Vocalisations of Captive Sumatran Tigers
(*Panthera tigris sumatrae*)

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Courtesy of Carnivore Keepers Taronga Conservation Society Australia

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Research.

To the examiners,

The style and formatting of this thesis has been written according to the author guidelines for the journal Bioacoustics. Due to the nature of this research, this thesis varies from a typical format by the inclusion of acoustic sound descriptions and vocalisation contexts. This format, along with embedded tables and figures, is used to improve clarity and avoid redundancy regarding the specific vocalisations and related information presented. Vocalisation figures may not reflect tabulated averages, but are the highest quality representation to assist the reader. Supervising Dr. Jennifer Clarke provided feedback on the Introduction, Methods, and Results section, but did not have access to the Discussion section.

Declaration

I certify that the research presented in this thesis is my original work. Others that assisted include Jennifer Clarke, who provided assistance on the experimental design and related administrative work, Tim Pearson on recording equipment and sound analysis software techniques, and Drew Allen and Dan Noble on statistical analysis and interpretation. This work has not been presented for a higher degree to any other university or institution, and contains no material previously published or written by any other person except where due reference is made in the text.

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by

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Thesis

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Abstract

Wild tigers (*Panthera tigris*) are endangered with populations continuing to decline primarily due to humans. Acoustic communication research is a recommended enhancement to current tiger conservation efforts. Tiger acoustic communication research is extremely limited with a solitary study quantifying a single tiger call. This study investigated the acoustic characteristics and behavioural context of tiger vocalisations. Remote audio recordings of five captive Sumatran tigers (*Panthera tigris sumatrae*) in two separate enclosures at Taronga Zoo, NSW Australia were obtained March-July 2014 and reviewed with sound analysis software. Tigers were most vocal between 0100-1100 hours. From peak vocalisation times, 547 high quality recordings of tiger vocalisations were separated into seven vocalisation types ('moan', 'arf', 'mrr', 'chuff', 'growl', 'roar', and 'hiss'). Tiger experts provided suggested contexts and functions for these vocalisations. Classification of frequent laryngeal sounds including moan, arf, and mrr were verified with a multinomial logistic regression based on peak frequency (Hz), fundamental frequency (Hz) and duration (s) measurements. This research represents the first quantitative study of multiple tiger vocalisations. Descriptive literature on tiger communication lacks 'mrr' and 'arf' descriptions and acoustic characteristics of tiger vocalisations. Future research is needed to standardize vocalisation terms and further quantify the tiger vocal repertoire.

Keywords: Panthera, tiger, acoustic, communication, chuff

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1. Introduction

Tigers (*Panthera tigris*), including all subspecies, have been continually listed as an endangered species since 1986 (IUCN 2013). It is estimated that they have declined approximately 50% over the last 21-27 years (Walston et al. 2010). This continuous decline in tiger populations is primarily due to humans. Surveys from people living near wild tigers in the Chitwan District of Nepal (n=5400) revealed that nearly 82% had multiple encounters with the tigers and 17% of them had livestock attacked or been physically threatened by tigers (Carter, Riley, and Liu 2012). The threats tigers pose on livestock and humans as well as the illegal trading of tiger products such as skins, bones, and meat has resulted in heavy hunting of this species (Chundawat et al. 2011). The hunting of these endangered animals can quickly lead to extinction as tigers require large populations to persist in the wild (Chapron et al. 2008). There are many conservation efforts in place with hope to save the species such as tiger habitat preservation, illegal trade eradication, community education on human-tiger conflicts, and captive breeding programs. Nevertheless, there is still little understanding about tiger behaviour and communication, which may assist current conservation plans.

Research on this endangered species is of great importance in order to improve conservation efforts. Much of the conservation research on tigers has focused on estimating population sizes and understanding evolutionary relationships, which assists in monitoring population declines (Mazák 2010; Borthakur et al. 2011). Efforts have been made to understand and improve the human-tiger conflicts that are severely reducing current tiger populations (Goodrich et al. 2011; Carter, Riley, and Liu 2012). The Russian Federation created a team to investigate and assist with human-tiger conflicts in 1999 called the Tiger Response Team, but the Amur or Siberian tigers (*P. t. altaica*) in the area continue to have fewer numbers (Goodrich et al. 2011). These conflicts and poaching are unfortunately doing more than reducing tiger populations. They are also influencing a loss of genetic diversity in the species (Kenney et al. 1995; Mondol, Bruford, and Ramakrishnan 2013). This could lead to individuals being sterile or poor reproductivity and will subsequently cause captive breeding programs to struggle, as has occurred with cheetahs (*Acinonyx jubatus*) (Bertschinger, Meltzer, and Van Dyk 2008). Currently, there are more tigers in captivity than are estimated to be in the wild (Szokalski, Litchfield, and Foster 2012). However, this unfortunate fact provides an opportunity to undertake studies of captive individuals to scientifically investigate tiger behaviour and communication. I aimed to describe captive tiger vocalisations qualitatively with audible and visual spectrogram characteristics and quantitatively with numerical measurements, in addition to the contexts in which vocalisations occur. Quantifying the acoustic signals used by *P. tigris*, and describing contexts in which they occur will enhance current and future conservation efforts by revealing critical aspects of individual and social behaviour and improving our understanding of the species.

1.1 Acoustic Communication in Conservation

Acoustic communication can be invaluable in various ways for conservation. Research on acoustic signalling is an economic, efficient, and non-invasive method for studying a wide range of ecosystems and animals as it involves recording and playback devices with very little human interaction (Gerhardt and Huber 2002). A recent study found automated bioacoustic recorders to be significantly more accurate than human wildlife surveys at detecting endangered European nightjars (*Caprimulgus europaeus*) and suggested this method to be preferable and more accurate at monitoring and protecting endangered species (Zwart et al. 2014). Recording acoustic communication can also help illuminate many behaviours and behavioural patterns (Robbins 2000). Important behaviours including foraging, orientation, anti-predator defense, and habitat selection are often facilitated by acoustic communication (Laiolo 2010). In captive conditions, studies have revealed that lighting and chemical conditions affect zoo animal welfare and breeding success (Morgan and Tromborg 2007). Bioacoustic studies are needed, not only to determine how vocalisations can indicate zoo animal welfare, but also to investigate the impact of sound on zoo animal welfare and breeding success. Acoustic communication involved in various behaviours can help assess animal welfare as well as provide a greater understanding of animals and their relationships with conspecifics. Additionally, much of this type of behavioural information may be difficult, if not impossible, to obtain without the use of bioacoustic research methods.

Individual behaviour and communication of a species can also further enhance conservation efforts. In many cases, studies investigating specific vocalisations have found evidence of vocal individuality (Palacios, Font, and Márquez 2007; Trimble and Charrier 2011; Morisaka et al. 2013). For example, the fundamental frequency and variability of frequency between howls of captive wolves (*Canis lupus*) allowed for reliable individual discrimination (Tooze, Harrington, and Fentress 1990). Similarly, a study on the acoustic structure of the carnivorous spotted hyena (*Crocuta crocuta*) laugh found that this call can provide information about an individual’s age, identity and status (Mathevon et al. 2010). Individual vocalisations gathered from acoustic communication research can assist in providing a marking technique and possibly help monitor populations over time by providing range and fitness information (Terry, Peake, and McGregor 2005; Tripp and Otter 2006). In captive environments, the use of recording and playing individual or group vocalisations has been useful in enhancing captive breeding programs (Curio 1996). It is evident that studies of acoustic communication can provide enrichment of captive animals, wild population monitoring, or extensive ethology and acoustic knowledge, which are essential parts of any conservation plan.

1.2 Vocal Repertoires of Carnivorous Mammals

The initial step in studying the acoustic communication of any species is to qualitatively and quantitatively identify the sounds produced by the animal and the contexts in which the sounds occur in order to identify their function. This acoustic communication research has been partially explored in carnivorous mammals. Peters (2006) described unique acoustic signals in relation to sound production mechanisms across a wide range of carnivores such as ‘prusten’ in Felidae, ‘chuffing’ in Ursidae, ‘chuckling’ in Herpestidae, and ‘barking’ in Pinnipedia. Although specific vocalisations were described for each family this study did not expand on other vocalisations that may exist in the vocal repertoire of the species examined. For example, ‘chuffing’ and ‘humming’ were two calls identified in Ursidae (Peters, Owen, and Rogers 2007; Peters 2006), but recent research of Asiatic Black Bear (*Ursus thibetanus*) cub vocalisations revealed seven separate call types including ‘whine’, ‘moan’, ‘yelp’, ‘grunt’, and ‘snort’ as well as ‘chuffing’ and ‘humming’ (Pokrovskaya 2013). Similarly, three distinct calls were initially described for killer whales (*Orcinus orca*) (Ford 1989) until further scientific investigation distinguished 14 discrete calls (Saulitis, Matkin, and Fay 2005). Acoustic form and function research has also been explored with other mammalian carnivores including yellow mongoose *Cynictis penicillata* (Le Roux, Cherry, and Manser 2009), Northern quoll *Dasyurus hallucatus* (Aitkin, Nelson, and Shepherd 1996), spotted hyena *Crocuta crocuta* (East and Hofer 1991; Mathevon et al. 2010), white-nosed coati *Nasua narica* (Compton et al. 2001) and various Canidae (Palacios, Font, and Márquez 2007; Tooze, Harrington, and Fentress 1990; Robbins 2000; Déaux and Clarke 2013). The documented vocal repertoires of multiple species allows for acoustic communication comparisons as was performed in one comprehensive study comparing the vocal repertoire of dingoes (*Canis lupus dingo*) with other canid species (Déaux and Clarke 2013). Such inter-species comparisons are useful in understanding evolutionary relationships, behaviours and life-history traits (Déaux and Clarke 2013). However, these acoustic comparisons of related species are unfortunately limited in many carnivores, and particularly the Felidae.

1.3 Feline Acoustic Communication

A review of the literature on acoustic communication in felids reveals many gaps. Much of the research has investigated call mechanisms, but there remains limited understanding of the acoustic features and contexts of felid vocalisations. In an early published abstract, Wallschläger (1981) referred to similar elements in the vocal repertoires of felids, including many of the genus *Panthera*, but the full details of his research are unpublished. Members of the genus *Panthera*, in particular, are distinct from many other cats as they have a unique long-distance call (Peters and Peters 2010). The anatomical structure of the larynx of various *Panthera* species has been analysed to further understand the mechanisms behind these 'long-distance calls' (Hast 1989). Analysis of 'roar' acoustic features of lions (*Panthera leo*) in Tanzania have shown differences relative to sex and body size (Pfefferle et al. 2007). The vocal folds of the larynx are specialized in *Panthera*, allowing them to produce a loud, low frequency roaring sound (Hast 1989; Klemuk et al. 2011). In particular, the tiger larynx has a size and structure that is very efficient in producing roars (Titze et al. 2006; Titze et al. 2010). Additionally, the hyoid apparatus and pharynx of lions, tigers, jaguars, cheetahs, and domestic cats have been compared to investigate further morphological differences (Weissengruber et al. 2002). Understanding the physiology and morphology with animal vocalisations is important, but along with this, knowledge of numerical acoustic characteristics and functions of vocalisations is needed.

