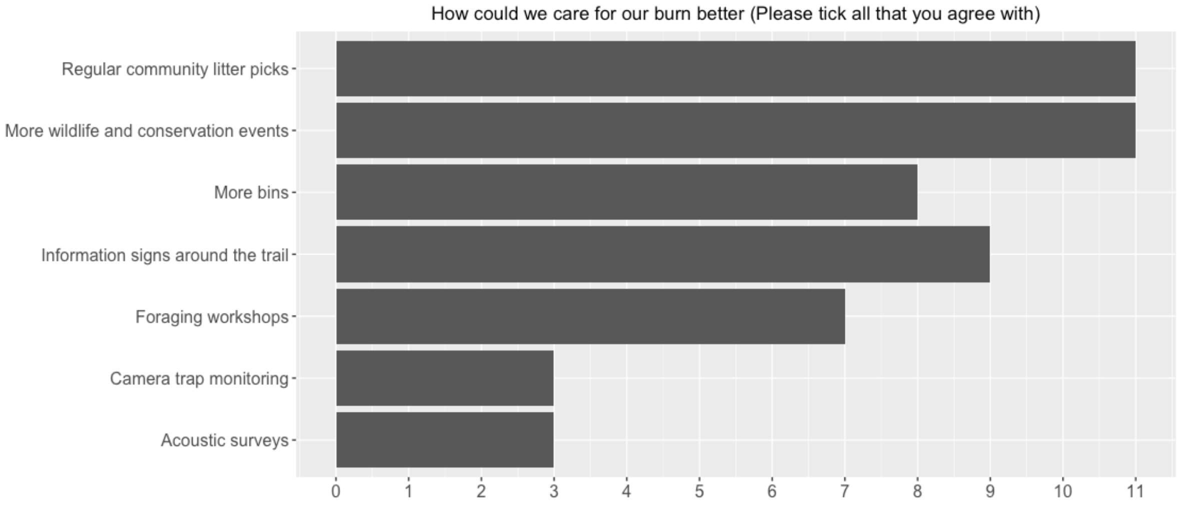


Figure 5.4.13: How could we care for our burn better? Number of votes for each option. Participants could tick all that they agreed with. Regular community litter picks and more wildlife and conservation events received the maximum of 11 votes each.

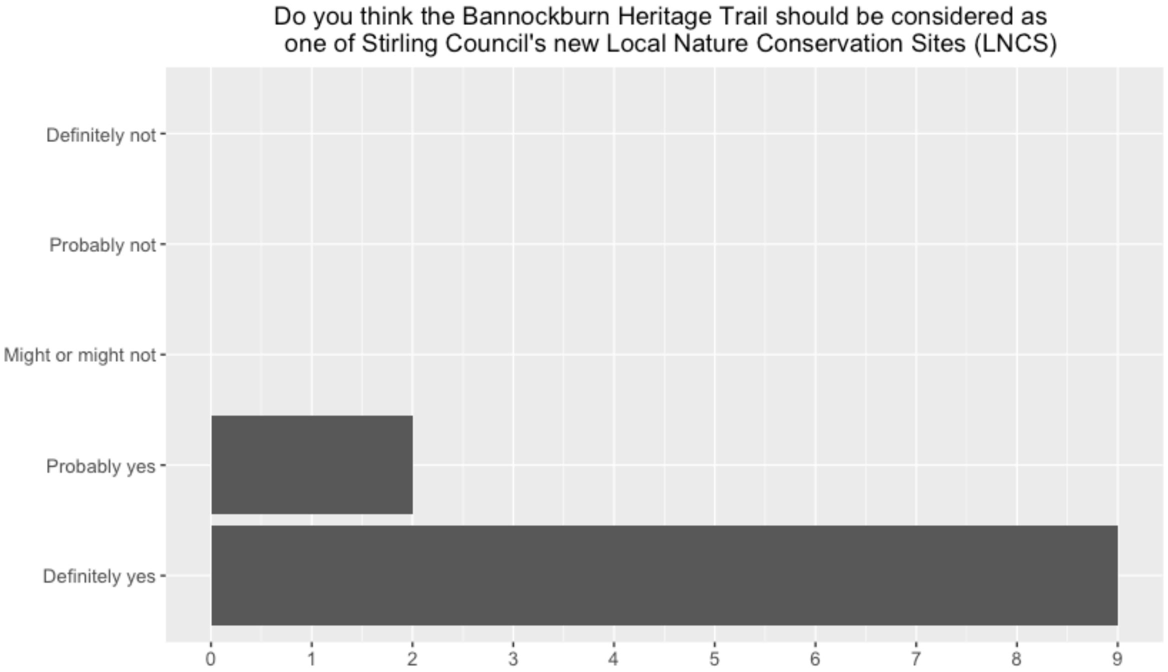


Figure 5.4.14: Do you think the Bannockburn Heritage Trail should be considered as one of Stirling Council's new Local Nature Conservation Sites (LNCS)? Number of votes for each option. All participants voted for 'yes' to varying degrees.

The Bannockburn BioBlitz has had significant medium to long-term impacts on both local and global scales. With its success and recognition, the project has been brought to world stages, such as the prestigious COP26 concert for the climate, gaining international attention and support. Locally, the event has become an eagerly anticipated annual occurrence, approaching its third year, with the community now expecting the BioBlitz as an enriching experience for their children and the environment. The event has garnered media attention, being featured in a local newspaper, further spreading awareness and engaging the broader public. Additionally, the BioBlitz has catalysed the establishment of a local river guardians group, demonstrating the lasting legacy of the initiative. As the project continues to flourish, it has been fortunate to receive small grants, enabling its ongoing efforts. Looking ahead, there is a strategic vision to register the group as a Scottish Charitable Incorporated Organization (SCIO) or a charity. This step aims to unlock access to larger grants and ensure the long-term sustainability of Wild Bannockburn's endeavours, ultimately future-proofing their commitment to environmental conservation and education. See Figure 5.4.15 for more examples of the medium to long-term impacts achieved by the

Bannockburn BioBlitz and the Wild Bannockburn project.

