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Vocalisations of the New Zealand Morepork (*Ninox novaeseelandiae*) on Ponui Island

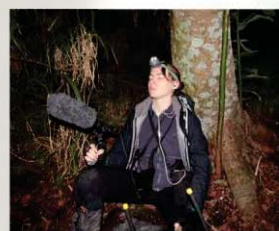
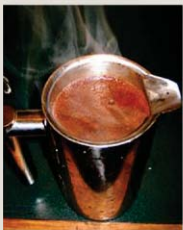
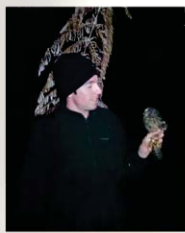
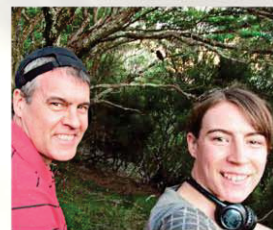
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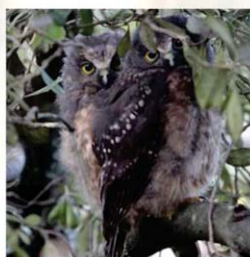
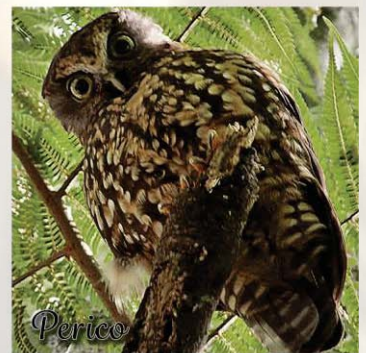
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Abstract

Vocalisations provide an effective way to overcome the challenge of studying the behaviour of cryptic or nocturnal species. Knowledge of vocalisations can be applied to management strategies such as population census, monitoring, and territory mapping. The New Zealand Morepork (*Ninox novaeseelandiae*) is a nocturnal raptor and, to date, there has been little research into their vocalisations even though this offers a key method for monitoring morepork populations. Although not at risk, population monitoring of morepork will help detect population size changes in this avian predator which may prey on native endangered fauna and may suffer secondary poisoning.

This study investigated the vocal ecology of morepork on Ponui Island, Hauraki Gulf, New Zealand from April 2013 to April 2014. The initial goal was to develop a monitoring method for morepork. However, due to a lack of detailed basic knowledge of their vocalisations, the primary objective shifted to filling that knowledge gap and providing baseline data for future research. The aims of this study were thus to characterise all of the calls given by the morepork on the island; to investigate spectral and temporal parameters of three main calls; to plot the amount of calling across a night and a year; and to study the responses of morepork to playback calls.

Eight morepork were caught using mist-nets and subsequently tracked by radio-telemetry. Vocalisations were recorded using manual and automatic digital sound recorders and calls were analysed with manual and automated sound analysis software. I described eleven distinct calls, referred to as *more-pork*, *trill*, *rororo*, *more-more-pork*, *weow*, *low trill*, *copulation squeal*, *single hoot*, *distress squeak*, *chicketting* and *juvenile begging trill* and I further analysed the spectral and temporal characteristics of three main calls, *more-pork*, *trill* and *rororo*. I found variation between individual morepork in acoustic parameters of these call types. I found no evidence of sexual variation in the fundamental frequency, fundamental duration nor inter-syllable duration of the three call types. However, sample sizes were small (2 males to 7 females) and a larger sample size would be needed to confirm these results.

The average number of all morepork call types showed temporal variation both nightly and monthly. A low amount of calling in winter months compared to summer

appeared to coincide with the morepork breeding cycle. The highest numbers of call were heard from November to January, with the numbers of calls during this period being significantly higher than in all other months. The number of calls per hour showed two peaks: one around the middle of the night and the other during the last hour of darkness. The number of calls heard in the first two hours after sunset were significantly lower than during the rest of the night.

Playbacks were effective in eliciting responses from morepork, but the proportion of responses to playback was lower than to natural calls. Response rates did not seem to be affected by season. Session time and order of playback had an effect on proportional responses as well as playback call-type whereby *rororo* elicited the most responses and *trill* elicited the fewest.

This project broadened our knowledge of morepork vocal ecology and therefore contributes to our knowledge of raptor vocal communication. The study also presents information and recommendations that will be useful to future research and also in management of morepork. In particular, this project provides background information needed to help develop protocols for acoustic monitoring of morepork. The techniques used in this study and the general results can be used or applied to studies of other nocturnal species.



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I have so many people to whom I'm indebted a little or a lot for their varied assistance over the course of this little, not so little, project. When I began this thesis I thought I could do it by myself, without needing to trouble anyone else, save annoying my supervisors of course. How wrong I was. Without so many people's help and support, this thesis simply would not exist. I hope I have not missed anyone, but if I have, thank you, blame the sleep deprivation.

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Chapter 1 - General Introduction & Literature Review



There was no wind

The trees stood still

As giant statues.

And the moon was so bright

The sky seemed to shine. (Yolen, 1992)

Animal Communication: An Overview

The ability to transmit and receive signals is essential to enable animals to interact with their environment. Animals communicate in varied ways using modes of communication that are highly adapted to their lifestyle. Depending on their niche and environment, particular senses are more appropriate for effective communication than others. An important example is the challenge to communication posed by a nocturnal lifestyle. Low-light restricts effective communicative options to mainly olfactory and auditory. The line between diurnal communication and nocturnal communication is blurred by the varying amount of light during one night, and between different nights, depending on moon, clouds, and habitat. Studies of crepuscular animals, for example, which are most active at dusk and at dawn, show that vision may also play a role in communication.

Communication is described as being ‘difficult to define succinctly’; however, it entails a behavioural process whereby the probability of an animal’s behaviour occurring is influenced by the behaviour of another animal (Catchpole, 1979). The communication system consists of the ‘sender’, which is the animal producing a signal; the ‘signal’ that is produced; the ‘medium’ (or mode), which is the way the signal is produced and propagated; and the ‘receiver’, or the animal receiving the signal (Catchpole, 1979). Freeberg & Lucas (2010) define “animal communication” as the “sharing of information between a sender and a receiver through the form of a signal that must be constructed in such a way that the signal retains its information after propagating through the environment” (p. 337). However, depending on the receiver, a signal such as a vocalisation can have different meanings. For example, a vocal male can convey a ‘keep out’ message to potential rival males and territory invaders, but also convey a ‘come in’ message to females as potential mates (Catchpole, 1979). The function of a certain call depends largely on the context of the situation and the behaviour accompanying the vocalisation (Catchpole, 1979).

Communication is very important to the lives of animals for many reasons including creating and maintaining social bonds; advertising reproductive status; attracting a mate; maintaining pair-bonds; indicating hunger to parents; using aposematic signals to warn predators; communicating resource presence and quality; communicating

danger and alarm; encoding information on identity or sexual status; and expressing aggression via threats (Catchpole, 1979; Freeberg & Lucas, 2010).

The signals involved in communication can be divided into five primary modes: chemical, sound, visual, tactile and electrical (Freeberg & Lucas, 2010). However, signals are not necessarily so clear cut that they can be grouped into single categories and are often multi-modal. The types of signals that animals use are closely tied to their lifestyle and surroundings (Campbell & Reece, 2008). Freeberg and Lucas (2010) discuss how different signalling modes have varying benefits and costs to the signaller and the receiver. Likewise, they examine the influence of environmental factors and habitat of the animal on which mode of signalling the animal can use effectively to communicate.

Examples of animal communication are numerous and diverse (Alcock, 2009), including both intra- and inter-specific communication (Marler, 1961; Alcock, 2009). The more obvious examples of sound, colouration and body language usage include the loud ultrasound impulses produced by wing-flapping in Whistling Moths (*Hecatesia exultans*) (Alcock, 2009); the 'seet' call - an almost identical and universal inter-species general-alarm call - a result of convergent evolution in many oscine (or song) birds (Marler, 1961; Alcock, 2009); and the encoded 'waggle dance' used by Honey Bees to communicate resource location and quality (von Frisch, 1956, as cited by Marler, 1961).