Understanding the evolutionary relationships of the many cat species can be possible with the use of acoustic comparisons. A study comparing the acoustic sounds and perceptual comparisons of domestic cats (*Felis silvestris catus*) and African wildcats (*F. s. lybica*) demonstrated distinct differences (Nicastro 2004). The domestic cat 'meows' are shorter and more pleasant sounding to humans than the African wildcat 'meows', suggesting there may be anthropogenic selection for meows in domestic cats (Nicastro 2004). A comparison of 'mew' calls in various members of the genus *Felis*, including the European wildcat (*F. s. silvestris*), Asiatic steppe cat (*F. s. ornata*), jungle cat (*F. chaus*) and sand cat (*F. margarita*), demonstrated that the dominant frequency differences are correlated with body weight, with larger individuals producing lower frequency sounds (Peters et al. 2009). Additionally, the sound types of Felidae have been plotted according to phylogeny and the distinct differences suggest the acoustic signals may evolve at different rates (Peters and Tonkin-Leyhausen 1999). These sound types and calls have been suggested to have evolved relative to the felids' habitat type which may also be correlated to body size (Peters et al. 2009; Peters and Peters 2010). The sound comparisons of various Felidae have provided useful information in understanding evolutionary relationships, but understanding the form and function of calls may provide further associations.

The form and function of vocalisations in felids is extremely limited. Opportunistic recordings of wild cougar (*Puma concolor*) vocalisations were measured and compared (Macarrão, Corbo, and Araújo 2012), but only two recordings from potentially the same individual does not provide much information. An earlier study investigated the vocalisations and behaviour responses of male cheetahs in relation to separation and reunion events (Ruiz-Miranda et al. 1998). Three distinct calls, 'chirps', 'eeaows', and 'stutters', were analysed in the study using spectrograms to visually categorize and measure acoustic features of vocalisations (Ruiz-Miranda et al. 1998). When males in a coalition were separated, chirps, eeaows, and stutters were common, and upon reunion only stutters were heard (Ruiz-Miranda et al. 1998). A possible function of the 'chirps', based on the context in which they occurred, may be to communicate desire to reunite and encode individual identity (Ruiz-Miranda et al. 1998). This information has helped discover possible psychological attachments between non-sibling male cheetahs and the value of raising and maintaining male cheetah coalitions in zoos (Ruiz-Miranda et al. 1998). A later study further explored the cheetah vocal repertoire and identified eight sound types including 'churtling', 'purring', 'growling', 'gurgling', 'miaowing', 'chirping', 'howling' and 'hissing' and reported the quantified characteristics and context of each (Volodina 2000). These studies have assisted in our understanding the form and function of cheetah vocalisations, and demonstrate the usefulness of this research in understanding animal behaviour and well-being (Volodina 2000). Similar research investigating call form and function in other felids is greatly needed, and particularly with endangered species such as tigers.

1.4 Tiger Acoustic Communication

Tiger acoustic communication research is extremely limited. To date, only one study has used spectrogram analysis to quantify and compare a single call type, the 'long distance roar', between individuals (Ji et al. 2013). Ji et al. (2013) revealed evidence of vocal individuality in this call with duration to be the most distinguishing measurement.

Nevertheless, the function for ‘long distance roars’ is not well understood, as stated in an old publish abstract (Walsh et al. 2010), and other vocalisations exist in the tiger’s vocal repertoire that have not been explored. Additionally, ‘long distance roars’ seem to also be described as a ‘long distance call’, ‘territorial roar’, ‘estrus roar’, ‘intense mew’, or ‘moan’ (Peters and Peters 2010; Walsh et al. 2010; Mills 2004) with the majority of these terms describing functions that have not been scientifically verified. The lack of standardized terminology and scientific evidence of the context of this vocalisation leaves a poor understanding of its acoustic characteristics and functions.

Much of what is currently understood regarding the vocal repertoire of *P. tigris* is comprised of scientifically unverified statements from sources that have not been peer-reviewed. Multiple books have stated a wide range of tiger vocalisations including ‘roars’, ‘prustens’ or ‘chuffs’, ‘growls’, ‘snarls’, ‘grunts’, ‘moans’, ‘meows’, ‘spits’, and ‘hisses’ (Sunquist and Sunquist 2002; Mills 2004; Thapar 2004; Schaller 1967). Unfortunately, there is nothing further than written descriptions of these calls to assist researchers in correctly identifying each individual vocalisation. A recent scientific study that investigated the behavioural impacts of different tiger housing practices measured the number of ‘chuffing’ and ‘roaring’ vocalisations that occurred (Miller, Leighty, and Bettinger 2013), but again the vocalisations were only verbally described. The tiger vocal repertoire has never been fully documented or quantified regarding its form and function (Hollien 1987; Walsh 2004), which would resolve these concerns of reliably identifying and describing individual tiger vocalisations. Since tigers are primarily solitary animals, it would be useful to understand the purpose of such a wide range of vocalisations and their individual functions. It is expected that this information will significantly contribute to the conservation of *P. tigris* as well as assist future research in accurately identifying tiger vocalisations.

1.5 Conservation Applications

Research on acoustic communication provides useful behavioural and biological information with conservation applications. Using vocal individuality for population monitoring, or using vocalisation playbacks for enhancement of breeding programs are applicable to current conservation efforts for tigers. The animal welfare of captive tigers, which are regularly housed in social groups although they are solitary in the wild (Miller, Leighty, and Bettinger 2013), may also be assessed by monitoring recorded vocalisations and related behaviours that indicate stress or frustration. For example, various species of farm animals have been documented to utter specific calls when in stress (Manteuffel, Puppe, and

Schön 2004) but similar studies are lacking for many zoo animals including tigers. Furthermore, the use of acoustic communication in making comparisons with other related species could be imperative in finding relationships and understanding differences. This can help to identify successful conservation efforts in one species, such as the cheetah, and be able to apply those same methods with another species like the tiger. Many aspects of tiger conservation could benefit from acoustic communication research.

1.6 Study Objectives

In this study, I investigated the acoustic form and context of captive purebred Sumatran tigers at Taronga Zoo, Mosman, NSW Australia over a three-month period. These captive tigers provided an ideal setting for obtaining high quality audio recordings as well as visual observations. Through the use of audio recordings and audio analysis software, I aimed to identify the distinct acoustic sounds produced by tigers and quantify their acoustic characteristics. I also aimed to create a model based on relevant acoustic measurements that can reliably discriminate between vocalisation types. This research will provide the basis for further investigations of tiger call functions and will assist in future research as well as explain unknown elements in previous research, particularly with standardizing vocalisation descriptions. Knowledge of the form and functions of tiger vocalisations will aid in tiger conservation in a wide variety of ways including revealing critical social behaviours associated with reproduction, parental care and territoriality, improving captive animal welfare, population monitoring, and comparisons with other felids.

2. METHODS

2.1 Site

This study was conducted at the Taronga Zoo, Mosman, NSW Australia. The main tiger enclosure (approx. 500 m^2) in this study housed three to four tigers at a time (Enclosure 1), and the other enclosure (Enclosure 2) was another neighbouring habitat (approx. 230 m^2) housing one adult male tiger (Figure 1). Enclosure 1 had an electric fence surrounding it and bordered the lion (*Panthera leo*) enclosure. Enclosure 2 was completely enclosed with a mesh cover above and was near the Sun bear (*Helarctos malayanus*) enclosure. Both enclosures had naturalistic settings with rock and water features, large trees and other vegetation, and a "cave". Additionally, the enclosures had public viewing windows frequented by zoo visitors daily from 0930-1700 hours. These enclosures complied with the Australian animal welfare standards and guidelines for exhibited animals.

Figure 1: Satellite image of the tiger enclosures at Taronga Zoo, NSW Australia

2.2 Subjects

Five captive-bred Sumatran tigers (*Panthera tigris sumatrae*) were the subjects for this study. This included an adult female (Jumilha) born at Taronga Zoo in October 2003 with her three cubs born in August 2011 in Enclosure 1, and the father (Satu), born at Wilhelma Zoo in Stuttgart, Germany in May 2005 in Enclosure 2. The three siblings included two males and one female (named Sakti, Kembali, and Kartika respectively). Jumilha or Sakti was rotated every 24 hours into dens off public display leaving only three tigers in Enclosure 1 at a time. All tigers were locked into dens and fed between 0715-0830 hours and again from 1400-1500 hours (Table 1). At all other times, the tigers had free range of the enclosure.

Table 1: Daily schedule of Sumatran tigers at Taronga Zoo, NSW Australia

Time	Activity
0715-0830 hrs.	Locked in dens and fed
0930-1000 hrs.	Tigers locked in exhibit
1030-1200 hrs.	Dens cleaned
1400-1500 hrs.	Dens set up and tigers fed
1645-1710 hrs.	Exhibit tigers given access to dens

2.3 Ethical Considerations

All research was conducted in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (NHMRC, 1997). The specific methods of this study were approved under Macquarie University Animal Ethics Committee protocol number 2014/010-2 (Appendix B).

2.4 Data Collection

A pilot trial was conducted over two consecutive days in late March 2014 to determine the types of information that could be gathered from audio and video recordings as well as what equipment settings would be needed. To collect audio recordings, a Wildlife Acoustics, Inc. Song Meter SM2+ (SM2) was used, which is a remote audio recording device that allows for continuous recording without human interference. The SM2 was placed in the keeper viewing area (VIP area) of Enclosure 1 (Figure 2) with one 10-meter cable on each side that extended the microphones and were attached to bars on each end of the VIP area. This provided high quality audio recordings of the entire enclosure without disturbing the tiger environment. Two high-resolution infrared trail cameras (UOV565HD) were placed at different angles in the VIP area to obtain video recordings of the tigers when they vocalised. All equipment ran continuously for a period of 48 hours. These audio and video recordings were reviewed over a period of approximately two months. Samples of different audio recordings were then reviewed with tiger keepers at Taronga Zoo to confirm tigers and not neighbouring animals uttered the acoustic sounds observed.