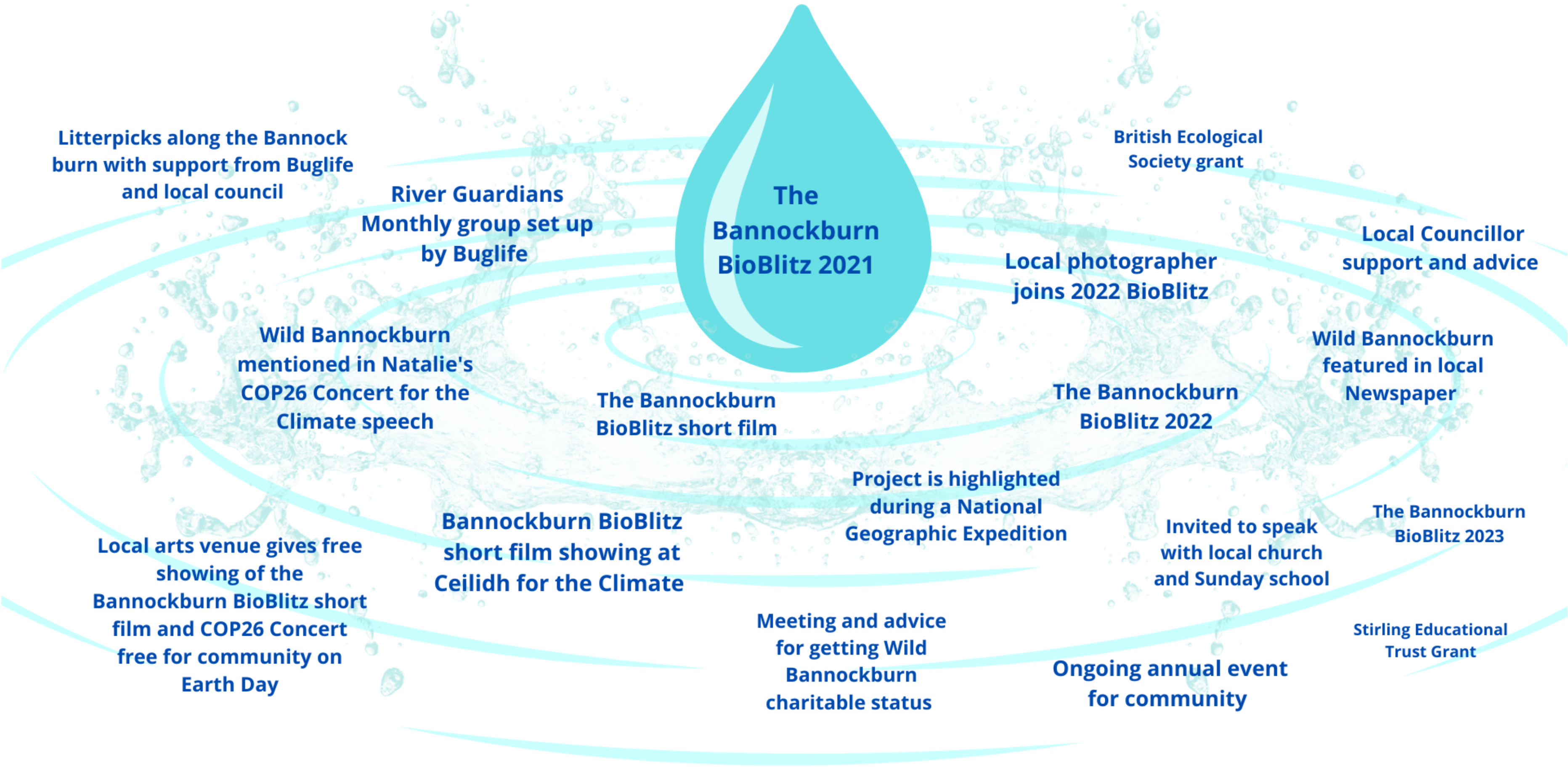


Figure 5.4.15: Long-term impacts from the Bannockburn BioBlitz

6.4 Discussion:

I embarked on the Wild Bannockburn project, partly in response to the Covid-19 restrictions that compelled me to relocate to Bannockburn and recognise the necessity for such a project in my area. The Wild Bannockburn project was also designed as an open-air event, making it less susceptible to changing Covid-19 restrictions. The Wild Bannockburn and Bannockburn BioBlitz projects were designed in a way that allowed for accessibility outside of a specific location and could be easily adapted for different settings and times. The activities offered transcended the limitations of a physical space and demonstrated the power of collaboration, creating materials, and establishing connections that extend beyond the confines of a single location. This highlights the importance of developing flexible and adaptable approaches to public engagement that can reach a wider audience and have a lasting impact, regardless of specific physical venues.

The success of the Bannockburn BioBlitz can be observed through the significant increase in attendance between year 1 and year 2, nearly doubling the participant numbers aligning with my aim to create a free to attend wildlife event that would be accessible to low SES and low science capital communities. Short-term impacts were evident based on responses from both questionnaires, indicating that participants intended to make behavioural changes as a result of their involvement in the event. Many participants explicitly mentioned their intention to modify their behaviour after attending the Bannockburn BioBlitz. These responses had a tangible effect on the community, as they were implemented during a community litter pick, representing medium-term impacts stemming from the event aligning with my aim to nurture ongoing engagement within the community. Moreover, due to the positive feedback received from participants regarding their enjoyment of the river-dipping sessions and their desire to contribute to the health of the Bannock burn and surrounding areas, a "river guardians" group is being established and is scheduled to launch in summer 2023. This initiative further demonstrates the lasting impact of the event. It is worth noting that a significant number of respondents to the first-year evaluation form mentioned that they found out about the BioBlitz through word of mouth. This suggests that participants from the first year actively spread the word, resulting in an increased attendance in the second year. Furthermore, the fact that many participants from the first year returned for the second year serves as another testament to their enjoyment of the events.

Assessing the success of the Bannockburn BioBlitz solely based on written answers proved challenging. Additionally, I discovered from the first year's event that many adults who participated with small children found it difficult to provide written answers in a public setting due to the logistical demands of caring for their children. Moreover, I recognised that some individuals might not feel confident writing in a public environment or could experience pressure to respond in a particular manner. Considering these factors and the low response rate for the paper form in the second year, I opted to create an online questionnaire using Qualtrics. This approach allowed me to update the questions and gain a better understanding of the event's attendees. Furthermore, it enabled me to pose additional questions that aligned with the project's long-term goals. It's worth noting that encouraging participants to fill in forms and provide feedback can be challenging across various evaluation techniques, and my experiences are not unique in this regard. In the future, a modest financial incentive to stimulate greater participation in the evaluation process could be offered. This could potentially lead to increased response rates and a more comprehensive understanding of participant perspectives. Furthermore, individual qualitative comments proved tremendously useful in assessing the quality of the event. Many of these comments captured the meaningful impact of the events on community cohesion and educational outcomes for both children and adults and were just as important as the quantitative data derived from the evaluation forms.