Communication is often used to avoid direct combat. Animals use threats, including vocalisations, posturing, and other visual displays, to settle disputes and conserve energy that would be lost in fighting a rival (Alcock, 2009). In 1935, Kohts described body language and facial expressions used by chimpanzees to communicate (as cited by Marler, 1961). Marler also cites Leyhausen's 1956 study of domestic feline body language showing graded fear-aggression postures. Animals not only communicate the presence of emotional responses such as aggression, but also the absence of them, which Darwin outlines in his antithesis (1872). Darwin describes how dogs show submission – or a lack of aggression – which is a reverse signal (Marler, 1961). The expression of pain via facial expressions, most commonly attributed to humans, has

recently been found by developing grimace scales in mice (Langford et al., 2010), rats (Sotocinal et al., 2011), and horses (Dalla Costa et al., 2014).

Sensing vibrations is central to the experience and survival of almost all animals and the vast majority of these diverse vibrations are embodied as sound, used by animals not only to communicate but also to monitor their environment (Campbell & Reece, 2008). For example, nocturnal vertebrates such as owls, alligators, geckos, rodents, bats, most felids and canids to name a few, use auditory communication (Crawford, 1934). Auditory communication can be divided into vocal and non-vocal sounds. Vocal sounds dominate with a vast range of noises including song, calls, cries, roars, screams, barks, howls, hisses, grunts and growls, as well as mimicry. Non-vocal sounds are produced when the animal uses other body parts to make noise, for example using air sacs (Kakapo, *Strigops habroptilus*, Powlesland et al., 2006), body vibrations and stridulations (many insects) or body spines (hedgehog-like Madagascan Tenrec, family Tenrecinae, Zherebtsova, 2006). Body parts, such as extremities, bills, beaks, tails, and flukes or fins, can be used for percussion, or to create sound with tools, for example drumming objects with a stick.

Vocal communication can be used for territoriality, mate attraction, pair-bond maintenance, and for a variety of other social reasons. It is of major importance to most bird species, and especially to nocturnal avian species because visual displays are of limited value in low light conditions.

Avian Communication

Birds employ all of the modes of communication outlined above. Examples of non-vocal avian communication include birds that ‘boom’ and those that use wind resistance to produce sounds. Rather than using their syrinx, the New Zealand Kakapo, as well as bitterns such as the Australasian Bittern (*Botaurus poiciloptilus*), use their air sacs, which they inflate, to create deep, resonant booms (O’Donnell et al., 2013). Species such as Ruffed Grouse (*Bonasa umbellus*) (Garcia et al., 2012) and Snipe (family Scolopacidae) (Sutton, 1981) create sound with their wing beats (grouse) or tail feathers (snipe) using air resistance. Woodpeckers drum their bill on tree trunks, and

parrots knock sticks against logs. Most commonly, however, birds rely heavily upon vocal communication, primarily song.

Avian Vocalisations

Avian vocalisations are numerous and varied with almost all bird species communicating vocally in some way and an entire clade – oscine or song birds grouped by their vocalisations, song, and which comprise close to 40% of all extant bird species (Birdlife International, 2014a). To list a few examples of avian vocalisations would not do justice to their diversity. Bird vocalisations can be grouped, however, and it is traditionally accepted that they can be split into song and calls. The line between these two groups has recently become less defined as research into avian vocalisations advances, leaving some traditional definitions, such as ‘songs are learnt’ and ‘calls are innate’, somewhat outdated.

Study of Bird Song

Catchpole (1979) explains how bird song is commonly defined as being a longer and more complex vocalisation made mostly by males in the breeding season, compared to calls which are shorter and simpler, and uttered by both sexes in the breeding and non-breeding period. Penteriani (2002) initially states that song displays are widely believed to have just two main functions - territoriality and mate attraction. However, he goes on to suggest that this may be less true for species that are long-term monogamous and have less need for regular mate attraction and territoriality, than for species that form short-term pairings and are highly territorial. Møller (1988), as cited in Penteriani (2002), states that there may be more functions to bird song than the aforementioned two. Repertoires of calls can be constructed by studying calls and their relation to behaviours and context (Catchpole, 1979), and it has been shown by Thorpe (1961, p. 37), who tabulated various species’ vocabulary, that the number of calls in a repertoire and their function can vary for different species.

With advances in song theory and technology, the study of birdsong has progressed from anecdotal, descriptive discussions to sophisticated analysis of experiment-based studies carried out within a strong framework of evolutionary theory (Slater, 2003) at all levels of organisation: the individual; population; neurobiological; and natural

history. From humble beginnings, the study of bird song can now be grouped into seven study areas: bird-song description methodology; individual song development; physiology of the syrinx; vocal neurobiology; song learning in populations; the communication system as a whole; and the evolution of song learning (Baker, 2001). These areas continue to be built upon as technology and sound analysis techniques improve.

Study of Bird Calls

The study of bird calls is underrepresented compared to bird song in the literature, with the focus in avian vocalisation study directed at oscine birds and their songs. Calls have long been regarded as strictly basal, innate behaviours, although recent studies are proving this to be more myth than fact. Marler and Slabbekoorn (2004) suggest that the structural simplicity of calls is not a definitive indicator of innateness; it simply makes learned nuances less easily detected, though not necessarily non-existent.

Calls are not limited to reproduction and territoriality, but are more deeply involved in the daily lives of birds, for example alarm, foraging, sociality and group dynamics, which are described by Marler and Slabbekoorn (2004) as more “involved than song with immediate issues of life and death” (p. 132). They also caution about the challenge to researchers in describing an avian call repertoire due to the varying number of calls in a repertoire, which can consist of alarm, separation, distress, food-sharing, aggression, and contact maintenance calls. When describing and cataloguing repertoires, necessary considerations include the active space of a call, its acoustic structure, and motivational states behind each call type, as well as silence that communicates information by the cessation in calling.

Nocturnal Avian Communication

For nocturnal birds, the night-time environment poses barriers to visual communication, yet they have the same reasons for communication as diurnal birds with territories to defend and breeding status to announce. Accordingly, vocalisation is very common among nocturnal avian species and has the advantage of travelling long distances. Some nocturnally vocal species include: Frogmouths (*Podargidae*), Nightjars

(*Caprimulgidae*), Potoos (*Nyctibiidae*), Kiwi (*Apterygidae*) and, of course, Owls (*Strigidae* and *Tytonidae*).

In New Zealand there are seven well known nocturnal vocal birds, the five Kiwi species (*A. mantelli*, *A. australis*, *A. owenii*, *A. rowi*, *A. hastii*), Kakapo, and Morepork (Ruru: *Ninox novaeseelandiae novaeseelandiae*). In addition to these there are other species which are more active and vocalise at night and during crepuscular times, including Little Owls (*Athene noctua*), Weka (*Gallirallus australis*), Kaka (*Nestor meridionalis*), Auckland Island Snipe (*Coenocorypha aucklandica*), Blue Ducks (Whio: *Hymenolaimus malacorhynchos*), Little Blue Penguins (*Eudyptula minor*) and a fair number of other New Zealand seabirds.

The number of studies into nocturnal avian vocalisations has increased in the past few decades thanks to advances in technology that have increased the practicality of such studies, such as more affordable and improved quality of recordings and ease of sound analysis. Owls are a common subject in the literature on nocturnal avian vocalisations, mirroring that they are the most common birds associated with nocturnal vocalisation. Owls are nocturnal and/or crepuscular and the majority are highly vocal, relying on vocalisations as their primary mode of communication. Day-hunting owls are less vocal than nocturnal owls (Everett, 1977; Leach, 1992), but most species produce at least one vocalisation with some possessing considerable vocal repertoires (Everett, 1977). Most owls show little sexual dimorphism, so sex-specific vocal characteristics often play an important role in advertising sexual identity, especially in the primary stages of courtship (Leach, 1992). Owl behaviour at night is commonly inferred from studying their vocalisations, as it is difficult to observe these species' other behaviours in darkness without causing disturbance. Their low visibility poses a challenge to surveying their populations too, so vocalisations are a commonly used technique for population monitoring. However, before an accurate estimate of abundance can be attempted, it is first necessary to understand the behaviour underlying each species' vocalisations and the factors that may influence the relationship between number of vocalisations and number of individuals. These include movement habits, territory size and sociality of the subject, and also effects of weather and lunar cycles. When

planning a survey of a vocal nocturnal species, the seasonality of vocalisations needs to be known to choose an appropriate time of year to conduct the survey.