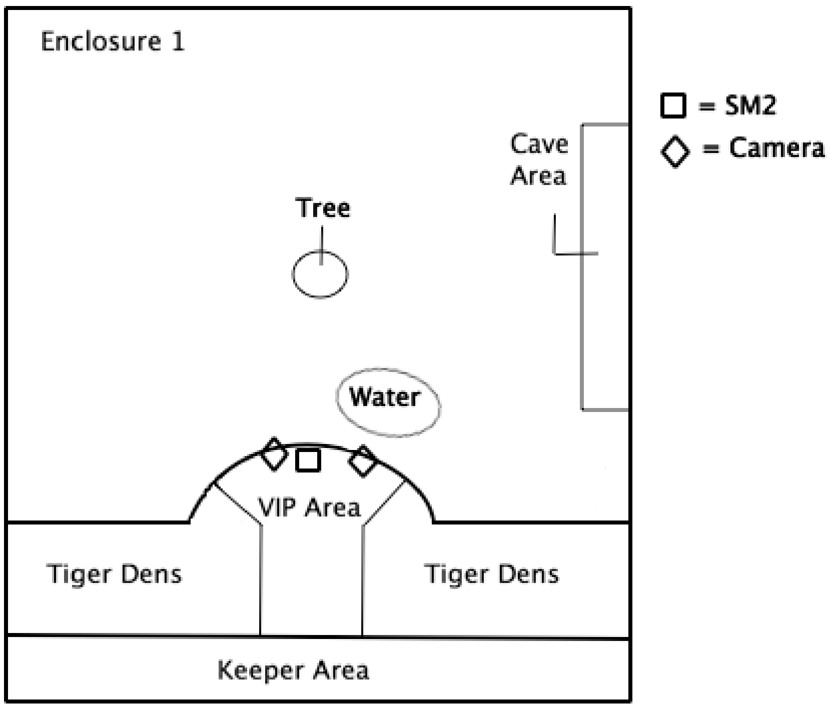

Figure 2: Tiger habitat diagram of Enclosure 1 indicating location of audio recording device (SM2) and video recording cameras during pilot trial at Taronga Zoo, NSW Australia

After the data from the pilot trial had been reviewed, audio recording resumed and continued in Enclosure 1 from May-July 2014. Another SM2 audio recording device was placed in Enclosure 2 early June-July 2014 to record the single male in that enclosure. As the

SM2 could not be safely located inside Enclosure 2, it was attached to a small barred open window located in the keeper area (Figure 3). To prevent any disruption to tiger behaviour, tiger keepers maintained the audio recording equipment on site. Both SM2 devices for this study were set to record continuously and were only stopped for periodic battery and SD card changes. All recordings throughout the duration of this study were made at a 44.1 kHz sampling rate and 16-bit depth as uncompressed .wav files.

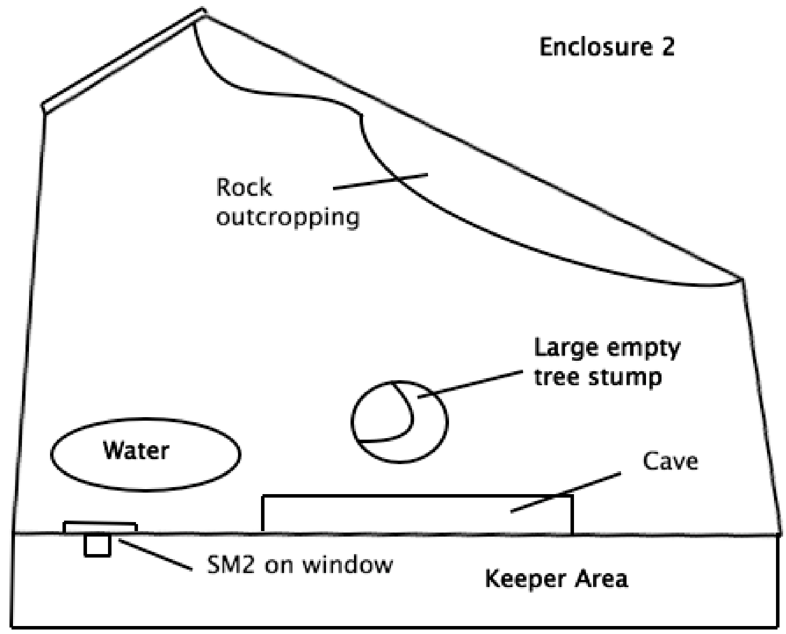

Figure 3: Tiger habitat diagram of Enclosure 2 indicating location of main features relative to SM2 recording device at Taronga Zoo, NSW Australia

2.5 Data Analysis

Audio recordings from the two enclosures were filtered for high quality tiger vocalisations with a high sound to low noise ratio (SNR) using Audacity 2.0.5 (Audacity Team 1991). No standard SNR was used, but each high quality sound had little to no background noise and was visually and audibly clear. Vocalisations were analysed through spectrograms created using Raven Pro 1.5 (Bioacoustic Research Program 2013). Each spectrogram was set at a DFT size of 2048, Hann window of 1084 samples, and overlap of 50% for measurements to be taken. The peak frequency (Hz) (specifically referring to the average peak frequency of the entire vocalisation), fundamental frequency (Hz), duration (s), and number of visible harmonics for each vocalisation observation were measured using automated procedures with Raven Pro 1.5 (Figure 4).

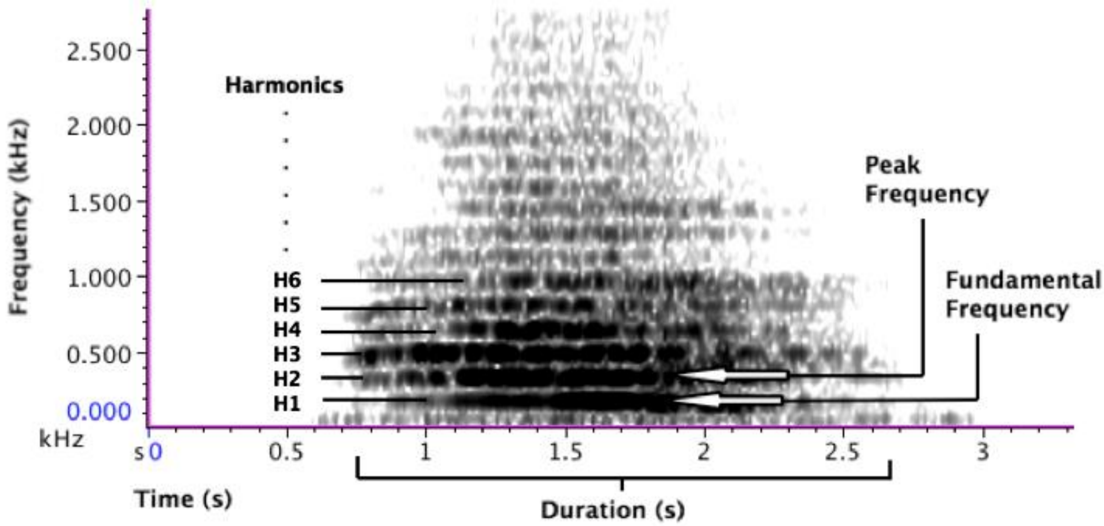

Figure 4: Sample vocalisation from a Sumatran tiger indicating the measurements that were taken from a spectrogram

Sounds were classified, prior to measurement, as per Robbins (2000) and Le Roux et al. (2009) where separate categories are created based on the spectral and audible differences of each sound. For example, large audio files were reviewed until a tiger vocalisation was visually and audibly identified on the spectrogram. The entire vocalisation was exported as a smaller audio file and classified according to the vocalisation type, or category, it is most similar to. Grouping vocalisations with the same audible and visual features together created separate vocalisation types. Each unique type was labelled relative to zoo keeper, onomatopoeic, and other tiger literature descriptions (Sunquist and Sunquist 2002; Mills 2004; Thapar 2004; Schaller 1967). To determine if the four measurements would be useful predictor variables for discriminating between vocalisation types, a Kruskal-Wallis rank sum test and a pairwise comparison using the Wilcoxon rank sum test (p-value adjusted with FDR control method) were conducted (data did not conform to parametric assumptions). The variable harmonics was not used further in the analyses due to the number of visible harmonics on a spectrogram may not be an accurate representation for each vocalisation (i.e. if the tiger was not facing the audio device fewer harmonics will be visible on the spectrogram).

The classification of the vocalisations based on the measurements of each acoustic sound were further explored with a multinomial logistic regression, which is a statistical classification method that determines the probability of category membership based on a model. This statistical test has been suggested as more appropriate for acoustic category classification than other methods, such as the discriminant function analysis (DFA), where many strict assumptions must be met (Taglialatela, Savage-Rumbaugh, and Baker 2003; Field 2013). The DFA assumes normality, linearity, and homoscedasticity of the data and not meeting these assumptions could result in inaccurate category membership. The predictor variables (peak frequency (Hz), fundamental frequency (Hz), and duration (s)) were not normally distributed and the multinomial logistic regression is more robust with these types of data, thus avoiding many potential errors that could occur with another statistical test.

All predictor variables were natural log transformed and likelihood ratio tests were implemented to compare the inclusion of linear and quadratic terms for the multinomial logistic regression model. A backward elimination with step-wise regression method was used to eliminate non-significant terms until all remaining linear and quadratic variables in the model were significant contributors to the model (where $p<0.05$). The regression model used only laryngeal sounds where more than 10 vocalisation observations were recorded. The male tiger in Enclosure 2 uttered only one vocalisation type and was not included in the model due to potential differences between the enclosures. The observations for this vocalisation type were compared and tested for significant differences between the two enclosures with a Wilcoxon rank sum test.

2.6 Contexts and Potential Functions

Video and direct observation of tiger behaviour associated with vocalisations could not be obtained during the course of this study. Although remote filming was attempted, the design of the tiger habitat was such that the cameras had to be placed in areas that could not view the entire enclosure. Invariably, the tigers vocalised from locations out of view of the cameras. To obtain a basis for possibly contexts and functions of tiger vocalisation types, two tiger experts were consulted: Deborah Price, senior keeper of the carnivore unit at Taronga Zoo, NSW, Australia with 11 years of tiger experience and Pat Craig, executive director at The Wild Animal Sanctuary in Keenesburg, Co, USA with over 20 years of tiger experience. Keeper assessments regarding animal behaviour, have been demonstrated to be reliable and valid across a variety of species (Whitham and Wielebnowski 2009). Each expert was given a high quality audio sample of each vocalisation type and was asked to provide the context in which they would expect to hear the vocalisation as well as the potential function. Additionally, tiger vocalisation descriptions or contexts as well as suggested functions were extracted from available literature (Mills 2004; Sunquist and Sunquist 2002; Thapar 2004; Walsh 2004; Schaller 1967). These literature sources are primarily based on field observations of wild tigers and are commonly referenced descriptions of tiger vocalisations. The information from experts and the literature are observational and can only be considered suggestions until scientifically confirmed, which is particularly necessary in the case of contradicting observations or suggestions.

3. RESULTS

3.1 Pilot Trial Results

After the initial 48-hour pilot trial, the time periods during which tigers in Enclosure 1 were most vocal were determined based on the number of vocalisations per hour. The peak period of vocalising was between 0400-0500 hours (Figure 5). Eleven potentially distinct acoustic sounds were initially identified and, when reviewed with tiger keepers, ten were confirmed as sounds produced by tigers and one was confirmed as the neighbouring lions roaring. Ten acoustic categories were then created for tiger sounds: ‘moan’, ‘arf’, ‘mrr’, ‘groan’, ‘chuff’, ‘puff’, ‘roar’, ‘growl’, ‘hiss’, and ‘cough’.

During the pilot, 263 video clips (each ~ 1 minute in length) were captured from the two trail cameras. In 133 videos (51% of total) a tiger was in view, but only once was a tiger vocalising. The infrared video, which recorded during peak vocalisation hours, also had limited tiger visibility. Because trail cameras did not provide sufficient information on tiger behaviour or the context in which vocalisations occurred, the use of this equipment was discontinued. Unfortunately, an alternative of obtaining and setting up a high quality video surveillance system within the timeframe of this study could not be achieved. Additionally, due to the tiger vocalisation hours occurring outside regular zoo operating hours, direct visual observation of the vocalisation contexts was not possible.