Another form of evaluation involved documenting the community's involvement in creating the community art projects. In the first year, we had the 'WILD' boards adorned with fallen leaves collected by BioBlitz participants. In the second year, we crafted a 'Bannockburn' banner using linen bunting. Both children and adults engaged in lino-printing plants and animals found around the Bannock burn onto the bunting pieces, which were then threaded together to form the banner. We captured photographs of the event's participants alongside the WILD sign and the Bannockburn banner, serving as a visual record of the community's collaborative effort during the event aligning with my goal to demonstrate shared purpose within the community. I observed that participants were highly enthusiastic about participating in both of these activities. To enhance this aspect for future events, we could consider incorporating an evaluation element. For instance, I could ask participants to write down words they associate with the Bannock burn directly onto the art project itself. This approach would allow us to combine the enjoyable experience of the community art project with the collection of responses from the participants, providing a more comprehensive evaluation of their perceptions and associations.

Another avenue for enhancing evaluation in future events involves utilising photographs as a method of assessment. In each Bannockburn BioBlitz event, I collaborated with local photographers to capture the enchantment of the event through both posed and candid shots. The candid photos prove particularly valuable in documenting participants' engagement in the activities. However, it's important to note that these photos are subject to the photographer's discretion and may present a bias toward more positive interactions. Exner-Cortens *et al*. (2021) have employed self-based photography as an evaluation method in their project, which focuses on participatory evaluation with adolescents. This approach would involve collecting photos from the participants, encompassing not only the wildlife they have discovered and identified but also their personal interactions with nature and other community members. It is essential to obtain explicit consent from adults to utilise photographs featuring their children for such a study. Additionally, rigorous privacy guidelines would be followed to anonymise the data to the greatest extent possible.

6.4.1 Personal reflections on outreach

Working as a team member on the Sea Symphonies project and leading the evaluation of the exhibition provided me with the necessary experience and confidence to initiate the Wild Bannockburn and Bannockburn BioBlitz projects. Through my involvement in Sea Symphonies, I gained valuable experience in collaborating with team members from diverse disciplines. I worked closely with the project manager, Ken Boyd, and the graphic designer, Steve Smart, to design various elements such as the Floor Piano sheet music, the 'whale passport,' the whale post box, postcards, whale song badges, the 'Respond' station, and the tags used for responses. Upon assessing the exhibition area and available equipment, I worked in conjunction with the team to develop a cohesive approach that unified the multiple exhibits (a total of 8) into a single, immersive experience. Drawing on my background in animal communication research, I assigned verb titles to each exhibit, reflecting behaviours that could also be observed in whales (e.g., Communicate, Respond, Play, Evolve, etc.).

I discovered a talent for effective collaboration with individuals from diverse sectors, particularly outside of the university environment. This skill was further cultivated and applied in the Wild Bannockburn project, where I forged enduring connections with local charities, businesses, and schools. Building upon my experience in designing materials for the Sea Symphonies exhibit, I assumed the role of graphic designer for Wild Bannockburn, taking charge of creating visually appealing assets such as the map, iNaturalist guides, and BioBlitz bingo cards. Additionally, I designed the captivating logo, eye-catching posters, and user-friendly website for the project. It was my collaboration with graphic designer Steve Smart during the Sea Symphonies project that instilled the confidence in me to independently create these materials. As for the Bannockburn BioBlitz event, I adopted a similar format, where participants were guided to different workshops along the Bannockburn nature trail. However, unlike the user-led experience within the Dundee Science Centre, this event was condensed into a single day and led by workshop facilitators. My role involved coordinating participants and ensuring their seamless transition between workshops, presenting a unique set of challenges distinct from creating a user-led experience.

In the Wild Bannockburn project, I achieved success by securing a small engagement grant from National Geographic/iNaturalist in the first year, followed by the British Ecological Society in the second year. Once again, I was entrusted with the task of creating evaluation stands and products within a limited budg*et* allocated from the overall Sea Symphonies exhibition budget. This experience heightened my awareness of maximising the value of my resources while maintaining quality. Furthermore, my ability to lead a project was strengthened as I successfully organised and coordinated a team of ten individuals both leading up to and on the day of the event. Building upon my previous experience in Sea Symphonies, where I had the responsibility of overseeing project timelines and collaborating with the project manager and team members, I continued to refine my project management skills. The Wild Bannockburn project also provided an opportunity for me to enhance my public speaking abilities. This included presenting in a short film and delivering speeches at live events, such as the COP26 Concert for the Climate, at which almost two thousand people attended. These experiences allowed me to cultivate effective communication skills and confidently engage with diverse audiences.

The primary challenge I encountered in my public engagement work was striking a balance between the continuous time commitment it required and my doctoral research. The skillsets needed for research and public engagement are distinct, and transitioning between the two mindsets (open, networking, coordinating, designing versus focused, analytical, solitary) could be challenging at times. However, engaging in both public outreach and research provided me with valuable opportunities to practice and refine the ability to switch between these diverse tasks, ultimately enhancing my time management skills.

I used the Researcher Development Framework (RDF) planner to track how my qualities as a researcher evolved through my leadership roles in the two aforementioned public engagement projects. The RDF was developed based on empirical data obtained from interviews with researchers, aiming to identify the key attributes of exceptional researchers. It consists of four main domains and 12 sub-domains. Within these domains, a total of 63 characteristics are identified. Each characteristic is divided into five phases, ranging from 'Phase 1' indicating the lowest level of performance or development to 'Phase 5' representing the highest level. To evaluate my growth, I reflected on my experiences throughout the two public engagement projects and assessed my development across all 63 characteristics before and after completing the projects. Notably, my progress was most pronounced in the domain of 'public engagement.' Initially, I was at Phase 2, contributing to promoting public understanding of my research area. However, I advanced to Phase 4, where I began establishing a reputation for public engagement, as evidenced by receiving the University of St Andrews Public Engagement award in 2021 and becoming recognised as an advocate for public engagement. Moreover, my skills in communication and dissemination have shown significant improvement. Additionally, my abilities in working with others, including people management and collaboration, have substantially increased.

Working on both of these projects has played a significant role in helping me articulate and deepen my passion for engaging communities with low socioeconomic status (SES) and limited science capital. Through my involvement, I have gained a deeper understanding of the educational landscape in Scotland and the UK, particularly in relation to my own primary and secondary education. It has become clear to me that there are significant disparities in both formal and informal learning opportunities for individuals across the country, often based solely on their place of birth and their limited exposure to science. An eye-opening realisation came when I discovered that during the year I left Bannockburn High School, fewer than 16% of pupils achieved 5 or more Highers (the requirement for pursuing higher education from a Scottish high school system). This placed my high school within the bottom 5% of state schools in Scotland. The chances of a student from my high school, with limited science capital, going on to study science-related subjects at prestigious universities like St Andrews were incredibly slim. This realisation further fuelled my determination and passion to give back to my community and inspire children growing up in similar circumstances, showing them that they too have the potential to develop their science capital and achieve remarkable things. By actively engaging with communities and fostering educational opportunities, I hope to contribute to breaking the cycle of inequality and empowering individuals with low science capital to explore the world of science, technology, engineering, and mathematics (STEM). Through my work, I aim to demonstrate that science is accessible and to empower individuals to pursue their dreams and aspirations, regardless of their socioeconomic background or inherited science capital. Furthermore, to underscore the importance of public engagement alongside active research as a scientist.