In Australia, the morepork's close relative the Southern boobook (*Ninox boobook*) has been the focus of a few vocalisation studies (Olsen & Trost, 1997, 2007; Olsen et al., 2002a; 2002b; 2010; 2011) and there have been a few vocalisation-focussed studies into other *Ninox* owls such as a comparative study of the Sumba boobook (*Ninox rudolfi*), Little Sumba Hawk-owl (*N. sumbaensis*) and Southern boobook ("*Ninox novaeseelandiae*") (Olsen et al., 2009) and short vocal descriptions of the Togian boobook (*N. burhani*) and comparisons to other boobook of Sulawesi, Indonesia (King, 2008) and Northern boobook (*N. japonica*) (King & Icaragnal, 2008) and the Philippine Hawk-owl Complex (*N. philippensis*) (Rasmussen et al., 2012). These studies include the use of passive call surveys, playback induced call studies, sound recording and spectrographic analysis, repertoire studies, and temporal and environmental influences on calling.

History of Avian Vocalisation Studies

Although there were some insights made into bird vocalisations and behaviour before the twentieth century, the focus of ornithology in earlier times was based largely on description and classification. Early methods of describing bird vocalisations before recordings could be made and visualised via spectrograph, involved employing words or musical notation to represent bird sounds (Baker, 2001). The study and knowledge around the area of bird behaviour and vocalisations increased exponentially after World War II due to technological advances. Two such advances are credited by Baker (2001) as being pivotal in the change of pace in knowledge acquisition and study of bird vocalisations; these are the tape recorder and sound spectrograph. While the tape recorder had been available for longer than the spectrograph, the necessity for military grade sound visualisation and analysis brought about by the war meant that once the war ended, scientists could combine the two technologies to great effect in studying bird song. Such was the growth in knowledge that Baker (2001) describes it as mirroring the great leap forward that the invention of the microscope facilitated.

Prior to the mid-twentieth century, technology for studying and describing bird vocalisations was virtually non-existent and methods were basic. Using words as notations for animal vocalisations, especially bird song, is the oldest description method, records of which, according to Baker (2001), date back to the 1200s. Baker stated that, although a scientifically limited form of description, assigning onomatopoeic words to bird song is very effective for bird identification in field ornithology at any experience level, and this method is still used today. Musical annotation was also an early form of bird song description spanning into the twentieth century, whereby composers and then ornithologists attempted to transcribe bird song into a musical composition. Baker (2001) described a method used by Saunders in 1915 which used a combination of the above two methods. Using an amended version of standard musical notation - which allowed for the time, pitch and intensity variation in bird song - and writing accompanying phonetic descriptions gave a visual result highly comparable to those produced by modern voice analysis equipment. However, with so little equipment with which to describe and study bird song, little progression was made because it was not a priority ornithological subject until the mid-twentieth century. A pioneer in the recording of bird song, A. R. Brand, used a movie camera to record singing birds and, by analysis of the movie film with a microscope, produced the first published film-derived bird song visualisations. He went on to record the vocalisations of more than 300 species (Baker, 2001).

Technological Advances

Around the 1930s, advances in recording technology saw the invention of magnetic tape recorders and by the mid-thirties a recording/playback device, the Magnetophon, had been developed. With this as a base, the equipment for recording bird vocalisations began to grow with advances in technology (Baker, 2001).

World War II and the consequential technological arms race served as a catalyst for technological invention and some of these would prove beneficial to post-war society. One such invention was the sound spectrograph which was developed during the war for military intelligence in the analysis of enemy sounds and communication. Once made available to the scientific community after the war, the spectrograph was to revolutionise the way animal sounds were studied, allowing quantitative descriptions

of sound where before only verbalisation and musical notation had been possible (Marler & Slabbekoorn, 2004). The machine evolved from spying on humans to spying on animals.

The inception of the tape recorder and spectrograph meant that animal sounds, in particular those made by birds, could be studied in far greater depth both quantitatively and qualitatively. Varied parameters could now be measured from recorded sound using the spectrograph and then used to analyse the sound and conduct comparisons. From humble beginnings, bioacoustics and its use in the study of animal communication broadened and diversified, and with further technological advances it is now a large and growing field of study.

Definitions

Marler and Slabbekoorn (2004) discussed how there is no clear line separating bird calls from bird song. However, the majority of the literature agrees that traditionally, **calls** are shorter, simple vocalisations (often monosyllabic) which do not follow an orderly pattern, but are given at random. **Song** displays higher acoustic structural complexity and has a longer duration, delivered in a statistically significant pattern. **Song** is commonly given by one sex, most often the male, whereas **calls** are uttered by both sexes. **Song** tends to be more related to territoriality and mate attraction, where **calls** have a much broader purpose and occur in a wide yet specific range of contexts, including roles in foraging, sociality, and alarm, as well as lesser roles in reproduction and territoriality. There is debate between owl vocalisation researchers as to whether owl vocalisations are calls or song.

It is very difficult to define exactly the distinction between calls and song. Tinbergen (1939) found such diversity in song and calls that there was little defence for their separation by duration or aesthetics, suggesting function could be a more appropriate distinction (as cited in Baker, 2001). Indeed, as knowledge and insight into bird vocalisations grows, the line between the two becomes more blurred. Song can be as short as some calls and likewise calls can be as complex and rich in harmonics as some songs (Baker, 2001). In this study, I will refer to more complex vocalisations as **calls**, because they are largely acoustically-simple vocalisations and are uttered year-round

and by both sexes as opposed to being uttered only in the breeding season and by a single sex, from what I have discovered.

Song and calls themselves can be split into increasingly detailed parts, including phrases, syllables and elements. A **phrase** consists of a number of **syllables** (usually similar but sometimes different) in a series pattern. However, in simpler calls a phrase often does not occur, or it is not possible to distinguish a phrase level. **Syllables** in turn consist of **elements**; however the number of elements depends on the complexity of the syllable. In simpler calls, the two are often difficult to distinguish and therefore referred to as equal to each other, in which case **syllables** are the shortest part of the call (Duan et al., 2013; Somervuo et al., 2006). These three features are most commonly seen in complex bird song, whereas calls, being simpler vocalisations, can most often only be segmented into single or a few syllables and generally do not form detectable phrases (Somervuo et al., 2006).

A **bout** is a collection of calls by one individual that occur without a large gap separating them. Like Somervuo et al. (2006), in this study the smallest unit of a call will be referred to as a **syllable**. Baker (2001) describes how there are no standardised terms within avian bioacoustics research that have been developed to apply to all calls and song. While **note** is often used interchangeably with **syllable**, I find it implies a musical, tonal quality that some of the morepork call syllables seem to lack and therefore I will use the term syllables instead of notes when referring to smaller units of morepork vocalisations. Odom and Mennill (2010) defined a note or syllable as a structure separated by a silent interval and their definition will be adopted in this chapter.

Finally, a **repertoire** encompasses all the vocalisations that both sexes of a bird species – in the context of general avian communication – make over their lifetime (Baker, 2001). In bird song, however, repertoire can also be used to define an individual's unique versions of its species' song (Baker, 2001). The species level repertoire can vary in size from just a few to a great many vocalisations; however, there is a general lack of intensive study into repertoires (Marler & Slabbekoorn, 2004). Marler and Slabbekoorn (2004) explained that a high level of expertise in the species' ecology and behaviour

temporally, seasonally and throughout the course of its life is first required before being able to fully describe a species' repertoire. This is due to repertoire being affected by the caller's age, sex and status. The complexity of the task may offer a reason why species' whole repertoires have been less studied than their standalone vocalisations.