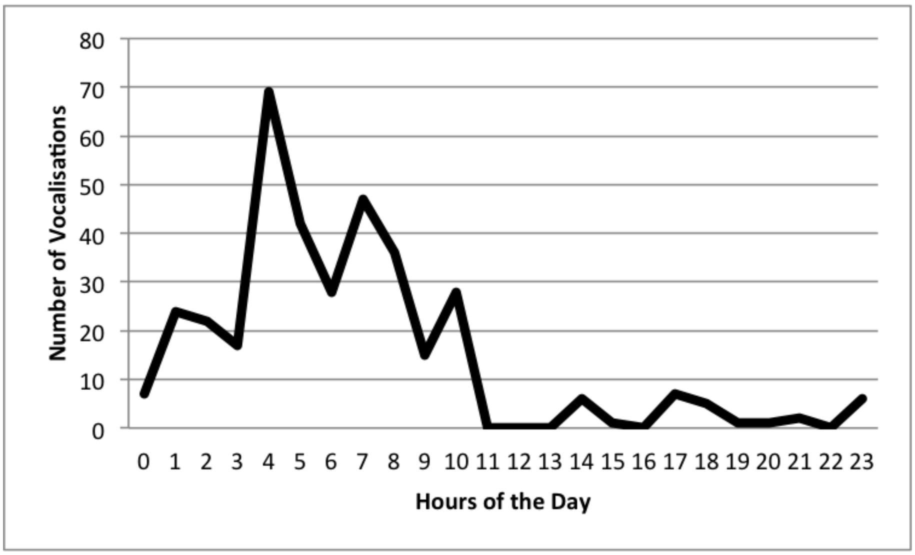

Figure 5: Peak tiger vocalisation times of Enclosure 1 based on the number of individual vocalisations observed over a 48-hour period for each hour of the day

3.2 Vocalisation Descriptions and Contexts

In 78 hours of audio recordings, 562 tiger acoustic sounds were documented. Of the initial ten sound types identified, ‘chuff’ and ‘puff’ were determined to belong to the same non-laryngeal sound type and ‘groan’ and ‘mrr’ had enough sound and measurement overlap that they were determined to be the same laryngeal sound type (confirmed by tiger keepers). Coughs and sneezes were not considered vocalisations and were not added as a vocalisation type. Therefore, I established seven distinct vocalisation types (547 observations) with six laryngeal acoustic categories (‘moan’, ‘arf’, ‘mrr’, ‘growl’, ‘roar’, and ‘hiss’) and one non-laryngeal category (‘chuff’). Quantifiable measurements of six of the seven vocalisation types ($n>5$) observed in Enclosure 1 (333 observations) were described with summary statistics performed in R (Table 2). The fundamental frequency and harmonics were not identifiable in ‘chuffs’ or ‘roars’; however, the number of staccatos and staccatos per second were measured for ‘chuffs’.

Tiger expert D. Price provided suggested contexts and potential functions on the seven identified vocalisation types and P. Craig reported on all but the ‘hiss’ vocalisation type (Table 3). These experts greatly differed in their descriptions of context and function for ‘arf’ and ‘mrr’. Both these vocalisations are poorly understood and experts can only refer to personal observations. Vocalisations ‘arf’ and ‘mrr’ were also not described in any of the tiger vocalisation literature (Table 4). However, other vocalisations are described in the literature that were not observed, or were not described sufficiently to correlate with the seven identified vocalisation types in this study.

Table 2: Summary statistics for the quantifiable variables of vocalisations ‘moan’, ‘arf’, ‘mrr’, ‘chuff’, ‘growl’, and ‘roar’, including standard deviation (s.d.), standard error (s.e.), minimum (min.), and maximum (max.)

Moan (n=109)	**mean**	**s.d.**	**median**	**min**	**max**	**range**	**skew**	**kurtosis**	**s.e.**
duration (s)	1.35	0.2	1.35	0.88	2.14	1.26	0.97	2.03	0.02
peak frequency (Hz)	347.31	173.46	344.5	150.7	689.1	538.4	0.37	-1.34	16.61
fundamental frequency (Hz)	177.41	37.05	172.3	86.1	301.5	215.4	0.64	1.78	3.55
harmonics	10.14	2.41	10	6	16	10	0.29	-0.38	0.23
Arf (n=54)									
duration (s)	1.12	0.3	1.1	0.47	1.96	1.49	0.21	0.04	0.04
peak frequency (Hz)	567.84	150.13	581.4	172.3	1055.1	882.8	0.28	2.4	20.43
fundamental frequency (Hz)	257.61	76.33	236.9	150.7	495.3	344.6	0.75	-0.09	10.39
harmonics	9.7	3.48	9.5	5	22	17	1.1	1.58	0.47
Mrr (n=83)									
duration (s)	1.87	1.12	1.6	0.41	6.21	5.8	1.59	2.87	0.12
peak frequency (Hz)	570.5	156.6	581.4	150.7	1335.1	1184.4	0.66	6.53	17.19
fundamental frequency (Hz)	222.86	77.16	193.8	129.2	559.9	430.7	1.24	2.53	8.47
harmonics	12.04	4.95	11	3	30	27	1.15	1.54	0.54
Chuff (n=70)									
duration (s)	0.37	0.08	0.36	0.2	0.61	0.41	0.59	0.39	0.01
peak frequency (Hz)	2480.94	1095.54	2088.7	366.1	7062.9	6696.8	1.87	5.28	130.94
staccatos	4.49	1.44	5	0	8	8	-0.82	2.3	0.17
staccatos/second	12.15	2.98	12.59	0	16.45	16.45	-2.83	9.15	0.36
Growl (n=9)									
duration (s)	2.42	1.23	2.41	0.73	4.24	3.51	0.09	-1.73	0.41
peak frequency (Hz)	284.7	233.36	258.4	64.6	646	581.4	0.37	-1.76	77.79
fundamental frequency (Hz)	267.96	208.25	258.4	64.6	538.3	473.7	0.28	-1.88	69.42
harmonics	3.89	0.6	4	3	5	2	-0.01	-0.64	0.2
Roar (n=6)									
duration (s)	0.75	0.37	0.64	0.5	1.49	0.99	1.22	-0.31	0.15
peak frequency (Hz)	265.58	151.44	290.7	64.6	430.7	366.1	-0.22	-1.92	61.83

Table 3: Context and proposed function of tiger vocalisations as suggested by two tiger experts

Vocalisation	**Context**	**Potential Function**
Arf[1]	Occurs when relaxed in social setting or sometimes when rubbing on mesh or another tiger.	Chatting
Arf[2]	Self-talk when a tiger is alone and potentially frustrated.	Frustration
Chuff[1]	When reuniting with another tiger or in close contact with other tiger(s).	Greeting
Chuff[2]	Occurs when in social setting or specifically when one tiger is approaching another.	Greeting
Growl[1]	Between two or more tigers advertising a possible attack	Warning
Growl[2]	When a female is early or late in reproductive cycle and is not accepting mating. Can also occur when a female appears unsure of mating with a male and this may progress to a roar.	Warning or fear
Hiss[1]	When keepers walk past tiger den, or when irritated or warning another tiger to retreat.	Warning
Moan[1]	Female or male calling for a mate often during peak mating times.	Reproductive
Moan[2]	Focused call when separated from other tigers.	Long distance advertisement
Mrr[1]	Occurs in relaxed social settings.	Chatting
Mrr[2]	Focused call when active and very frustrated.	Frustration
Roar[1]	When frightened or unsure of something	Conflict
Roar[2]	Escalating growl or squeal when in pain sometimes when tigers are mating. Also when multiple tigers are having a confrontation and biting is immanent.	Fear of or experiencing Pain

[1] Deborah Price, Carnivore Unit Senior Keeper, Taronga Zoo, NSW Australia
[2] Pat Craig, Executive Director, The Wild Animal Sanctuary, Keenesburg, CO USA.

Table 4: Comparison of tiger vocalisations with their accompanied behaviours and suggested functions as described in published tiger literature (Schaller 1967; Walsh 2004; Sunquist and Sunquist 2002; Mills 2004; Thapar 2004)

Vocalisation	Context	Function	Reference
Bark	Close-encounter vocalisation produced when tiger is agitated and conveying attack is imminent	Warning	Walsh 2004
Growl	Deep rolling rrr denoting an aggressive motivation or readiness to attack	(not stated)	Sunquist and Sunquist 2002
Growl	Occurs when mating	(not stated)	Thapar 2004
Growl	Similar to a roar but is missing a 300Hz peak and harmonics associated with a roar that occurs in close encounters prior an attack	Warning	Walsh 2004
Grunt	Short, sharp ur, ur, ur from mother to young	Call cubs to mother	Mills 2004
Grunt	Close-encounter vocalisation produced when tiger is agitated and conveying attack is imminent	Warning	Walsh 2004
Hiss	Agonistic close-range encounters	Attack or Defense	Sunquist and Sunquist 2002
Main call	Low to medium intensity call	Long-distance advertisement	Sunquist and Sunquist 2002
Main call with Grunt	High pitched with throaty grunt at the end that occurs in various behavioral situations	Long-distance advertisement	Sunquist and Sunquist 2002
Miaow	Emitted by unhappy cubs or courting adult tigers.	(not stated)	Mills 2004
Moan	Low-volume, subdued roar that occurs when cub approaches mother's kill uninvited, or during peak mating season.	Warning or advertisement	Mills 2004
Moan	Subdued roar that can be heard over 400 meters away and is made with mouth partly open or closed while tiger is walking with the head down	Long-distance advertisement	Sunquist and Sunquist 2002
Moan	Low-pitched moaning sounds from cubs wanting some of a mother's kill	(not stated)	Thapar 2004

(continued)

Table 4 (continued)

Vocalisation	Context	Function	Reference
Pook	Cross between hoot and deep bark that mimics the sound of the sambar alarm call.	Advertise animal's presence and prevent sudden encounters	Schaller 1967
Prusten/Chuff	Sneeze or prusten is a blowing action through the nose done in close contact with others.	Friendly greeting	Mills 2004
Prusten/Chuff	Staccato puffing sound done in close range with other tiger. Air is forced through mouth and nose and the lips flutter. Often occurs with mother and young and during courtship and mating.	Greeting call	Sunquist and Sunquist 2002
Prusten/Chuff	Occurs in social settings where small bursts of air are forced through the nasal cavity and have a fluttering sound like a neighing horse	Greeting	Walsh 2004
Purr	Emitted by mother when contented and being nuzzled by cubs.	(not stated)	Mills 2004
Purr	Emitted by mother when being nuzzled by cubs	(not stated)	Thapar 2004
Roar	When adults are vocalising to each other, advertising, or when showing signs of irritation.	Long-distance warning or advertisement	Mills 2004
Roar	Occurs after a kill, prelude to mating, or when a mother is beckoning young. Often heard during peak mating period.	Long-distance advertisements, sexual receptivity advertisement	Sunquist and Sunquist 2002
Roar	Intense close encounter call with a broad frequency range with the greatest power in low frequency range that occurs prior to an attack	Warning	Walsh 2004
Snarl	Occurs with older tiger cubs during play	(not stated)	Mills 2004
Snarl	Short harsh sound with teeth bared used when attacking	Defense	Sunquist and Sunquist 2002
Snarl	Associated with squinting eyes, flattened pinnae, furled muzzle, and showing of teeth that occurs in close encounters prior an attack	Warning	Walsh 2004

3.2.1 Moan: acoustic form and proposed context

A ‘moan’ was a loud *owwrr* sound (Figure 6) that occurred in 33% (109/333) of the sounds recorded in Enclosure 1 and was the only recorded vocalisation type in Enclosure 2 (118 observations). This vocalisation may also be termed a ‘main call’ or ‘subdued roar’ as described in other literature (Sunquist and Sunquist 2002). Moans were approximately 1-2 seconds long, had a median peak frequency of 344.5 Hz, and median fundamental frequency of 172.3 Hz, and 6-16 visible harmonics. Tiger experts suggested this call occurs during peak mating times potentially with a reproductive function or when a single tiger is separated from others suggestive of a long distance advertisement call. A long-distance advertisement function for this vocalisation is also suggested in other literature by Sunquist and Sunquist (2002), but has been described as a potential warning in other descriptions (Mills 2004; Thapar 2004).