Chapter 6 Appendices

Figure A6.1: Posters for the Bannockburn BioBlitz. (A) 2021 (B) 2022.

Appendix 6.2 2022 Qualtrics evaluation questions

List of questions on the online Qualtrics form for **Year 2** of Bannockburn BioBlitz

• What event or events have you attended with Wild Bannockburn? Please tick all that apply - The Bannockburn BioBlitz 2021 (25th September 2021) - The Bannockburn BioBlitz 2022 (18th June 2022) - The Bannockburn Litter Pick (12th March 2022)
• How many people attended the event/events as part of your group/family? (if you attended more than one event please fill in for the most recent event) - Options from one to ten
• Please indicate your age range and gender? (the person filling in this form) - 12 - 18 years - 19 - 35 years - 36 - 65 years - 65 + years

• If also filling in on behalf of a group: What age ranges attended the event as part of your group/family (including yourself)? Tick all that apply - 0 - 5 years - 6 - 11 years - 12 - 18 years - 19 - 35 years - 36 - 65 years - 65 + years
• What did you find most useful about this event? - Open question with text box
• How likely are you to make a change as a result of attending this event? - Likert Scale (Very Likely to Very unlikely)
• What actions will you take as a result of this event? - Open question with text box
• How likely are you to recommend the event to a friend? - Likert scale (Very likely to Very unlikely)
• How could we care for our burn better? (Please tick all that you agree with) - More bins - More wildlife and conservation events - Information signs around the trail - Regular community litter clean ups - Camera trap monitoring - Acoustic surveys - Foraging workshops
• Do you think the Bannockburn Heritage Trail should be considered as one of Stirling Council's new Local Nature Conservation Sites (LNCS)? - Likert scale (Definitely not to Definitely yes, including Don't know)
• What's your postcode? - Open question with text box • Would you like to tell us anything else? - Open question with text box

7 General Discussion

7.1 Summary of Findings

I began this thesis by outlining humpback whale song research to date and how this relates to debates in cumulative cultural evolution. Furthermore, I described how humpback whale song has been used as an effective took for engaging the public in science and conservation.

In Chapter 2 I developed a conceptual analysis of the compatibility of cumulative cultural evolution (CCE) with aesthetics across different fields. Current thinking on cumulative cultural evolution and aesthetics was brought together by an interdisciplinary team to discuss how aesthetic culture fits into the concept of cumulative cultural evolution. I argued that the concept is problematic to reconcile with dominant views of aesthetics in philosophical analysis and struggles to characterise aesthetic cultures that evolve over time. A tension arises from fundamental differences between cultural evolution in aesthetic and technological domains, which contributes to current debates between reconstructive and preservative theories of cultural evolution. In addition to our interdisciplinary exploration, I presented a case study involving nonhuman animals to assess the implications of our findings within the realm of nonhuman animal culture. By doing so, I aim to spark further discussions and investigations into the concept of cumulative culture evolution within the domain of aesthetics. This chapter serves as a catalyst, opening up new avenues of discourse and collaboration between different disciplines. I hope that it marks the beginning of a fruitful exchange that will deepen our understanding of CCE and its implications across various domains.

In Chapter 3 I tracked the evolution of one humpback whale song unit type across different themes within one song type over the breeding season. I utilised the natural hierarchy of the humpback song to track the same song unit (the basic building block of the song) in different themes (a higher level of the song). I identified a unit type that was able to be tracked over multiple theme types. I made a number of methodological efficiencies, building on previous humpback whale song research, to enable a much larger number of units to be processed for analysis. Over the time scale examined (one month of the breeding season) I found that the 'groan' unit was generally stable and there was no divergence in overall acoustic similarity between the same unit in different theme types. More variability in unit trajectories between different themes was detected within song sessions both between and within individuals providing more support for the vocal production learning hypothesis. Examining unit evolution across themes within individuals may control for interindividual variation however current acoustic technologies do have constraints that prevent more than 48 hours of the same individual being captured at a time. The methodologies utilised in this chapter (and Chapter 4) open up possibilities for investigating much larger datasets of humpback whale song units with a fine-scale analysis, which was challenging to address before due to the significant time investment it required.

In Chapter 4 I built on Chapter 3 through examining the evolution of one humpback song unit type but over a longer time frame - over two seasons and locations – and a different ocean basin, the North Atlantic. Firstly, I matched the song types present in the Eastern Caribbean in 2020 and Scotland in 2021. I then tracked the evolution of one unit type present in this song, again over two time-scales: within the song session and over two seasons (2020 breeding and 2021 migration). I found a clear match in song type between the two locations which enabled exploration of a unit type over multiple seasons and locations. This match in song type and evolutionary timing also supported photographic data of the cross Atlantic migration of humpback individuals from the Eastern Caribbean breeding population and confirms the extraordinary scale of humpback song cultural evolution processes. Across the longer time scale of two seasons much larger changes in overall acoustic structure were detected however this did not add up to a significant divergence between theme types. Nonetheless when analysing discrete measurement types 6 of the 8 measurement types showed significant change across the season. This provides evidence against the presence of an innate template of units and supports the vocal production learning hypothesis, as the same unit undergoes different changes across different themes, suggesting separate updates of acoustic templates. This study contributes to the empirical investigation of vocal learning in humpback whales by utilising the natural structural hierarchy of their songs. Unlike captive experimental vocal learning assessments, which are neither feasible nor ethical, this approach relies on passive acoustic recordings to gather valuable insights into the vocal learning abilities of humpback whales.