Duetting and Duelling

An interesting aspect of calling behaviour in birds is the separation of **duetting** and **duelling**. As with defining repertoires, this too requires an understanding of the species' behavioural ecology, because the two calling behaviours are related to two different aspects of the species' biology - mate attraction and territoriality respectively. Olsen et al. (2002b) defined **duetting** as a mated pair calling in co-ordinated, overlapping bouts. **Duelling** on the other hand involves two unmated birds from different territories calling in overlapping but non-coordinated bouts. Olsen et al. (2002b) reviewed the literature on Southern boobooks (*Ninox boobook*) and whether they duet or duel and found a debate on both sides. In 1997, Olsen and Trost reported how some researchers may have misidentified rival territorial males duelling as a mated boobook pair duetting. In Higgins' review (1999), duetting was concluded to occur based on evidence from both Australia and New Zealand, however, it is noted that none of these studies actually defined duetting.

Bioacoustics and Wildlife Monitoring

Animal bioacoustics, the study of biological sounds, has become an important tool for monitoring animal populations, and is becoming increasingly common in the field of conservation at many levels, from environmental monitoring to identification and study of individuals. Bioacoustics is common in the study of bird populations and is very useful in nocturnal bird studies. As a survey technique, it is less invasive than mark-recapture, and also requires less effort (Baptista & Gaunt, 1997). Two well-used examples of bioacoustic methods of monitoring populations are call surveying and sound recording, both having positive and negative aspects in regard to wildlife management and monitoring programmes. In their community-based urban acoustic morepork study, Morgan and Styche (2012) discuss how involving the general public in call surveys can be a powerful conservation advocacy tool. Before bioacoustics can be

applied in the context of conservation, however, the basic underlying ethology in the character and contexts of vocalisations must first be studied and understood.

Sound Recorders

Manual sound recorders are user-operated recording devices which use highly sensitive and directional microphones. These can be used in the field to obtain high quality recordings for later sound analysis. Recording calls manually enables identification of the calling bird and behavioural observations to be obtained whilst recording.

Automated sound recorders remotely record and store sound in the field and can be programmed to record at certain times and for certain durations (Rognan et al., 2012). They can greatly increase effective field survey effort and site coverage due to the ability to operate automatically (Steer, 2010).

Playback Experiments

Playback is a popular technique in the study of animal communication and cognition. Deecke (2006) defined playback as “the experimental presentation of recorded sensory stimuli to animals to investigate their behavioural or psychophysiological responses”. The general aim of using sound playback is to elicit a response from the target animal which may be vocal or behavioural. Applications of acoustic playback cover a broad range of areas. These include studying territorial behaviour and mapping, general communication, predator-prey interactions, personality and motivational states, dominance, function and context of vocalisations, seasonality of certain behaviours and finally population census; including presence/absence of cryptic species as well as abundance and density. Experiments using playback allow hypotheses from questions of call meaning and function to be tested in the field and the laboratory and elicited responses used to infer answers to these questions (Douglas & Mennill, 2010). With cryptic animals, playback experiments offer the ability for scientific study of aspects of ecology and behaviour which are otherwise difficult to study in the wild.

Study Species: New Zealand Morepork

The Morepork (*Ninox n. novaeseelandiae*) or Ruru in Maori, named after its distinctive, repetitive, disyllabic call, is New Zealand's only native owl after the extinction of the New Zealand Laughing Owl (*Sceloglaux albifacies*) at the beginning of the 20th Century. Morepork, one of the most well-known nocturnal birds in New Zealand, are common throughout most of the country and are classified as 'Least Concern' by the International Union for the Conservation of Nature (IUCN) species conservation status classifications (Birdlife, 2009). The Department of Conservation lists the morepork as not threatened (Robertson et al., 2013), however, there is suspicion that numbers may be in gradual decline (Department of Conservation (DOC), n.d.). While common, the deterioration of many of New Zealand's habitat types means morepork face the same threats that have brought many other New Zealand species to the brink of extinction, including habitat destruction, habitat modification, and mammalian predation of eggs, chicks and adults. However, they have also benefitted from certain human-introduced pest mammals as a prey source - mainly mice and rats - which pose a huge threat to New Zealand's avifauna. To this end when rodent numbers boom, morepork populations often do well as a result. Yet, as predators that occupy a higher trophic level than many of New Zealand's birds, morepork often consume mammalian prey that are targets of pest-control poisoning efforts, and hence they may be at risk of secondary poisoning, either from consuming poisoned rodents directly, or from bioaccumulation of toxins (Stephenson et al., 1999). Morepork are also susceptible to being hit by road traffic.

Morphology

The morepork is a relatively small owl, on average less than 30 cm tall and weighing around 200 g (Stephenson & Minot, 2006; Denny, 2009). It is similar in appearance to the Australian Southern boobook, which is slightly bigger, has lighter plumage and feet, and paler yellow eyes (Olsen, 2011). Morepork have predominantly brown plumage with interspersed white breast feathers, and brown and white barred primaries, secondaries and retrices. There is a high degree of morphological variation in their plumage, including shade of brown and amount of light feathers on the breast (Imboden, 1985; Stephenson, 1998). They often have white feathers that define the

ridge above the eyes, but this varies individually (Pers. obs.). Male and female morepork are similar in appearance and very difficult to distinguish in the field (Haw & Clout, 1999). However, Stephenson's (1998) observations suggest that females can be slightly heavier with broader beaks and longer wings, although colouration is not correlated to sex.

Taxonomy

The morepork belongs to the hawk owl genus *Ninox*, classified for their small size and hawk-like characteristics, in the family Strigidae (Higgins, 1999). Certain morphological characteristics common to the *Ninox* genus include a long tail, subtle facial disk, front facing nostrils as opposed to either side of the cere and a certain degree of emargination to the primary feathers. The genus of 37 species is well represented in the Indonesian Archipelago (ten species: *N. hantu*, *ios*, *hypogramma*, *sumbaensis*, *ochracea*, *squamipila*, *punctulata*, *rudolfi*, *forbesi*, *burhani*); the Philippines (eight species: *N. leventisi*, *rumseyi*, *randi*, *philippensis*, *spilocephala*, *mindorensis*, *spilonotus*, *reyi*); Australia (five species: *N. connivens*, *strenua*, *boobook*, *leucopsis*, *rufa*); Papua New Guinea (five species: *N. variegata*, *theomacha*, *meeki*, *odiosa*, *rufa*); the Solomon Islands (four species: *N. granti*, *roseoaxillaris*, *malaitae*, *jacquinoti*); the Indian Andaman and Nicobar Islands (two species: *N. affinis* and *obscura*); Christmas Island (one species: *N. natalis*) and New Zealand (one species: *N. novaeseelandiae*) (Olsen, 2011; BirdLife International, 2014). Finally, two species are geographically widespread: the Brown boobook (*N. scutulata*) which occurs in India, Indonesia, Thailand, Nepal, Myanmar, Vietnam and Malaysia, and the Northern boobook (*N. japonica*) which occurs in Indonesia, Taiwan, Japan, North and South Korea, Eastern China and Eastern Russia (BirdLife International, 2014b). Of these 37 *Ninox* species, BirdLife international (2014b) reports conservation statuses of 19 to be of Least Concern, nine to be Vulnerable, seven as Near Threatened and two as Endangered. With regard to population trends, 70.3% are decreasing (26 species) and 29.7% are stable (11 species).