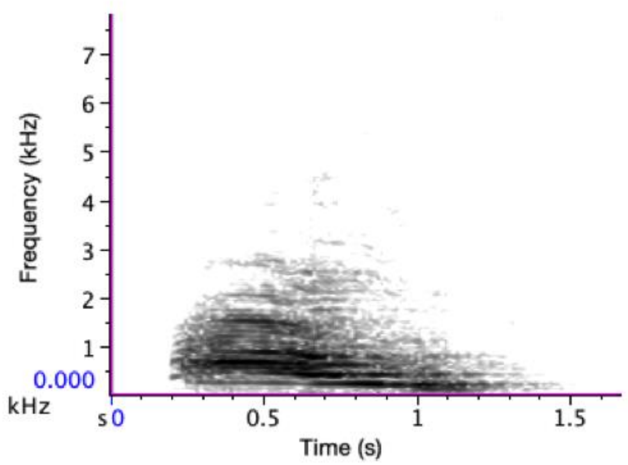

Figure 6: Spectrogram of a ‘moan’ vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro)

3.2.2 Arf: acoustic form and proposed context

An ‘arf’ vocalisation was a short and abrupt *ar-arf* or *ar* sound (Figure 7) that was observed in approximately 16% (54/333) of the sounds recorded in Enclosure 1. It was relatively short in duration (0.5-2.0 seconds), with a median peak frequency of 581.4 Hz, a median fundamental frequency of 236.9 and with 5-22 harmonics. This sound was suggested to be a “relaxed” vocalisation “with no real purpose” or a vocalisation associated with “frustration”. This vocalisation has not been previously described in tiger literature.

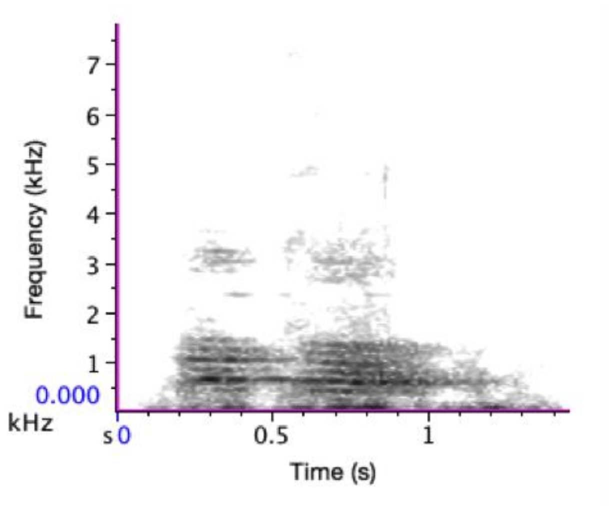

Figure 7: Spectrogram of an 'arf' vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro)

3.2.3 Mrr: acoustic form and proposed context

A 'mrr' was a drawn out *mrr* or *urr* sound (Figure 8) that was the second most frequent vocalisation observed in 25% (83/333) of the sounds recorded in Enclosure 1. Mrrs greatly varied in duration (0.4-6.2 seconds) with a median peak frequency of 581.5 Hz, a median fundamental frequency of 193.8 Hz and visible harmonics ranging from 3-30. Very similar to 'arf', D. Price suggested this to be a relaxed social setting vocalisation, while P. Craig suggested this to be a very focused call when the tiger is active and is possibly vocalising "frustration". This vocalisation has not been described previously in other tiger literature.

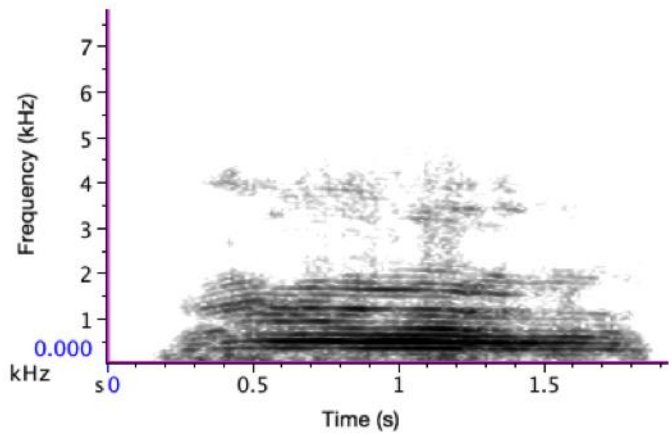

Figure 8: Spectrogram of a 'mrr' vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro)

3.2.4 Chuff: acoustic form and proposed context

A 'chuff' vocalisation involved quick staccato, or short, repetitive puffs of air like a *huf-huf-huf* sound (Figure 9), which was the only observed non-laryngeal vocalisation and represented 21% (70/333) of the sounds recorded in Enclosure 1. Chuffs were distinctive from other vocalisations with a very short duration (0.2-0.6 seconds) and a median peak frequency of 2088.7 Hz. The number of individual staccatos for each chuff was not always visually discernible, but could be distinguished when the audio speed was reduced by 50%. This sound had a median of 5.0 staccatos and a median of 12.6 staccatos per second. Experts and the literature described this as a close-range greeting vocalisation that occurs in social settings when one tiger is approaching or reuniting with another tiger. The literature also terms this vocalisation as a 'prusten' and described it as a puffing or blowing action where air is forced through the mouth and nose creating a fluttering sound used as a greeting call.

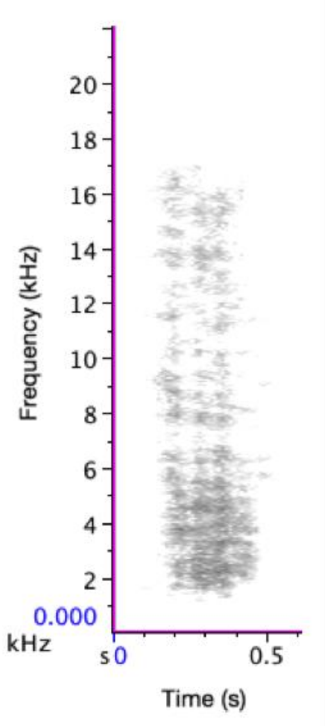

Figure 9: Spectrogram of a 'chuff' vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro). Note: Frequency scale has been adjusted to show full range of the vocalisation.

3.2.5 Growl: acoustic form and proposed context

A 'growl' vocalisation was a guttural *grrr* sound (Figure 10), which only occurred with approximately 3% (9/333) of the sounds recorded in Enclosure 1. With the growls observed, the average measurements were as follows: peak frequency = 284.7 Hz, fundamental frequency = 268.0 Hz, duration = 2.4 seconds, and 4 visible harmonics. Experts agreed that growl vocalisations occur as a potential warning due to conflict between two or more tigers or when mating. The suggested context of a ‘growl’ occurring with mating individuals is also described in Thapar (2004). Walsh (2004) also suggests growls are used as a warning.

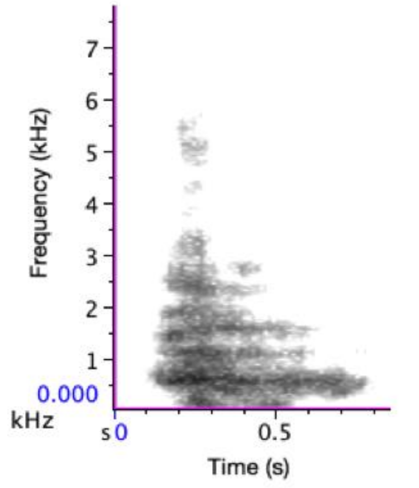

Figure 10: Spectrogram of a ‘growl’ vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro)

3.2.6 Roar: acoustic form and proposed context

A ‘roar’ was a loud burst *roar* sound (Figure 11) that had only 6 observations. Roars did not have observable harmonics or a measurable fundamental frequency. The average peak frequency was 258.4 Hz and the average duration was 0.7 seconds. Experts described this infrequent vocalisation as an advertisement of fear, pain, or warning. In the literature ‘roar’ descriptions vary from the vocalisation occurring between mother and young, during the mating period, when adults are vocalising to each other, or as a close encounter warning.

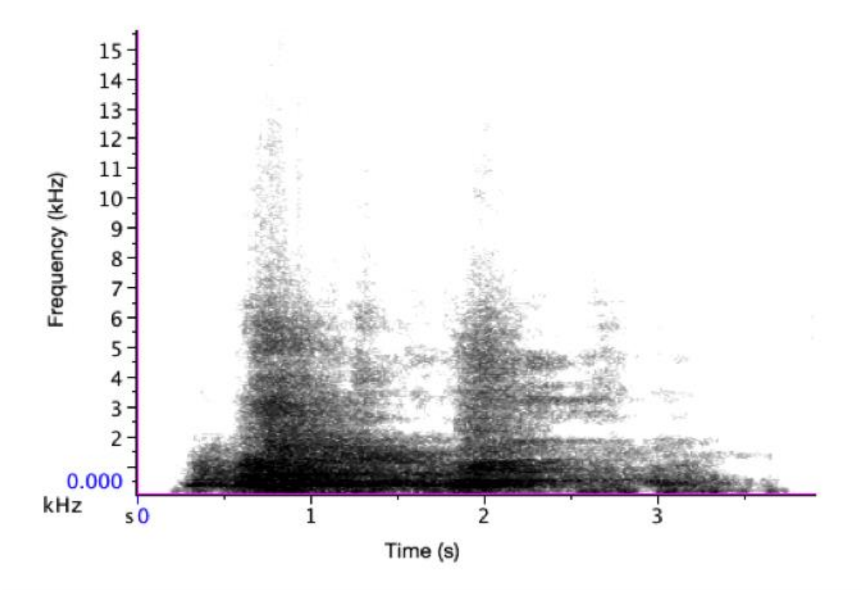

Figure 11: Spectrogram of a 'roar' vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro). Note: Frequency and time scales have been adjusted to show the full ranges of the vocalisation.