In Chapters 5 and Chapter 6, I ventured into a thematic and methodological divergence from the preceding chapters by conducting two case studies in the realm of public engagement in science. Chapter 5 revolved around the development and implementation of an interactive science exhibition, which took place over several months within a science centre. Chapter 6 focused on a one-day annual event complying with outdoor meeting during the COVID19 guidelines. Both projects showed evidence of wide success in engaging public groups. The science centre exhibition was well attended and showed evidence of meeting the learning outcomes in whale song research. The annual community science event doubled in number from the first to the second year and has built long lasting collaboration with local charities and schools. Impact has included national events, such as at the Concert for the Climate during COP26. One noteworthy finding from my observations is that the level of funding allocated to a public engagement project does not necessarily correlate with its level of impact, particularly in the long term. This observation was especially evident during the COVID-19 restrictions imposed on the Sea Symphonies exhibition. As the exhibition could only be accessed within the physical premises of the Dundee Science Centre, any closure of the centre meant that no one could benefit from the exhibition. In contrast, the Wild Bannockburn and Bannockburn BioBlitz projects were designed in a way that allowed for accessibility outside of a specific location and could be easily adapted for different settings and times. The activities offered transcended the limitations of a physical space and demonstrated the power of collaboration, creating materials, and establishing connections that extend beyond the confines of a single location. This highlights the importance of developing flexible and adaptable approaches to public engagement that can reach a wider audience and have a lasting impact, regardless of specific physical venues. The impact on the public groups engaged with the projects was evident as too was the impact on me professionally. My ability to manage projects has improved dramatically and this can be seen in the before and after Research Development Framework spider plots in which I have seen a clear link between my leadership in the public engagement projects and sharp increases in the public engagement, communication and dissemination and working with others criterion. I am proud to include these chapters as a first for Biology PhDs at St

Andrews and to show the benefit and responsibility of researchers to engage with those outside of the university environment alongside their active research, while also showing the impact on the researcher themselves.

7.2 Limitations and Caveats

In Chapter 2, it is important to note that our conceptual analysis has a limited scope, specifically focusing on selected case studies of human aesthetic cultures and potential cumulative culture in animals. It is essential to recognise that these examples, such as music in human aesthetic cultures and humpback whale song as an animal culture case study, do not encompass a comprehensive analysis of all nonhuman cultural phenomena or the entirety of aesthetic cultures in humans. Additionally, it is crucial to acknowledge that while humpback whale song is examined as a potential instance of cumulative culture in nonhuman animals, the findings and conclusions derived from this case study may not be universally applicable to all species. This aspect will be further elaborated upon in the subsequent section on future directions for cumulative culture and animal songs, particularly when referencing a recent study on Savannah sparrow song. Lastly, this chapter delves into the philosophical debates surrounding the nature of aesthetic value and improvement. These debates involve multiple perspectives and interpretations, and it is important to acknowledge that the conclusions drawn are influenced by the specific philosophical stance taken in this study. Alternative philosophical perspectives may lead to different interpretations and conclusions.

In Chapter 3 and Chapter 4, one notable limitation of these studies was the difficulty in obtaining high quality humpback whale song recordings. The scarcity of high-quality song recordings restricts the sample size and potentially introduces bias in the analysis. This was also connected to the limitation of controlling for the effects of overall time in the season and individual differences is essential but challenging due to their intertwined nature. The scarcity of high-quality song recordings limits our ability to fully disentangle the influence of these variables on unit type changes. It is also important to acknowledge that this study focused on a specific population in a particular ocean basin. The generalisability of the findings to other humpback whale populations and ocean basins may be subject to regional and ecological variations. Replication of these studies across different populations would enhance the robustness and generalisability of the rate of change in acoustic structures across one (Chapter 3) and two (Chapter 4) seasons. In Chapter 4, the robustness of the song connection between the Caribbean and Scotland, as indicated by song type and evolutionary dynamics, is evident. However, it is crucial to conduct a thorough investigation of concurrent recordings of songs originating from the eastern breeding grounds in the North Atlantic (specifically Cape Verdes) to assess the similarity of songs across these breeding locations. Lastly, while the findings of this study lean in support of the vocal learning hypothesis, it is important to consider alternative explanations for the observed unit type changes. Factors such as environmental influences and individual variation in learning abilities could also contribute to the observed patterns. Further investigations and experimental manipulations are necessary to disentangle these potential confounding factors which are discussed in the subsequent section on future directions.

In Chapter 5, an unavoidable limitation of the Sea Symphonies exhibition was due to the early closure of the exhibition due to the COVID-19 pandemic. This meant that the exhibition was not able to meet some of its original targets and goals. This closure and the associated restrictions prevented the completion of planned activities such as changing the question at the "Respond" station and conducting school workshops and follow-up questionnaires to monitor medium to long-term impacts. There may have been a potential bias in the data analysis of Sea Symphonies tags and postcards as tags for younger participants may have been filled in by adults. Similarly, in Chapter 6, the evaluation forms for the Bannockburn BioBlitz were not filled in by all participants, and there could be biases in the responses collected. Some adults with small children may have faced logistical challenges in writing answers publicly, and others may have felt pressure to answer in a particular way. Lastly, postcode data was not collected during the Sea Symphonies exhibition, and it was only collected in year 2 of the Bannockburn BioBlitz event by a limited number of people. Therefore, it is challenging to assess the specific socio-economic backgrounds of the participants reached. However, it is assumed that many of the participants reached were within our target demographic due to the events' location.

7.3 Future Directions

7.3.1 Cumulative Culture in human aesthetic cultures and animal songs

Since publishing my second chapter, it has become relatively rapidly cited. For instance, Williams *et al*., (2022) used it in framing their claim for cumulative cultural evolution in the songs of wild Savannah sparrows (*Passerculus sandwichensis)*. They found that males replaced “high note clusters” with “click trains” and then later modified the “click trains” by adding more clicks over time, a change which apparently made the song more effective. They claim that these two sequential changes in the same part of song satisfy Mesoudi and Thornton’s (2018) 4th criterion that “steps 1, 2 and 3 are repeated to create sequential improvement over time” because their mathematical modelling shows that the changes in the song were due to selection (specifically sexual selection) rather than drift or frequency-dependent bias. Williams *et al*., (2022) also note in their discussion that the sexual selection of the click train and subsequent increased number of clicks is likely caused by some combination of demonstrator or payoff bias and/or female sensory predispositions (which may themselves be learned). They therefore liken the cumulative evolution they have found in Savannah sparrow songs to CCE observed in human social artefacts such as language, pottery, ornamentation styles or music (in which they cite our paper), rather than to human material technology.

However, I am unsure whether an increase in fitness by one change in the song, followed by another increase in fitness by another change in their song at a later time, would qualify as “sequential improvements” to satisfy the 4th criterion of Mesoudi and Thornton (2018)’s framework. The ‘improvement’ in fitness that some individuals confer by adopting the trait early on, is lost when the majority of the population have adopted the trait. In other words, the alleged turn of the ratchet steadily turns back to its starting position as time goes on and this resembles more the notion of a ‘cultural trap’ outlined by Lachlan and Slater (1999). Thus, we find ourselves in a similar starting point as before any song modification was adopted, in terms of any advantage that the first song modification (e.g., replacing “high note clusters” with “click trains”) may have provided. At this stage, another change may happen (e.g. adding more clicks to the “click trains”) that confers a new advantage, as documented by Williams *et al*., (2022).