The New Zealand morepork are the nominate race of the species *novaeseelandiae* as *N. n. novaeseelandiae*, which also includes the subspecies *N. n. albaria* (extinct Lord Howe boobook), and *N. n. undulata* (Norfolk Island boobook). The Norfolk Island boobook is also sometimes referred to as morepork, as they are a hybrid population

with two New Zealand morepork translocated to save the sub-species (Konig et al., 1999). There is considerable debate over the classification of the Southern and Tasmanian boobooks. Higgins (1999) groups the New Zealand morepork, Australian Southern boobook and Tasmanian boobook together as the same species (*N. novaeseelandiae*) following Mees' taxonomy of 1964. However, Olsen (2011) reports how Mees described the classification of the Southern boobook as "one of the most difficult taxonomic problems he had encountered" (Olsen, 2011, p. 15). In 2005, Olsen and Debus reported how the boobook and morepork were wrongly split into two species by Konig et al. (1999) and del Hoyo et al. (1999) due to "misinterpretation of DNA evidence", and even with the improvement of DNA analysis techniques, the classification problem is still being debated. It remains a contentious subject as to whether the Southern boobook should be classified as *N. novaeseelandiae* or *N. boobook* and the classification varies according to the taxonomist. Of the six publications Olsen cites, ranging from 1980 to 2008, there is an even split between the two species names for the Southern boobook. However, in classifying the Tasmanian boobook, four use *novaeseelandiae*, one uses *boobook* and the other *leucopsis*. Two of the most recent publications Olsen cited, Christidis and Boles (2008), classify the three as *N. Novaeseelandiae*, and Wink et al. (2008) classify them as three separate species. Olsen suggests that Wink et al. have a stronger case as they used both morphological and genetic (cytochrome b) analyses, whereas the other publications used more primitive methods. Interestingly, the current thinking is that the two should be split and BirdLife International (2014b) follows del Hoyo et al. (2014) by splitting the two as separate species. Therefore, in this study the Southern boobook and New Zealand morepork will be treated as separate species, *N. boobook* and *N. novaeseelandiae* respectively.

Ecology in Brief

Distribution

Morepork are widespread throughout New Zealand on the North Island, much of the South Island, and offshore islands such as Stewart Island, Little Barrier and Great Barrier Islands, Three Kings Island and Kapiti Island (Konig et al., 1999; Haw & Clout 1999). They have, however, encountered strong competition from the introduced

Little Owl (*Athene noctua*), as well as habitat loss, leading to their decline in the Canterbury and Otago regions in the south east of the South Island (Haw & Clout, 1999; Higgins, 1999).

Diet

In general the *Ninox* owls have varied diets consisting of both invertebrate and vertebrate prey (Konig et al., 1999). The morepork is no different, as an opportunistic generalist carnivore with a tendency towards being insectivorous depending on the relative abundance of other prey. Studies have consistently shown morepork diet mainly consists of insects, especially lepidopterans (moths), coleopterans (beetles), orthopterans (weta) and spiders. However, their diet also includes small mammals and birds, and sometimes amphibians and reptiles (Saint Girons et al., 1986; Clark, 1992; Konig et al., 1999; Haw & Clout, 1999; Higgins, 1999; Denny, 2009). Denny (2009) suggested that vertebrate prey items may involve higher time and energy costs to locate and capture, explaining their preference for invertebrate prey. Conversely, morepork have been reported to feed chicks a higher proportion of vertebrate prey than is included in the usual adult diet. Denny (2009) suggested this could be due to energy conservation in trips to and from the nest to deliver prey. Morepork are reported to rarely take native vertebrate species (Haw et al., 2001), except when they are abundant or easy prey. For example, morepork have been reported to take fledgling shearwaters (*Puffinus assimilis*) on off-shore islands (Anderson, 1992), released captive-bred NZ Shore Plover (*Thinornis novaeseelandiae*) (Aikman, 1999), and skinks and geckos (Parish & Gill, 2003). They have been reported to prey on New Zealand's only native mammals, short-tailed bats (*Mystacina tuberculata*) (Konig et al., 1999) and long-tailed bats (*Chalinolobus tuberculatus*) (Borkin & Ludlow, 2009). Morepork have been reported to exploit the higher abundance of avian prey items during breeding seasons of both native and non-native birds (I. Castro, Pers. comm., 2015). In an urban setting, morepork will take advantage of street lights, hunting the light-attracted insects by hawking them from about the light (McCann, 1959). Morepork have also been known to take advantage of researchers' mist-netting efforts by hawking birds from the nets, for example, during a 1991 study on Little Barrier Island (Hauturu) in New Zealand (I. Castro, Pers. Comm., 2014).

The morepork has adapted to exploit introduced small mammals as part of its diet, however, introduced mammals have mixed impacts on these owls. While introduced small mammals generally have only negative impacts on New Zealand's avian fauna, their impacts on the morepork are a mix of positive and negative. Small mammals such as mice and small or juvenile rats can be useful as prey for the generalist morepork who can exploit changes in prey availability. Conversely, small mammals such as mice, rats and small mustelids are nest and chick predators, food competitors, deadly poison vectors via secondary poisoning, and the subjects of conservation pest-control, which results in prey population crashes. As competitors and predators, larger mammals such as cats and ferrets pose only negative impacts to the morepork. Morepork are vulnerable to predation while nesting both as adults sit on the nest but also when chicks are left alone as both parents leave to hunt. Cats can prey on morepork and it is behaviours such as hunting on the ground or being caught off guard while roosting that makes morepork vulnerable to predation not only while nesting, but year-round.

Owls have been suggested as useful biomonitors by Sheffield (1997), but their potential has been understudied. Sheffield (1997) defines biomonitors as species which serve as an early warning system of environmental change such as toxic contaminants. Characteristics common to those species commonly suggested as biomonitors include being territorial, non-migratory, having a wide distribution, high trophic status and high reproductive rates, many of which raptor species possess (Sheffield, 1997). While his discussion relates to larger northern species of owls, which have a higher trophic classification and eat predominantly mammals and birds compared to the morepork that favour invertebrates, the morepork should not be excluded from consideration. Morepork are known to take advantage of the most abundant prey source, which may coincide with rodent population booms and subsequent poisoning effort intensification. Fox and Lock (1978) found little cause for alarm regarding morepork when studying the residue bioconcentration of DDT and organochlorides in New Zealand's raptors, mostly due to morepork consuming fewer vertebrate animals than the native falcon (*Falco novaeseelandiae*) and harrier (*Circus approximans gouldi*). Fraser and Hauber (2008) suggest that poisoning from 1080 (sodium monofluoroacetate) does not have a significant detrimental effect on

morepork population numbers in the short term, and they found that their numbers may even increase due to improved breeding and survival following poisoning operations. In addition, Greene et al. (2013) found only one morepork (out of 27 monitored) to have died over five aerial 1080 drops. Conversely brodifacoum, an anticoagulant poison, has been found to build up as residue in live target mammals and also non-target birds including morepork (Murphy et al., 1998). Stephenson et al. (1999) studied the effects on morepork of a poison drop to control rodents on Mokoia Island, Rotorua, and found 21% mortality in radio-tracked morepork due to brodifacoum, 51 days after the poison drop. Furthermore, Stephenson and Minot (2006) found morepork breeding success decreased after a poison drop although they advise caution in interpreting this result as their sample size was small and they recommend that morepork breeding success in relation to poison drops requires further study.

Breeding

Until Stephenson's study (1998) of morepork breeding biology, much of the information on this subject was based on anecdotal reports, short papers and studies of the Australian boobook (Stephenson & Minot, 2006). The morepork breeding season lasts from September to February (Higgins, 1999) with egg-laying occurring around the beginning of October. Although Stephenson and Minot (2006) reported that the morepork's low sexual dimorphism makes differentiating sex of the birds by sight difficult, their study using marked sex-known individuals confirms both Imboden (1985) and Heather & Robertson (2005) who state that only females incubate and that males provide food and roost nearby. Morepork nest sites were commonly hollows in both trees and tree-ferns, as well as scrapes in the ground and nest boxes intended for other, smaller birds (Stephenson & Minot, 2006; Denny, 2009). The usual clutch size of a morepork is two or three eggs (Higgins, 1999; Stephenson & Minot, 2006). Hatching is asynchronous, occurring after approximately one month of incubation and the chicks fledge at around 30-40 days old.