3.2.7 Hiss: acoustic form and proposed context

A 'hiss' vocalisation was a spitting *hiss* sound (Figure 12) that was rarely observed (2/323). This vocalisation averaged 1.5 seconds in duration. Hiss vocalisations were suggested to occur when a tiger is showing signs of irritation and warning another tiger or tiger keepers to retreat. This vocalisation was not specifically described by name in the literature.

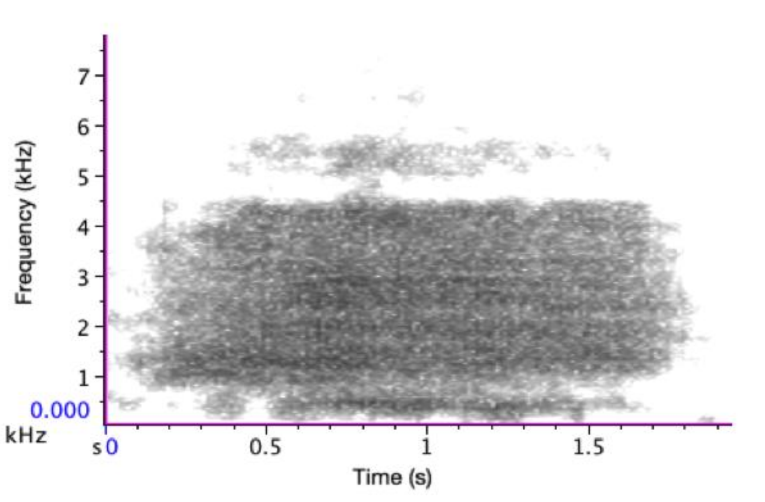

Figure 12: Spectrogram of a 'hiss' vocalisation of a captive Sumatran tiger, Taronga Zoo, NSW Australia (Raven Pro)

3.3 Regression Model for Moan, Arf, and Mrr

Non-parametric tests (Kruskal-Wallis rank sum tests of differences in medians) indicated statistically significant differences among vocalisation types with respect to median values for peak frequency ($p<0.0001$), fundamental frequency ($p<0.0001$), duration ($p<0.0001$) and harmonics ($p<0.01$) (Figure 13). Post hoc comparisons, using Wilcoxon rank sum tests (p-values adjusted using the FDR control method), indicated that the median peak frequencies of 'arfs' and 'mrrs' both differ significantly from that of 'moans', but not from each other (Table 5). Fundamental frequency and duration differed among all three vocalisation types. Harmonics differed between 'moans' and 'mrrs', and between 'arfs' and 'mrrs'. These statistically significant differences reported imply that these variables can be used to discriminate among vocalisation types.

The multinomial logistic regression model assisted in predicting the probabilities of vocalisation type based on predictor variables (peak frequency (Hz), fundamental frequency (Hz), and duration (s)). Using the log transformed linear and quadratic terms in the backward elimination process revealed ln peak frequency (Hz), ln fundamental frequency (Hz), ln duration (s) and (ln duration)^2 (s) terms to be very significant contributors to the model (Table 6). The results of plotting the model in relation to two variables with the third being held constant (mean value) confirm that these variables can reliably discriminate between 'moan', 'arf', and 'mrr' (Figure 14). These plots revealed the following:

- The probability of the vocalisation being a 'moan' was greatest at low peak and fundamental frequencies (Hz) (Figure 14A) and intermediate durations (s) (Figure 14B and 14C), as indicated by lighter colours (model predictions) and high fractions of all vocalisations (points) denoted as moans (filled points) in these panels.
- The probability of the vocalisation being an 'arf' increased with high fundamental and peak frequencies (Figure 14D). Additionally, vocalisations had a higher probability of being an 'arf' when durations were relatively short (-0.05-0.5 s on ln scale), particularly when this occurred with high fundamental frequencies (Figure 14E) or low peak frequencies (Figure 14F).
- The probability of the vocalisation being a 'mrr' was greatest with high peak frequencies and intermediate to low fundamental frequencies (Figure 14G). 'Mrrs' were also more likely when duration values were at either extremely low or approximately above 1.0 s on ln scale (Figure 14H and 14I). Original observations

classified as ‘mrr’ (filled in points for G-I) were mostly within 0.2 and 0.4 probabilities indicating a deviance from the model predictions (lighter regions). ‘Mrr’ observations were spread in low probability and high probability regions based on duration, indicating this to be an important predictor variable. When fundamental frequency was held at the median value, a large fraction of observations were in higher probability regions (>0.4), which suggests that ‘mrr’ classified vocalisations fit the model best according to peak frequency and duration measurements.

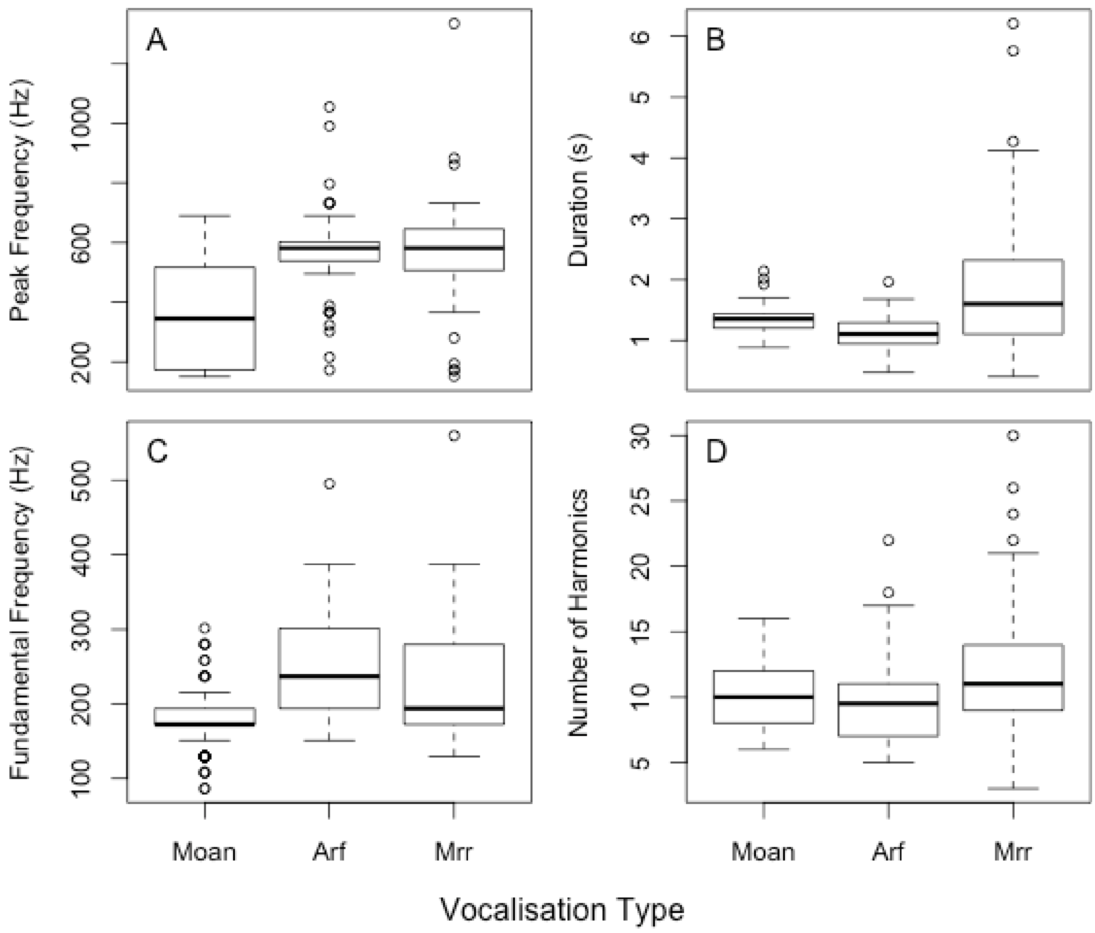

Figure 13: Boxplot comparison of each measured variable across vocalisation types: ‘moan’, ‘arf’, ‘mrr’. The boxplots depict the differences with the line representing the median, the box lines represents the upper and lower quartile (where 25% of the data above and below the median lie), the whiskers represent the data outside the 50%, and the dots represent potential outliers.

Table 5: Pairwise comparisons of the difference in medians for vocalisation type by each variable.

Variable	Moan-Arf	Moan-Mrr	Arf-Mrr
Peak frequency (Hz)	-236.9***	-236.9***	0.0
Fundamental frequency (Hz)	-64.6***	-21.5***	43.1**
Duration (s)	0.25***	-0.25***	-0.5***
Harmonics	0.5	-1.0*	-1.5**

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 6: Multinomial logistic regression results of the final model for the natural log transformed variables with moan as the intercept. Coefficient values are shown with the standard errors in parenthesis.

	Arf	Mrr
Moan (Intercept)	-31.4*** (5.68)	-27.9*** (5.53)
ln peak frequency (Hz)	2.73*** (0.70)	3.26*** (0.68)
ln fundamental frequency (Hz)	2.80*** (0.82)	1.48 (0.78)
ln duration (s)	-8.42*** (2.30)	-7.57** (2.31)
$[\ln \text{duration}]^2$ (s)	10.5*** (3.71)	14.1*** (3.56)