A similar question is discussed by Garland *et al*., (2022) in humpback whale song, who ask whether humpback song could be considered cumulative culture. Garland *et al*., (2022) describes the increase in complexity in humpback whale songs in evolution years followed by decreases in complexity when a new song is adopted (revolution years) in the South Pacific Ocean. I described this change as a case study of CCE in nonhuman animals in Chapter 2. Garland *et al*. (2022) built on the finding of Allen *et al*., 2018 in which complexity in humpback whale song was found to rise but then decrease when a new song was adopted in revolution years. This finding was confirmed in their study which analysed nine years of whale song in New Caledonia. Garland *et al*., (2022) claim that the increase in complexity over time in evolution years in the humpback whale songs may satisfy the Mesoudi and Thornton’s core criteria for CCE if this increase in complexity can be tied to fitness benefits of individual singers. This argument mirrors that described by Williams *et al*., (2022). However, even if an increase in complexity can be linked to an increase in fitness, I maintain that it does not qualify as cumulative cultural evolution (CCE) as per Mesoudi and Thornton (2018)’s core criteria. This is because the improvement in fitness is short lived and is in reference to the rest of the population. It is not the case that individuals possessing advantageous traits retain them and continue to accrue further advantages or in other words that the song gains beneficial modifications and then build on these modifications; rather, new traits emerge in the form of a new song or embellishment, which provides a temporary boost in attractiveness conveying a fitness advantage at that time. The trait then becomes widespread in the population and no longer conveys the same fitness advantage. Now that the effectiveness of the original change has worn off and another change may now be adopted to enhance fitness. In other words, the cycles of innovation can be likened to "running to stand still." At best, there may be a temporary advantage for individuals who exhibit the trait earlier, similar to a scenario where some individuals compete to win a 100m race faster than others. However, in the end, everyone reaches the finish line and the race resets, bringing us back to the starting point rather than progressing further to, for example, a 200m race.

Cumulative cultural evolution is characterised by a turning of the ratchet – as coined by Tomasello (Tomasello, 2000; Tomasello, 1994) – in which improvements are made and their advantage retained. In both the Savannah sparrow and humpback whale song examples the cycles of innovation do not continually progress in one direction but lose their effectiveness over time, which refutes the core of cumulative cultural evolution in marking the idea of progress over time. While in the Savannah sparrow example there is a change in element of the song, this is more markedly illustrated in the humpback whale song in which the change is quantified as an increase in complexity which drops on the adoption of a new song. On the other hand, in technological examples of CCE when an innovation spreads through the population *everyone* is better off (e.g. we can all use faster computers, we can all use more efficient cars); competition is not required to retain the advantage – we can continue to improve- sequential improvement. Williams *et al*., 2022 define Mesoudi and Thornton's fourth criteria as "a later repetition of steps 1 – 3 that results in different increments of change in the same behaviour" which I think masks the true meaning of Mesoudi and Thorntons original fourth criteria which states "steps 1, 2 and 3 are repeated to create *sequential improvement* over time" (my emphasis).

It may be that Mesoudi and Thornton's core criteria have to be clarified to make clear that the sequential improvement continues to move in one direction rather than having different increments of change that result in no overall improvement over time. This is similar to our analysis of music in Chapter 2 in which the possibility of some small-scale improvements may be tracked over time within a particular musical niche or, in other words, within a bounded context. For example, Grunge music in 1990s in Seattle encapsulates a particular time, place and group of people interested in one particular activity. Within this scenario we may be able to determine that there is shared sense of progression within the music scene (this band is good vs this band is bad) but we couldn't generalise this change to another musical niche. This may be because aesthetic cultures depend so much on the observer we have to also tightly bound the context of the observer as well. This idea is also illustrated in current work on literature from Pianzola *et al*., (2020) in which CCE is used as a framework to assess potential improvement in fan fiction (such as in Harry Potter fan fiction online). This work has the benefit of being able to amass great amounts of literary content that has reactions from the community – such as likes, comments and etc. However, even if the ‘likes’ or ‘kudos’ that a particular piece of fan fiction receives can be accurately quantified as an indication of how good the writing is, the ‘improvement’ in a piece of writing is not maintained over time and the improvement is only significant within the tightly bound confines of the harry potter fan fiction readership at that time, much like 1990s Grunge listeners in Seattle.

Returning to animal song, in a similar fashion to 1990s Grunge progression or Harry Potter fan fiction, the change in humpback song may convey a fitness advantage for the males of a particular population due to the preference of the females of that particular population, but this is only true for a particular place and time. The song sung in The Cook Islands in 2019 wouldn’t convey the same advantage if the male sang in a different location or at a different time (e.g. in New Caledonia, or in 2023). The ‘improvement’ is only significant within the defined system. On the other hand, for technological cultures, it doesn’t matter who has the technological improvement, when or where they are in the world, the same improvement is retained. For example, technology that improves fuel efficiency in cars will work the same in the UK in 2022 as it does in Germany in 2023. In other words, the technological CCE is not culture dependent.

Something interesting about humpback whale song is that humpbacks are present in all of the world’s oceans, but the pattern of evolution followed by revolutions has only been documented in the South Pacific Ocean. If an increase in complexity does confer a fitness advantage to earlier adopters of the more complex song it remains to be understood why the same dynamics are not at play in other oceans such as the Atlantic. Could the South Pacific Ocean have a new mechanism of song evolution that has evolved independently from humpback populations in other parts of the world? Or is it that these differences are best understood as similar underlying systems in different spatial and ecological contexts – for example models by Zandberg *et al.*, (2021) show how the different spatial patterns of populations could switch the song system from evolutionary to revolutionary. This new process as a whole could be indicative of CCE, in that this population have changed their process of song evolution to be able to switch their songs at a faster rate. However, it is not clear when this pattern of revolutions began in the South Pacific Ocean. Comparisons of song evolution between oceans is required to further explore this. The difference in song dynamics between oceans provides an excellent natural experimental setting to compare the same species performing the same behaviour but producing very different population level outcomes.

7.3.2 Aesthetic Preference

The rise in complexity in humpback whale song in evolution years in the South Pacific may also gain from further interdisciplinary dialogue such as those researching factors influencing aesthetic preference in humans. Aesthetic preference in humans has been linked to several traits including complexity, novelty and unpredictability. Berlyne (Berlyne *et al.*, 1968; Berlyne, 1971) showed evidence for complexity playing an important role in the 'interestingness' and 'pleasingness' of a stimulus. Berlyne proposed the concept of an inverted U-curve (or 'bell-shaped') relationship, suggesting that preference for complex stimuli increases until reaching a peak, after which preference diminishes. This relationship implies that intermediate levels of complexity are most preferred. However, recent studies, including the one conducted by Nadal *et al.*, (2015), which carefully manipulated the complexity level of stimuli, have shown that the inverted U-shaped curve is not consistently observed. The relationship between complexity and preference can vary, with patterns of increase, decrease, or U-shape depending on other factors.