Habitat

Morepork naturally inhabit native forest, but also exploit farmland, non-native forest and plantations, and suburban parkland habitats (Higgins, 1999; Haw & Clout, 1999;

Haw et al., 2001). Their tendency towards a generalist opportunistic predatory strategy means that morepork can exploit these various habitats, resulting in the species' widespread success and distribution. Roost trees favoured by morepork reportedly vary, however, overhead cover appears to be a recurrent key roost characteristic (Imboden, 1975; Stephenson, 1998; Denny, 2009). In fact, Denny (2009) suggested that the selection of roost site height, on average around 4 m, depended on the largest amount of overhead cover. High overhead cover allows reduced detection both by predators of morepork and prey species, which may mob a roosting morepork. Denny (2009) found that in her study site, a regenerating kauri (*Agathis australis*) forest, the most commonly selected roost trees were silver fern or ponga (*Cyathea dealbata*) and tree coprosma (*Coprosma arborea*), but that many other species were used too.

Territories and Home Range Size

The home range size of the morepork is reported at between three and five hectares (Imboden, 1975; Stephenson, 1998). Morepork are nocturnal, territorial and non-migratory (Stephenson, 1998; König et al., 1999; Higgins, 1999; Haw et al., 2001). They are territorial throughout the year, favouring specific parts of their home-range and defending their territories with vocalisations and aggressive behaviours (Stephenson, 1998). In a telemetry study in 1975, Imboden reported that morepork were highly mobile during the night. Following them on foot proved to be a challenge, as birds often traversed the extent of their home range and back several times within an hour, rendering hourly location data of little use. Imboden (1975) also commented on the birds appearing to be disturbed and moving more frequently when followed too intensely.

Activity

Morepork roost during the day, becoming active around dusk, and returning to the roost around dawn (Imboden, 1975; Stephenson, 1998; Denny, 2009), but they are sometimes observed being active during the day (Stephenson, 1998). In a study of morepork activity time-budgets, Stephenson (1998) found hunting to be the dominant activity. When hunting, the morepork, like most owls, are able to fly silently due to soft, serrated, comb-like edges to their wing feathers (König et al., 1999). This is widely accepted to reduce the noise caused by air turbulence over their wings, allowing them

to approach prey undetected. There is some controversy around this generally accepted explanation for owl's silent flight; a study by Neuhaus, Bretting and Schweizer (1973 as cited in Geyer et al., 2014) found that even without the serrated edge, the flight of Tawny Owls (*Strix aluco*) remained silent. In their review of the literature, Geyer et al. (2014) concluded that the serrated comb edge to the wings served mainly an aerodynamic purpose as opposed to being directly involved in flight noise reduction. Morepork are perch hunters or 'sit-and-wait' predators (Stephenson, 1998), waiting on a perch and hawking insects from the air or picking them off nearby vegetation.

Senses are critical to the morepork's hunting success. Vision is important and in owls this sense is sharp due to a very large retina, a more oval shaped, large eye, and high density of rod cells, which reduces colour vision, but heightens the outlines of objects. Sharp vision combined with acute hearing, maximises the ability to detect prey (Konig, et al., 1999), and sharp claws and powerful talons assist the morepork in plucking winged prey from the air (Haw & Clout, 1999; Konig et al., 1999; Higgins, 1999). Hunting usually occurs in the evening and before dawn. Morepork have been documented to be able to learn to manipulate sensor lights to attract insects (Haw & Clout, 1999; Higgins, 1999). Higgins (1999) also reported other methods used to capture and kill prey, including startling prey from trees or bushes by deliberately disturbing them with wings, or a rough landing. Morepork kill vertebrates by restraining them with their talons, severing the spinal cord and crushing the base of the skull with their beak. Small prey will often be swallowed whole, or dissected into smaller parts and excess food will be cached nearby the nest to be eaten later (Higgins, 1999). Hunting activity during the day has been recorded in the wild in times of food shortage, but it is also a common occurrence in some places for morepork to hunt during the day (Higgins, 1999).

Hearing is well developed and often critical to an owl's lifestyle. Of all bird groups, owls have arguably the most acute hearing, which is very important to a bird that is mostly active around the hours of darkness (Mikkola, 1983). Owls show intriguing anatomical adaptations which enable such acute hearing. One such adaptation is the facial disk created by separate feathers arranged concentrically around the eyes and ears that

give the owl its characteristic wide, round face. These feathers can be controlled with fine motor muscles and assist the directing of sound towards the ears. Owl ears have wide apertures often surrounded by a fold of skin to reflect sound (Mikkola, 1983). The facial disk can be more or less pronounced depending on the species. Another adaptation is the phenomenon of bilaterally asymmetrical ears, only seen in species from nine owl genera: *Tyto*, *Phodilus*, *Bubo*, *Ciccaba*, *Strix*, *Rhinoptynx*, *Asio*, *Psuedoscops* and *Aegolius* (Norberg, 1977). Bilateral asymmetry means that these owls' ears differ in size and position with one ear usually being larger than the other and being positioned higher or lower on one side than the other (Mikkola, 1983). This asymmetry is external in most species with only four species of owl (Ural, Great Grey, Tengmalm's and Saw-whet) having been reported to show internal ear asymmetry in skull anatomy (Mikkola, 1983). This bilateral asymmetry enhances directional and localised sound detection (Norberg, 1977), and is important to owls which rely on locating prey largely by sound. Owls of the *Ninox* genus, however, are part of the other 16 owl genera (Mikkola, 1983) which have not been found to display auditory bilateral asymmetry (Olsen, 2011). This is perhaps due to their use of vision as well as hearing when hunting, and their active periods extending either side of dusk and dawn.

There is not a large amount of literature addressing the frequency range sensitivity of owls, but, there have been two studies which looked at the subject in Barn Owls (*Tyto alba*) (Konishi, 1973) and Eastern Screech Owls (*Megascops asio*) (Brittan-Powell et al., 2005). When using the data to look at owl vocal communication, an interesting difference between these two studies, as pointed out by Brittan-Powell et al. (2005), is the two species' differing vocal behaviour. The Barn Owl shows limited territoriality and vocal repertoire and only communicates with vocalisations over short distances, whereas the Eastern Screech Owl is territorial and highly vocal (Brittan-Powell et al., 2005). Most birds are more sensitive to sounds between 1000 Hz and 5000 Hz with peak sensitivity generally occurring between 2000 Hz and 3000 Hz (Brittan-Powell et al., 2005). Konishi (1973) found Barn Owls to best hear frequencies of between 4000 and 8000 Hz up to 10,000 Hz. In their study of Eastern Screech Owls, Brittan-Powell et al. (2005) found peak sensitivity to lie at a higher frequency than fundamental frequency (500-1500 Hz) of its calls. They suggested that perhaps prey-detection is

more important than vocal signal detection where peak sensitivity is concerned. They found Eastern Screech Owls, like other owl species to have a broad range of high sensitivity, which served both the purpose of hunting and long-distance communication using low frequency sounds.

Hearing is not just used for detecting prey and for vocal species, but is very important to their communication across long-distances. Hearing therefore serves a dual purpose for owls and is important for both hunting and communication. Morepork frequency range sensitivity has not been studied. In his activity and time-budget analysis, Stephenson (1998) found that morepork spent considerable time calling, but most of the time hunting. Hunting and calling times did not seem to follow a pattern during the night, and further study linking the two is necessary.

Calling

There has been little study of the New Zealand morepork's calling behaviour directly, with the focus being on call surveying. However, as part of a larger ecological study of morepork, Stephenson (1998) described the different calls he heard and associated behaviours on Mokoia Island, Rotorua. He identified seven different calls which he named 'More-pork' (location call); 'More' (agitated location call); 'Purr' (contact call); 'Peow' (series location call); 'Pew' (alarm call); 'Chitter' (chick alarm call); and a juvenile begging call. Stephenson reported both pair duetting and rival duelling calling behaviours, and that the use of playback calls in the field successfully elicited responses. He also found that the pitch of calls varied greatly, and suggested that this was related to the sex of the bird calling, with certain call types uttered more frequently by one sex than the other. Debus (1996) and Olsen (1997) also suggested a link between call pitch and sex in Southern boobook. In morepork, Imboden (1975) reported an increase in calling just before the beginning of the breeding season around the end of August and early September, as well as calling episodes during late afternoon before dark early in the breeding season.