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

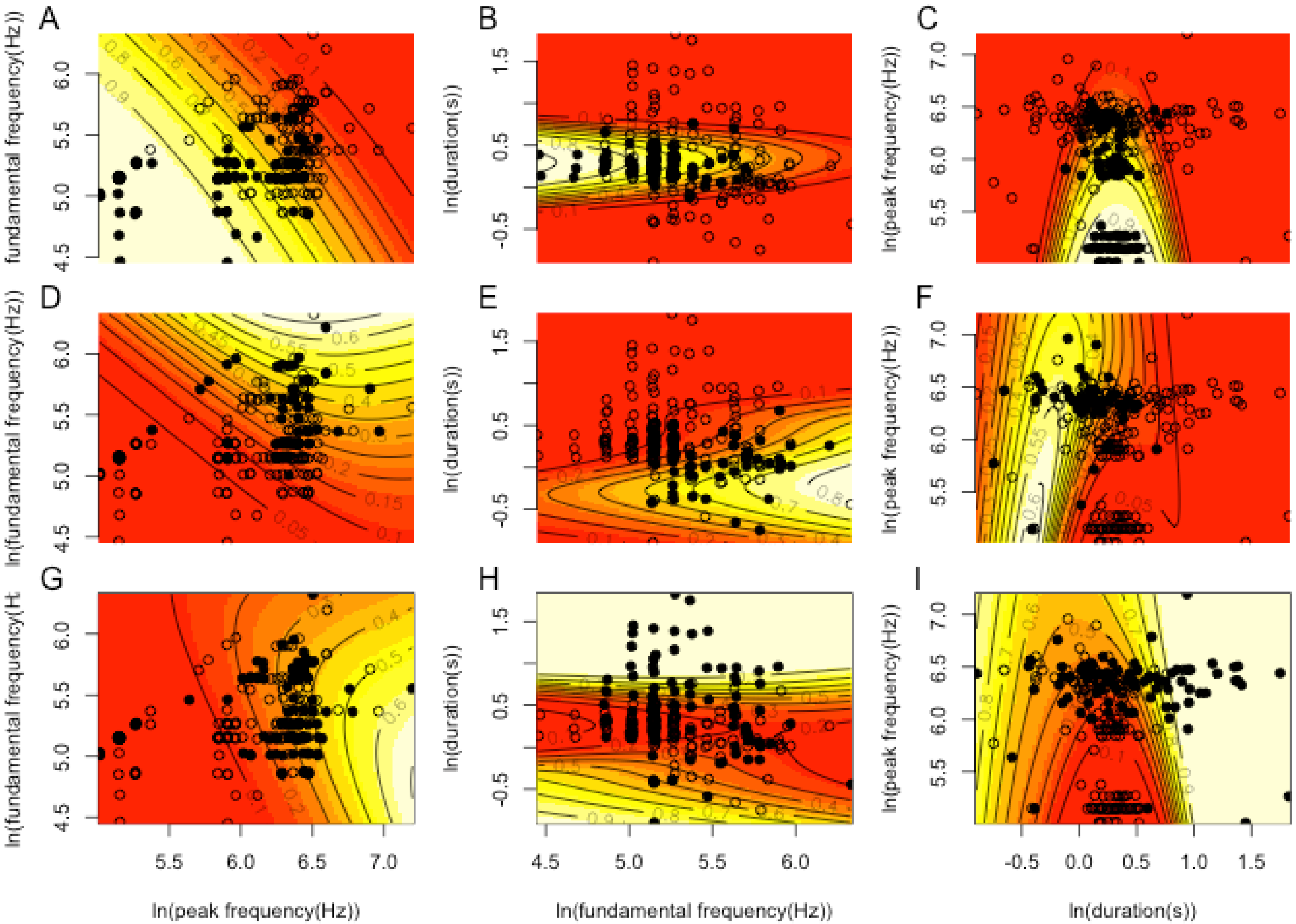

Figure 14: Contour plots of predicted probabilities from the multinomial logistic regression relative to two variables with the third term being held at the median value. A-C are plots relative to moan, D-F are relative to arf, and G-I are relative to mrr vocalisations. The model predicted probabilities of the vocalisation type increase from red to light yellow with probabilities above 0.9 being the lightest region. The points display the actual observations with the filled in points showing the observations for the vocalisation of interest

3.4 Moan Comparison by Enclosure

Enclosure 2 contained one adult male tiger that emitted only one vocalisation type (‘moan’). Moans in this enclosure were 1-3 seconds long with a median peak frequency of 301.5 Hz, a median fundamental frequency of 150.7 Hz, and 6-40 harmonics (Table 7). Comparisons of the ‘moans’ for both enclosures highlight potentially significant differences (Figure 15). The Wilcoxon rank sum test revealed that moans for Enclosure 2 had a significantly lower peak frequency ($W=8047.5$, $p<0.002$) and fundamental frequency ($W=10595$, $p<0.0001$). Enclosure 1 was found to have a significantly shorter duration ($W=341$, $p<0.0001$) and significantly fewer harmonics ($W=4209$, $p<0.0001$) than Enclosure 2. It is important to note that these differences, although significant, did not account for the difference in the number of individuals per enclosure or potential noise level differences due to the location of the SM2 audio recording devices.

Table 7: Summary statistics of variables for ‘moans’ uttered by the one adult male tiger in Enclosure 2, including standard deviation (s.d.) standard error (s.e.), minimum (min.), and maximum (max.)

Enclosure 2 (n=118)	mean	sd	median	min	max	range	skew	kurtosis	se
duration (s)	2.24	0.41	2.3	1.2	3.34	2.15	0	-0.16	0.04
peak frequency (Hz)	295.25	119.09	301.5	129.2	710.6	581.4	0.74	1.05	10.96
fundamental frequency (Hz)	147.43	17.26	150.7	107.7	279.9	172.2	3.34	27.75	1.59
harmonics	12.75	4.78	12	6	40	34	1.93	7.6	0.44

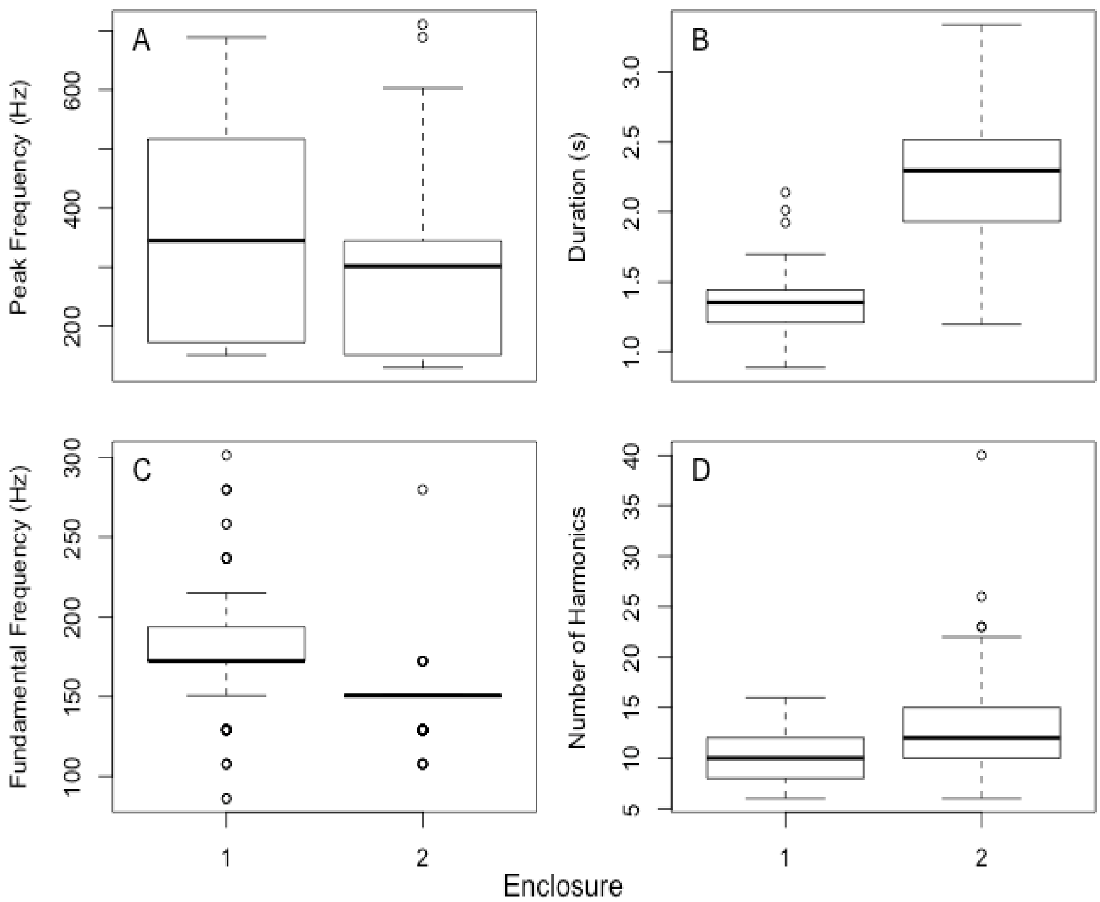

Figure 15: Boxplot comparison of each measured variable between the two tiger enclosures. Enclosure 1 contained four tigers and Enclosure 2 contained one male tiger that only moaned. The boxplots depict the differences with the line representing the median, the box lines represents the upper and lower quartile (where 25% of the data above and below the median lie), the whiskers represent the data beyond the 50%, and the dots represent potential outliers.

4. DISCUSSION

This study represents the first investigation into tiger communication in which multiple distinct tiger vocalisations have been quantitatively measured and identified. In this study, I recorded, measured and quantitatively described seven vocalisations uttered by tigers, as well as presented the putative contexts in which these vocalisations occur. Of these seven, I statistically discriminated between the most frequent vocalisation types ('moan', 'arf', and 'mrr') using frequency (Hz) and duration (s) measurements. The results of these findings were also compared with published accounts describing tiger acoustic communication.

The peak vocalisation times for the captive Sumatran tigers in this study occurred early in the morning between 0300-0600 hours. Wild tigers are described as being most active at night (Sunquist and Sunquist 2002), which supports our findings. 'Moans' were the most frequent of all the vocalisations, accounting for 59% of all recorded vocalisations from both tiger enclosures. This was the only vocalisation observed in enclosure 2, which supports the tiger expert suggestion of this being a long distance advertisement call directed at other tigers, perhaps those in enclosure 1 in this case. Comparisons between the enclosure with four tigers and the enclosure with one tiger revealed potential individual differences in the acoustic characteristics of moans. If confirmed, this would support the vocal individuality found in tigers' 'long-distance roars' (Ji et al. 2013). Ji et al. (2013) also provided the spectrogram and average fundamental frequency of 'long-distance roars' (150 Hz), which is visually and numerically similar to the 'moans' in this study with an average fundamental frequency of 177 Hz in Enclosure 1 and 147 Hz in Enclosure 2. That 'moans' and 'long-distance roars' may be the same vocalisation is further supported with tiger 'roar' descriptions as a two-toned sound like *a-a-u-u-u* or *a-o-o-o-nh* (Miller, Leighty, and Bettinger 2013; Schaller 1967) closely resembling the 'moan' *owrrr* description in the present study. Other sources use the terms: 'main call' (Sunquist and Sunquist 2002) and 'intense mew' (Walsh et al. 2010); which may also be referring to the frequent 'moan' observed in this study. Sunquist and Sunquist (2002) stated 'roaring' was observed by a female 69 times within 15 minutes (~14 roars/min), which is not consistent with the mere six roars observed in this study over 78 hours of recording. These inconsistencies indicate the need for quantitative analyses in standardising the terminology used in referring to the vocal repertoire of tigers, as has been accomplished for other species (Favaro, Ozella, and Pessani 2014).

Two often recorded vocalisations, 'arf' (16% of vocalisations) and 'mrr' (25% of vocalisations), were not described in any of the literature on tiger communication. Other acoustic communication research has had this occur where new vocalisations were discovered that had not previously been described (Pokrovskaya 2013; Favaro, Ozella, and Pessani 2014; Powys 2010). Moreover, the tiger experts did not concur with their suggested contexts and potential functions for ‘arf’ and ‘mrr’, which may suggest that these vocalisations have not been closely observed prior to this study. ‘Arf’ and ‘mrr’ were described as “chatty” or “frustrated” vocalisations implying these could be a single call with graded variation. That these two types are variations of each other is a possibility, particularly given the non-significant difference in peak frequency (Hz) between ‘arf’ and ‘mrr’. Graded variations of vocalisation types with the same context or other relationships are an area for further investigation. Nevertheless, that these two types are variations of each other may be explained with the non-significant difference in peak frequency (Hz) between ‘arf’ and ‘mrr’. The expert information also proposes that these vocalisations may be unique to captive tigers and not observed in wild tigers. A study of captive African penguins (*Spheniscus demersus*) identified a ‘begging moan’ not previously described in literature, which similarly may be related to the animal’s captivity (Favaro, Ozella, and Pessani 2014). This highlights the importance of documenting the acoustic structure and context of all identified vocalisations for captive and wild individuals.