This led to Gucluturk, Jacobs and Lier (2016) to investigate the preference-complexity relationship and individual differences. Their study used digitally produced grayscale graphics to evaluate individual differences in the complexity and preference relationship. This study found an inverted u curve relationship when results were grouped together but when analysed more closely subgroups showed different complexity-preference relationships. Some individuals exhibit a decrease in preference with increasing complexity while others display an increase in preference with complexity. Their study made a compelling case against the inverted U-curve being a universal rule for the complexity-preference relationship.

Furthermore, the relationship between complexity and preference is not found to be an absolute measure (Steck & Machotka, 1975). The context of the available complexity in the environment plays an important part in the preference of a particular variant. Steck and Machotka (1975) found that the relationship between complexity and preference is relative such that the judgement of the preference of one stimulus is dependent on the other stimuli available within the group, in other words the range of complexity within the group is a dictating factor in overall preference of a specific object (in this case computer generated 'music like' compositions). This suggests that there is no particular complexity in which tend to prefer, but that the context in which the individual listens to a musical piece determines preference. This finding supports the idea that the aesthetic value is relative to the aesthetic environment.

7.3.3 Neuroaesthetics

A neural correlate of aesthetic experience may allow us to determine whether we can objectively measure change in aesthetic attractiveness or value over time. Neuroaesthetics is a discipline devoted to the study of neurological processes in aesthetic attention and is a new subbranch of cognitive neuroscience (Cattaneo *et al*., 2020). Both cognitive neuroscience of art and neuroaesthetics concern themselves with the aesthetic qualities of artworks. However, neuroaesthetics is broader in its scope in also evaluating aesthetics of nature, common place objects and design.

While there is some evidence for neural correlates in aesthetic responses to art it is not clear whether these may be extrapolated across populations and time. Salimpoor *et al*'s (2013) study found that the amount of activation in particular parts of the brain (the nucleus accumbens and connectivity of this region to others, including the auditory cortex the amygdala) was able to predict the amount of money a participant would bid to listen to a piece of music again. This 'bidding paradigm' played short pieces of novel music to participants, who were then able to decide how much money they would pay to listen to each piece again.

Importantly, Salimpoor *et al*'s study uses novel music fragments as the stimuli of interest and allows some level of control in familiarity. However, contextual factors have been found to clearly play a key role in our aesthetic appreciation of objects. Multiple studies have found that the attitude with which one approaches an object may change one's aesthetic experience of it, as has been found in Kirk *et al*'s (2009) study in which art works were arbitrarily labelled 'gallery' and 'computer'. This led to beliefs in the participant about the origin of the pieces which were found to influence their aesthetic appraisal of the item. Even though all images were computer generated, participants were more positive about those images that they believed had been taken from an art gallery. This has important insights as to a process-focused or product-focused definition of CCE in response to aesthetic appreciation and value. Huang *et al*., (2011) also investigated semantic framing through asking their participants to appraise a set of Rembrandt paintings of which some were labelled 'authentic' and others 'copies'. This study found that participants preferred those paintings labelled authentic and when considering a 'copy' areas of the brain linked to the visual cortex were enhanced, as individual's attempted to evaluate visual evidence that the painting was indeed fake.

Considering the crucial role of context in the aesthetic evaluation of art, it becomes challenging to ascertain whether aesthetic attractiveness has truly increased over time due to the vast variations in cultural and historical contexts. To address this issue, human aesthetic cultures are now recognising the importance of cross-cultural changes in music. Initiatives like GlobalPop, being developed by Lee *et al*. (2021), are working towards creating diverse datasets of open-access music. These efforts aim to capture the global musical landscape, enabling a more comprehensive understanding of aesthetic developments across cultures.

The emergence of new technologies for monitoring brain activation in free-ranging marine mammals offers potential for studying song-related brain activation in humpback whales. For instance, near infrared spectroscopy (NIRS) has been successfully employed in studying bottlenose dolphins and grey seals in their natural habitats (Ruesch *et al*., 2022). This non-invasive technology holds promise for adapting human measurement approaches to assess brain activity in various tissues, including skin, muscle, and the brain, of free-roaming marine mammals. McKnight *et al*. (2021) demonstrated the applicability of NIRS in monitoring neural responses to acoustic sensory stimuli in grey seals. However, the application of such approaches in wild humpback whales is currently challenging due to the need for close and well-fitting head gear, which may introduce unknown stress effects and potentially compromise the validity of results. Although the technology shows potential for smaller and more manageable species, further developments are required to make it suitable for studying wild humpback whales. Monitoring progress in this technology will be of great interest in the future. A more promising avenue of research is cultural transmission experiments in which humans can be used as a tool for investigating animal communication systems.

7.3.4 Vocal learning in humpback whale songs

Throughout a single season, I observed a general stability in the humpback whale song unit type known as the 'groan' across different themes. However, over the course of two seasons, I noticed a notable increase in changes. Surprisingly, I did not observe significant divergence, which contradicted my initial prediction that different changes within the same unit across themes would lead to acoustic dissimilarity. Nevertheless, examining changes within individual whales proved to be an intriguing aspect as it allowed for potential control of interindividual differences over time, given the intertwined nature of time and individual factors. Lamoni *et al*., (Lamoni *et al*.) explored this aspect through a modelling approach, studying individual variation and how males stand out while conforming to a single song type.

My study demonstrates that there is variation between individuals in how the same unit changes within a single song session, and furthermore, individuals exhibit consistent variation. However, it is crucial to account for the effects of overall time in the season and differences between individuals, as these variables are intertwined due to the limited availability of high-quality song recordings. Additionally, acquiring more data from specific individuals over an extended timeframe poses challenges due to current technological limitations, but it is not an insurmountable task.

The overall impression from my fine-scale song unit analyses suggests that changes within unit types, manifested differently across various themes, may support the vocal learning hypothesis. However, it is important to note that this conclusion is based on only one recording per individual. Conversely, when considering a longer time scale in the North Atlantic, we observed greater changes in unit types when analysing individual measurement types, further supporting the vocal learning hypothesis. Analysing additional data is imperative for a more comprehensive understanding of how song units are learned.

One approach to further investigate whether units are derived from an innate species-specific repertoire or not is to compare unit types from distinct ocean basins. This approach would eliminate the possibility that acoustic contact is responsible for the similarity or evolution of unit types. Cerchio *et al*., (Cerchio *et al*.) previously conducted research documenting similar unit trajectories in different breeding populations, such as those in Mexico and Hawaii, which was thought to be due to a predisposition for units to change in a certain way regardless of social input. However, subsequent evidence has emerged indicating that separate breeding populations come into acoustic contact during migratory pathways and shared feeding grounds (Schall et al., 2021; Stimpert et al., 2012). In my study in the North Atlantic, I confirmed acoustic contact across the ocean basin between the Caribbean and Scotland, and it is reasonable to assume this extends to Norway as individuals continue traveling northward to known feeding grounds.