There has, however, been considerably more study into the vocalisations of the Australian Southern boobook (*Ninox boobook*). The territorial call of the Southern boobook (*N. boobook*), '*Ninox novaeseelandiae*' in Olsen 2011, is a double hoot,

responsible for its name 'boo-book', given at intervals of 4-5 seconds in bouts lasting up to and over an hour. Olsen et al. (2002a) studied and confirmed the occurrence of ten different types of call uttered by the Southern boobook, described by Higgins (1999) as the boobook call; single hoot; por (croak); squeal; bray; trill; yelp; growl; scream and the squeak, and determined that both sexes use most calls. They categorised the calls as either territorial or contact, and found that call frequency varied the most according to season, social context and individual differences.

The other Australian *Ninox* species' calls have been less intensely studied than the Southern boobook, but have been well described by Olsen (2011) who provides an informative overview of each species, which I will summarise next. The main call of Rufous Owls (*Ninox rufa*) is a slow, subdued, disyllabic hoot lasting half a second and uttered at intervals of several seconds. Their other calls include a single hoot, guttural bleating, and juvenile cricket-like begging call. Their calls are reportedly often confused with the Powerful Owl (*N. strenua*) which also has a slow double 'woo-hoo' hoot, but each syllable is twice as long as that of the Rufous Owl. The Rufous and Powerful Owls also utter a single, deep, guttural hoot. The Powerful Owl's juvenile begging call is a falsetto trill. The Barking Owl (*N. connivens*) also has a disyllabic hoot, but this is described as a faster, hoarser 'wook-wook' which is higher pitched when uttered by females (Olsen, 2011). Interestingly, as its name suggests, Olsen describes the call as being difficult to distinguish between a distant dog barking and an owl, as each first syllable is often preceded by a growl, many records of presence/absence include misidentified dogs and foxes. In addition, the Barking Owl's repertoire includes growls, snarls, a wavering scream and an elongated, deep juvenile begging trill.

Hill and Lill (1998) have described the Christmas Island Hawk-owl's (*N. natalis*) vocalisations, which are similar to the Southern boobook and include a territorial double hoot, male 'por-por' in courtship and territorial defence, a juvenile begging trill, a female low trill 'chirr', a copulation squeal, and a male 'kar-kar' when delivering food to the female.

Studies of other *Ninox* species have not often focused on vocalisations directly, dealing more with broader ecological studies and population monitoring. Indeed, King (2002)

analysed the territorial calls of the debated 11 or 13 subspecies of Brown Hawk-owl (*N. scutulata*) and using evidence derived from their differing calls, he split the whole species complex into three separate species: the Brown Hawk-owl (*N. scutulata*); Chocolate boobook (*N. randi*) and Northern boobook (*N. japonica*). Verbal descriptions of vocalisations of many of the *Ninox* species can be found within these studies. Most *Ninox* owls give a disyllabic territorial call with some exceptions being the Sumba boobook (*N. rudolfi*) and the recently discovered Little Sumba Hawk-owl (*N. sumbaensis*) whose territorial calls are both monosyllabic (Olsen et al., 2002c). King (2008) compared the vocalisations of six *Ninox* owls which inhabit the region of Sulawesi, Indonesia, and found that the Northern boobook (*N. japonica*), Chocolate boobook (*N. randi*), Rufous boobook (a.k.a Cinnabar boobook) (*N. ios*), and the Ochre-bellied boobook (*N. ochracea*) all utter variations of a disyllabic territorial call. Whereas the subject of King's study, the Togian boobook (*N. burhani*), utters a territorial grating 'kuk kuk-kukukuk', which is more similar to the Speckled boobook's (*N. punctulata*) fast volley of 'too' syllables than to the disyllabic call common to many *Ninox* species.

Hill and Lill (1998) presented spectrograms of five separate call types of the Christmas Island Hawk-owl (*N. natalis*) (Figure 1.1). The following studies also presented spectrograms: a comparative study of the Sumba boobook (*Ninox rudolfi*), Little Sumba Hawk-owl (*N. sumbaensis*) and Southern boobook ("*N. novaeseelandiae*") (Olsen et al., 2009) (Figure. 1.2a); a study on short vocal descriptions of the Togian boobook (*N. burhani*) with comparisons to five other *Ninox* species of Sulawesi, Indonesia (King, 2008) and Northern boobook (*N. japonica*) (King & Icaragnal, 2008) (Figure. 1.2b). Another study which included a very large number of spectrograms was a study of the Philippine Hawk-owl complex (*N. philippensis*) (Rasmussen et al., 2012). Higgins (1999) included spectrograms in describing the calls of the Southern boobook and morepork and Stephenson (1998) included a spectrogram of the morepork's disyllabic call.

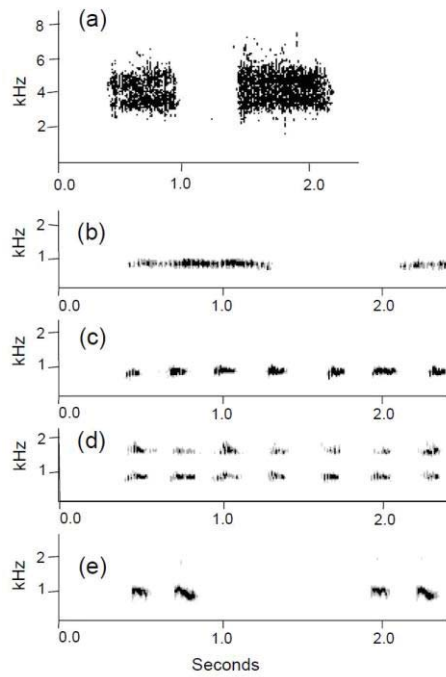


Figure 1.1 Spectrograms of vocalisations of the Christmas Island Hawk-owl a) begging call of young; b) chirring; c) *por por*; d) *kar kar*; e) *boobook*. (From Hill & Lill, 1998).

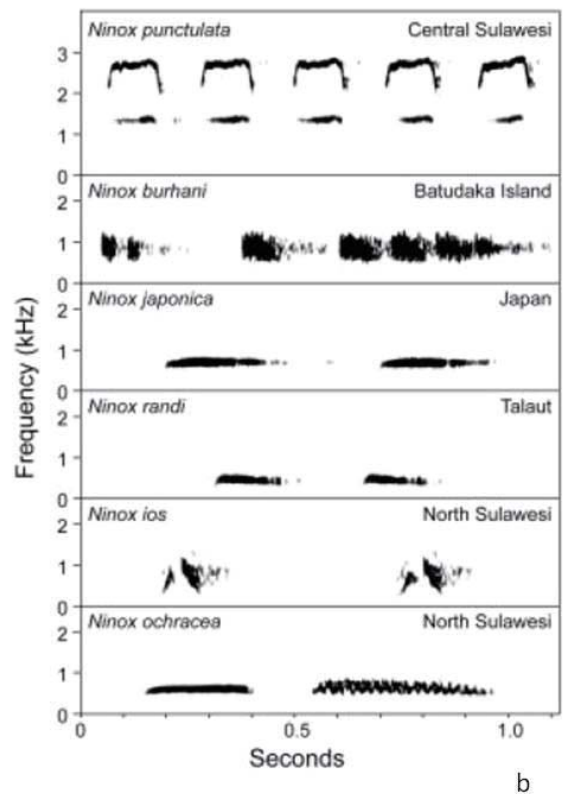
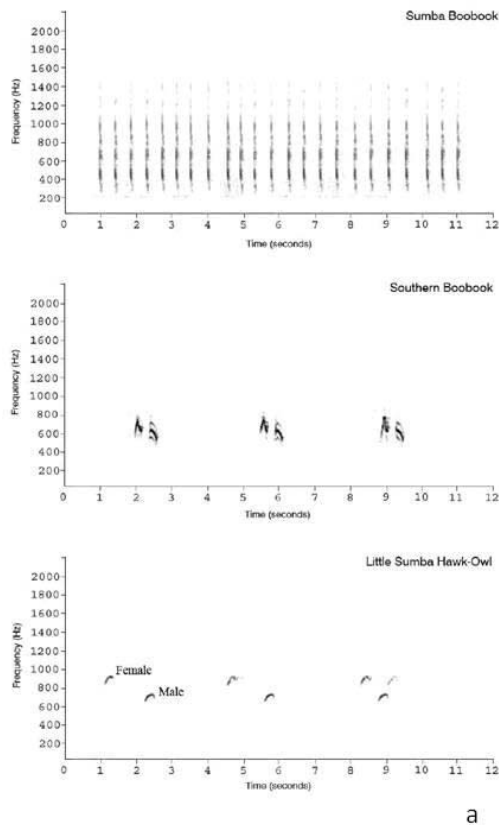