The ‘chuff’ or ‘prusten’ vocalisation was easily identified, as it is a non-laryngeal sound produced by air expulsion through the nose (and potentially mouth) that is commonly described as a greeting call. This non-laryngeal sound is distinctive from the other vocalisations and was recorded in Enclosure 1 with the group of four tigers, but not Enclosure 2 with a solitary tiger. Miller et al. (2013) also observed that tigers ‘chuffed’ more often while housed in groups versus individually. The differences between the chuffs and other vocalisations observed in the two enclosures could be due to the social setting or mother-young setting of Enclosure 1. Prior to this study, the numbers of staccatos, or repetitions, in a ‘chuff’ had not been measured and may provide additional information on this vocalisation. Chuff staccatos varied between individuals, but further investigation is needed to confirm this observation as well as its context and function.

The multinomial logistic regression and corresponding plots clearly demonstrated that ‘moan’, ‘arf’ and ‘mrr’ vocalisations could be reliably classified using measures of peak frequency (Hz), fundamental frequency (Hz), and duration (s) measurements. Duration appeared to be the major factor in differentiating between groups based on its highly significant contribution to the model. However, it is the combination of multiple variables that assist in reliably predicting acoustic categories (Terry, McGregor, and Peake 2001). It is also important to note that harmonics were also a significant variable, but in order to utilize this measurement in predicting categories, vocalisations need to have consistent power (Riede et al. 2001) (i.e. the audio recorder would need to be directly in front of the tiger's mouth for all recordings). Nevertheless, all measurements taken are useful in identifying and classifying different tiger vocalisations and will be beneficial for further investigation of tiger communication.

In this study, seven tiger sound types were identified: 'moan', 'arf', 'mrr', 'chuff', 'growl', 'roar', and 'hiss'. Other literature on tiger vocalisations suggests more than ten distinct vocalisations, some of which were not observed in the present study such as 'bark' (Walsh 2004) and 'purr' (Mills 2004; Thapar 2004; Peters 2002). Purring, as well as roaring, has been much debated with some suggesting neither are structurally possible in *P. tigris* (Walsh 2004; Weissengruber et al. 2002). I recorded a distinct, aggressive 'roar' sound, but with few observations (n=6) and no quantification from prior studies I cannot confirm or deny if tigers produce a 'roar'. Other vocalisations such as the 'chuff', 'growl', and 'hiss' are consistently listed as part of the tiger vocal repertoire (Muggenthaler 2000; Sunquist and Sunquist 2002; Thapar 2004; Walsh 2004). The documented vocal repertoire of cheetahs also includes 'growl' and 'hiss', where the acoustic structure of the 'hiss', in particular, is similar to that of the tiger's 'hiss' (Volodina 2000). According to a comparison of felid vocalisation literature by Sunquist and Sunquist (2002), the hiss and growl vocalisations are listed as consistent vocalisations across a wide variety of felids (Appendix A). Additionally, tigers share 'chuff' vocalisations with jaguars (*Panthera onca*), snow leopards (*Panthera uncial*), and clouded leopards (*Neofelis nebulosa*) (Sunquist and Sunquist 2002). Although this information is a useful basis for comparing tigers with other felids, without a standardized terminology and acoustic form and functions of felid vocalisations reliable comparisons cannot be made.

Multiple difficulties were encountered during the course of this study. Other facilities housing tigers were either unsuitable for audio recording or unable to participate, thus a small sample size of five individual tigers was used. However, it is common for acoustic research to gain useful information even with small sample sizes (Ji et al. 2013; Pokrovskaya 2013; Ruiz-Miranda et al. 1998; Leong et al. 2003), particularly when audio recordings are entirely opportunistic as performed with wild cougars (Macarrão, Corbo, and Araújo 2012). This research provides a basis for future studies, especially in regard to establishing a standardized lexicon of tiger vocalisations and record contexts and potential functions of these tiger vocalisations. Video feedback could not be obtained which prevented accounting for individual variation and hinders generalization of the findings to other tiger populations. Nevertheless, this study advanced our knowledge of tiger acoustic communication including peak vocalisation times, frequent vocalisation types, appropriate measurements to classify vocalisations and suggested contexts and functions of each vocalisation.

Tiger populations are severely declining in the wild and captive populations are increasing, thus any information that can improve captive animal welfare and wild tiger conservation is crucial. Currently, behavioural, stress hormone levels, and keeper assessments have been successful in evaluating captive animal welfare (Whitham and Wielebnowski 2009). Knowledge of vocal behaviour may also aid in monitoring animal welfare. For example, if 'arf' and 'mrr' vocalisations indicate frustration, they may provide a useful additional variable to captive animal welfare assessments. Experimental research may also find playbacks of other tiger vocalisations, such as 'moans', to be a form of auditory enrichment as found in lions (Kelling et al. 2012). The potential individual variation in 'moans' suggests this may be a key monitoring tool for wild tiger populations. Additionally, I can now provide specific times when tigers are most active as has been suggested with other endangered species (Zwart et al. 2014). This study has clearly revealed a strong foundation for the improvement of captive animal welfare and wild tiger conservation with the use of tiger acoustic communication.

CONCLUSION

In conclusion, this study is the first documented quantitative study on multiple tiger vocalisations. I described the acoustic form and suggested context of seven tiger vocalisations including 'moan', 'arf', 'mrr', 'chuff', 'growl', 'roar', and 'hiss'. Three of these ('moan', 'arf', and 'mrr') were reliably classified with the use of a multinomial logistic regression using peak frequency (Hz), fundamental frequency (Hz), and duration (s) measurements. This study presented two new vocalisations not previously described ('arf' and 'mrr'), and provided further information on the commonly described 'chuff' tiger vocalisation. Through the information given, I provide the basis for subsequent studies on the tiger vocal repertoire. Future research on tiger vocalisations should follow the terminology and acoustic forms in this study and further investigate infrequent vocalisations, contexts and functions of vocalisations, and vocal individuality. Once tiger acoustic communication is fully understood, useful comparisons can be made with other felids that have documented vocal repertoires. Most importantly, the documented form and function of all tiger vocalisations will allow for the application of bioacoustic surveys to be used for captive tiger welfare and wild tiger conservation. This is the first study to begin the process of scientifically documenting *P. tigris* communication and improving conservation efforts.

Appendices

Appendix A: Vocalisations compared across a wide range of felids as provided by Sunquist and Sunquist (2002) as "Table 73 Vocal Communication in Felids" in Appendix 4 (pp. 423-424)

Appendix B: Macquarie University Animal Ethics Committee approval for tiger vocalisation research (Protocol number 2014/010-2)

APPENDIX A

Species	Spit, hiss, growl, snarl	Gurgle	Prusten	Puff	Purr	Mew	Main call	Main call with grunt element	Roaring sequence	Grunt	Wah-wah
Lion	+,+,+,+	-	-	+	??	+	-	+	+	+	-
Tiger	+,+,+,+	-	+	-	??	+	+	+	-	-	-
Jaguar	+,+,+,+	-	+	-	??	+	+	+	+	+	-
Leopard	+,+,+,+	-	-	+	??	+	+	+	+	+	-
Cheetah	+,+,+,+	+	-	-	+	+	+	-	-	-	-
Puma	+,+,+,+	+	-	-	+	+	+	-	-	-	+
Snow leopard	+,+,+,+	-	+	-	??	+	+	-	-	-	-
Clouded leopard	+,+,+,+	-	+	-	??	+	+	??	-	-	-
Eurasian lynx	+,+,+,+	+	-	-	+	+	+	-	-	-	+
Canada lynx	+,+,+,+	+	-	-	+?	+	+	-	-	-	
Iberian lynx	+,+,+,+	+	-	-		+	+	-	-	-	
Bobcat	+,+,+,+	+	-	-	+	+	+	-	-	-	+
Caracal	+,+,+,+	+	-	-		+	+	-	-	-	+
Serval	+,+,+,+	+			+	+	+	-	-	-	+?
Asiatic golden cat	+,+,+,+	+	-	-	+	+	+	-	-	-	+
African golden cat	+,+,+,+	+	-	-		+	+	-	-	-	+
Fishing cat	+,+,+,+	+	-	-		+	+	-	-	-	
Jungle cat	+,+,+,+	+	-	-		+	+	-	-	-	-
Ocelot	+,+,+,+	+	-	-	+	+	+	-	-	-	
Margay	+,+,+,+	+	-	-	+	+	+	-	-	-	
Oncilla	+,+,+,+	+	-	-	+	+	+	-	-	-	
Jaguarundi	+,+,+,+	+	-	-	+	+	+	-			+
Geoffroy's cat	+,+,+,+	+	-	-		+	+	-	-	-	
European, African wildcat	+,+,+,+	+	-	-	+	+	+	-	-	-	-
Manul	+,+,+,+	+	-	-		+	+	-	-	-	
Leopard cat	+,+,+,+	+	-	-	+	+	+	-	-	-	
Marbled cat	+,+,+,+	+	-	-	+	+	+	-	-	-	
Sand cat	+,+,+,+	+	-	-		+	+	-	-	-	-
Flat-headed cat	+,+,+,+	+	-	-		+	+	-	-	-	
Rusty-spotted cat	+,+,+,+	+	-	-		+	+	-	-	-	
Black-footed cat	+,+,+,+	+	-	-	+	+	+	-	-	-	-

Note: + = present, +? = probably present, ?? = equivocal, - = absent, blank cell = no data

Note. Vocalisations of felids. Adapted from *Wild Cats of the World* (pp. 423-424), by M. Sunquist and F. Sunquist, 2002, Chicago: University of Chicago Press. Copyright 2002 by Fiona Sunquist and Mel Sunquist.

APPENDIX B

ANIMAL RESEARCH AUTHORITY (ARA)

MACQUARIE UNIVERSITY

AEC Reference No.: 2014/010 - 2 **Date of Expiry:** 28 February 2015

Full Approval Duration: *1 March 2014 to 29 February 2016 (24 Months)*

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) **and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).**

Principal Investigator:
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Other people participating:
Shannah Rose 0481 334 778

In case of emergency, please contact:
the Principal Investigator / Associate Investigator named above, or
Animal Welfare Officer - 9850 7758 / 0439 497 383

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: Pantheria tigris vocalisations: form and function

Purpose: 4 - Research: Human or Animal Biology

Aims: To audio-video record the vocalisations of captive tigers engaged in their normal, daily activities at two zoos in order to gain baseline data regarding the form and function of tiger vocalisations. These data can then be used to determine which vocalisations can be best used in acoustic monitoring efforts in the wild.

Surgical Procedures category: 1 - Observation Involving Minor Interference

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Age/Sex/Weight	Total	Supplier/Source
56 – Exotic zoo animals	Pantheria tigris (Tiger)	Any	13	Taronga Zoo (5) and Australia Zoo (8)
		TOTAL	13	

Location of research:

Location	*Full street address*
Taronga Zoo	Bradley's Head Road, Mosman, NSW 2088

Amendments approved by the AEC since initial approval:

1. Amendment # 1 – Removal of location in Australia Zoo. (Approved 17 July 2014 AEC meeting).

Conditions of Approval: N/A

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

Connor

Professor Mark Connor (Chair, Animal Ethics Committee) **Approval Date: 17 July 2014**

Adapted from Form C (issued under part IV of the Animal Research Act, 1985)

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