Consequently, when analysing breeding populations within the same ocean basin, we cannot exclude the possibility of acoustic contact. On the other hand, investigating the song dynamics between the North Atlantic and the South Pacific could prove fruitful since these populations are known to be acoustically isolated. Zandberg *et al*., (2021) have demonstrated the utility of this approach in modelling song dynamics. Previous empirical research on songs has primarily focused on broad-scale changes in song content and connections between sites within the same ocean basin. However, collaborative research involving scientists worldwide could enhance our understanding of the fundamental mechanisms underlying song learning. Such collaborations would allow us to account for population-specific processes and content, thus enabling an examination of the foundational aspects of song learning.

A logical next step following my studies would be to compare song unit repertoires between the Cook Islands in the South Pacific and the Caribbean and Scotland in the North Atlantic.

By building upon the methodology employed to track fine-scale changes in song units within a single song type, we can extend the analysis to encompass these distinct geographic locations to potentially find shared unit types and how often, if at all, these occur. The methodology utilised to track fine-scale changes in song units within one song type involved the ability to define a unit type that could be tracked across multiple theme types. This was achieved by combining fine-scale unit types. A similar approach could be employed to compare unit types across different song types and ocean basins, enabling the analysis of similarities in basic unit types among acoustically unconnected populations.

Obtaining humpback whale song recordings is challenging, resulting in limited accessibility for researchers, unlike the readily available online depositories for birdsong. Establishing an open library of whale song recordings would significantly enhance collaborative efforts among researchers worldwide. One potential approach could involve partnering with natural history museums, which would facilitate meticulous tracking of recording use and proper attribution. Developing an acoustic song library would also serve as an exceptional tool to involve public groups in song research. While there are existing online song libraries like the Google Whale Song Library, a substantial amount of song data remains in the possession of individual researchers. A more promising avenue of research is cultural transmission experiments in which humans can be used as a tool for investigating animal communication systems.

7.3.5 Humpback whale song and citizen science

Human transmission experiments offer valuable insights that can serve as foundational templates for creating innovative public engagement projects focused on humpback whale song. For instance, Anglada-Tort *et al*., (2023) conducted transmission experiments involving music-like song fragments in humans. The study examined two types of transmission chains: those within individuals, which involved self-copying of information, and those across individuals, which relied solely on copying from others. When comparing these two categories, distinct peaks of structure were observed across individuals, while such peaks were not apparent when individuals copied themselves. This suggests that the formation of this structure may require information to be passed among multiple individuals, possibly driven by a tendency to make the information more easily copyable by others.

The study presented an interesting approach by incorporating two different forms of copying. In one chain, participants were required to listen to a sound and then reproduce it by singing it back. In another chain, individuals listened to the sound and used an audio slider to match and replicate it, which eliminated the requirement for singing ability. This innovative approach opens up possibilities for applying similar experimental setups to animal sounds. By adapting this methodology, it becomes feasible to design experiments where human participants are tasked with transmitting humpback whale song phrases along chains. This approach holds great potential as a tool for investigating the evolution of humpback whale songs and exploring the cognitive constraints associated with singing. Moreover, it offers an excellent opportunity to engage the public and involve them as citizen scientists in the study of humpback whale communication.

Xanthoudaki and Blanton (2021) have presented their findings of open-ended creative learning environments. For example, a transmission task experiment in which contextual factors of previous innovations by other members of a group are considered. Participants were asked to view tablet screens of other individuals performing a set creative task with minimal instructions such as “create a machine that draws on paper using the materials provided”. Participants would then go on to create their machine with the option to use ideas they have learned from the group. The final machines were filmed in action and then added to a diary network of evolution to investigate how ideas are transmitted and built upon within the group. A transmission chain study of humpback whale song evolution could be achieved in the same way in which participants are given a provided with humpback whale song units and are tasked with designing a song based on the individuals singing around them. Instead of looking at videos of the other participants inventions participants would listen to humpback whale songs created by other participants and be tasked with copying the song using a variety of pre-recorded whale song units. They would also have the option of changing the whale song units to become lower or higher in frequency. This would build on the whale song copying and innovation stations within the Sea Symphonies exhibition in Chapter 5.

Public engagement events have the potential to generate innovative citizen science projects, such as the envisioned transmission chain study mentioned earlier. However, the public engagement events described in Chapter 5, which I led, faced challenges due to COVID-19 restrictions. As a result, the exhibition duration was shortened, impacting the long-term follow-up with visiting schools and school visits. Sustained community engagement is of utmost importance, and both of my public engagement studies underscored the significance of directing resources to communities that typically lack access to such initiatives. To enhance the future citizen science initiative mentioned above, careful consideration should be given to selecting locations and communities where participants can experience the greatest impact. For instance, prioritising schools or community groups in low socio-economic areas and expanding outreach beyond the immediate university vicinity would be beneficial. This approach would also foster long-term connections with local and national schools and community groups, ensuring sustained impact and future engagement in research initiatives. Moreover, when selecting these groups for informal learning opportunities, it is crucial to provide relevant and appropriate background materials both before and after the transmission chain experiments. This allows for monitoring of intended learning outcomes and ongoing impact, such as academic achievement among high school students. Utilising this methodology in public engagement projects would not only provide valuable insights into humpback whale song dynamics but also foster scientific collaboration and raise awareness about the fascinating world of these marine creatures. By actively involving the public, we can create a meaningful bridge between scientific research and broader communities, facilitating both scientific discovery and public appreciation for humpback whales.

7.4 Conclusions

In conclusion, this PhD thesis has demonstrated the importance of interdisciplinary dialogue in advancing our understanding of cultural evolution, specifically in humans and nonhuman animals. By embracing the power of passive acoustic monitoring and inventive non-invasive research techniques, this study has illuminated the previously hidden intricacies of wild animals' brains. Moreover, by linking datasets of humpback whale song recordings from across the globe, new insights have been gained into their complex communication systems and migration patterns. Additionally, this thesis underscores the importance of public engagement, not only as a means to improve our own research and give back to supportive communities but also to cultivate well-rounded researchers. The integration of these powerful approaches and considerations has strengthened the overall impact and contribution of this thesis which will hopefully continue to stimulate discussion in both human and animal cultural evolution research. I hope this thesis inspires future researchers to integrate public engagement as a key requirement alongside their research.

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