Figure 1.2 Spectrograms presented in other studies of *Ninox* owls: a) Spectrograms of three *Ninox* owls: Sumba Boobook (*Ninox rudolfi*), Southern Boobook (*N. novaeseelandiae*), Little Sumba Hawk-owl (*N. sumbaensis*) (From Olsen et al., 2009). b) Comparison of the songs of all six species of *Ninox* owls known from Sulawesi and its satellite islands. Speckled Boobook (*N. punctulata*), Togian boobook (*N. burhani*), Northern boobook (*N. japonica*), Chocolate boobook (*N. randi*), Rufous boobook (*N. ios*) (From King, 2005), Ochrebellied boobook (*N. ochracea*) (From King, 2008).

Social/Cultural

As a well-known nocturnal bird, common in urban as well as rural landscapes, the morepork is a popular bird among New Zealanders. Morepork are easily identifiable by their iconic call and many people often have a story about their encounter or experience of one. People can relate to hearing the morepork call, having listened to it at home, camping, walking, boating between small islands, or in wildlife sanctuaries and parks. Morepork inspire awe and intrigue at how it navigates in the dark, how silently it flies, and how indignant they can look if one disturbs their roost. They come with the air of mystery surrounding many owls that are more commonly heard than seen.

‘NINOX’ was a project for the improvement of night vision equipment for the Australian Armed forces, reportedly named after the Australian *Ninox* owls (Australian D.o.D, 2000; APDR, 2012).

Maori

The ruru (morepork) is steeped in Maori mythology and lore and is important in their spirituality and traditions. Many carved figureheads have wide eyes which are said to be based on those of the ruru. The theme of ruru eyes is also strong in Maori war dance, the ‘Haka’ and in the ‘pukana’ gesture. Ruru are thought to be guardians and advisors or ‘Kaitiaki’ (guardians of wildlife), and their appearance at certain times of day had significant meaning. If one appeared during the day, nearby or in the house, it could signify a death in the family. In Maori mythology the ruru are connected to the spirit world. Hineruru is the female spirit embodied in a ruru who is a “messenger from the world of death” (Schwimmer, 1963), and appears to Maori when relatives are dying, or when a visitor arrives (Maori spiritual return from the dead). In Schwimmer’s interviews (1963), local Maori had deep spiritual affection for Hineruru, as if she is part of the family. The ruru was described as ‘the bird’ of the Ngati Wai Iwi (Schwimmer, 1963).

The calls of the ruru had prophetic meaning to Maori who believe the “More-pork” call to herald good news and the “yelp” or weow to be an ominous sign of imminent bad news (Department of Conservation, n.d.). Morepork calls were also used to predict the

weather. A ruru calling once at night was a sign of bad weather. An interaction where ruru were answering one another meant an imminent storm. The appearance of many ruru in autumn was a sign of gales and a heavy winter and the noise of the hurried chuckling cry of the ruru was a sign of rain (Wingspan, 2013).

In the forest, their movement was noted too. If the bird flew straight ahead then there was no danger, but should it cross one's path then there was danger. This was also a forest species which was rarely eaten. It is clear that the ruru and its various calls are deeply spiritual to Maori and present in many New Zealanders' experience of nature at night. From heralding omens and offering spiritual advice to forecasting the weather, the natural history of the fascinating and varied calls of ruru have not been well studied and herein lies the reason for this study - curiosity.

This Study

Widespread distribution affords the opportunity to study the communication and behaviour of a nocturnal predatory bird, a fascinating owl with a loud voice disproportionate to its small size. The original motivation behind this study was to develop a more robust monitoring technique for morepork than a cold hill-side call-survey in the dark, where the magic of listening to these conversing owls is overshadowed by a feeling of uncertainty as to their actual abundance. However, to do this there was a need to find out more about their basic call characteristics and temporal calling patterns.

Aims

The aim of this study was to investigate the use of vocalisations as a mode of nocturnal communication, using morepork on Ponui Island as the study species in order to better understand the communication of this nocturnal predatory bird. The objectives of this study were: 1) to investigate the basics of morepork vocalisations to characterise their calls, and to compare their calls to published details; 2) to investigate temporal variation in calling behaviour; 3) to study the birds' behavioural responses to audio playbacks in different situations; and 4) to record and analyse vocalisations of morepork in captivity.

Study Relevance

Most studies on morepork focused on their diet and general ecology, (Cunningham, 1948; Clark, 1992; Haw & Clout, 1999; Brown & Mudge, 1999; Haw et al., 2001; Denny, 2009) including their breeding biology and home range (Imboden, 1975; Stephenson, 1998; Stephenson & Minot, 2006). Others combined the above with investigating the impacts of secondary poisoning from pest-control operations (Stephenson, 1998; Stephenson et al., 1999).

This study aims to broaden the knowledge base on this species and further the understanding of how nocturnal birds communicate in a dark forest environment. The results of this study may lead to data that can provide a baseline for further studies into identifying individual morepork and population surveying. This is important because, despite the morepork's current non-threatened status, the Department of Conservation believes the species is in a state of gradual decline (DOC, n.d.). Further study may involve improving morepork population monitoring (size, trends) to apply to morepork survival analysis, for instance to study further secondary effects of pest-controlling poison drops.

Population monitoring may also be important to the survival of endangered species that have been captive bred and released, but may fall prey to morepork if the release area has high morepork density. The release sites, often offshore islands, are chosen for reintroductions because they are introduced-predator-free. However, this creates a new challenge because on islands, the native predators such as morepork have a more restricted diet available to them. Morepork have been recorded preying upon the most abundant species, which in this case would be the reintroduced endangered prey species (Haw et al., 2001). High predation by morepork was highlighted as a key problem in Shore Plover (*Thinornis novaeseelandiae*) reintroductions by Haw et al. (2001), as well as release programmes on Motuora Island, which also encountered significant predation problems by morepork (Aikman, 1999). Often the habitat suitability surveys of potential release site areas regarding morepork rely solely on call surveying by ear and noting time and compass direction of calls, and then attempting to triangulate an estimate of morepork abundance. This has limitations, including human error, movement of morepork during the survey and miscalculating morepork

numbers. A survey method that includes sound recording and individuality recognition would greatly improve the estimate of suitability of potential release sites. Data on whether there is temporal variation in calling, both in time of night and time of year, as well as potential effects of weather and moon phase, would be useful baseline data for this.

Understanding the structure of morepork calls and the information they convey is also of interest in a comparative context: to better understand whether and how communication differs between New Zealand morepork and the Australian southern boobook and other *Ninox* owls and how this compares with other nocturnal bird species.

Study Site

Ponui Island (36° 55' S, 175° 11' E, Figure 1.3; top right) is located off the north east coast of New Zealand's North Island, around 30 km east of Auckland and south east of Waiheke Island in the Hauraki Gulf, within the Hauraki Gulf Marine Park (DOC, 2012a). It has an area of 17.7 km² approximately two thirds of which was converted to agricultural land in the early 1900s, leaving a third in its present cover of broadleaf-podocarp vegetation (Brown, 1979). Ponui Island has been privately owned and farmed by the Chamberlin family for five generations. The study took place in the forested gullies and pasture to the south of the island (Figure 1.3; bottom right).

Potential predators, nest predators, and resource competitors of morepork on Ponui Island include cats (*Felis catus*) and rats (*Rattus* spp.), but possums (*Trichsurus vulpecula*) are not present (Bellingham, 1979). There is also a population of mice (*Mus* spp.) and one other species of raptor, the diurnal Australasian harrier hawk (*Circus approximans*).

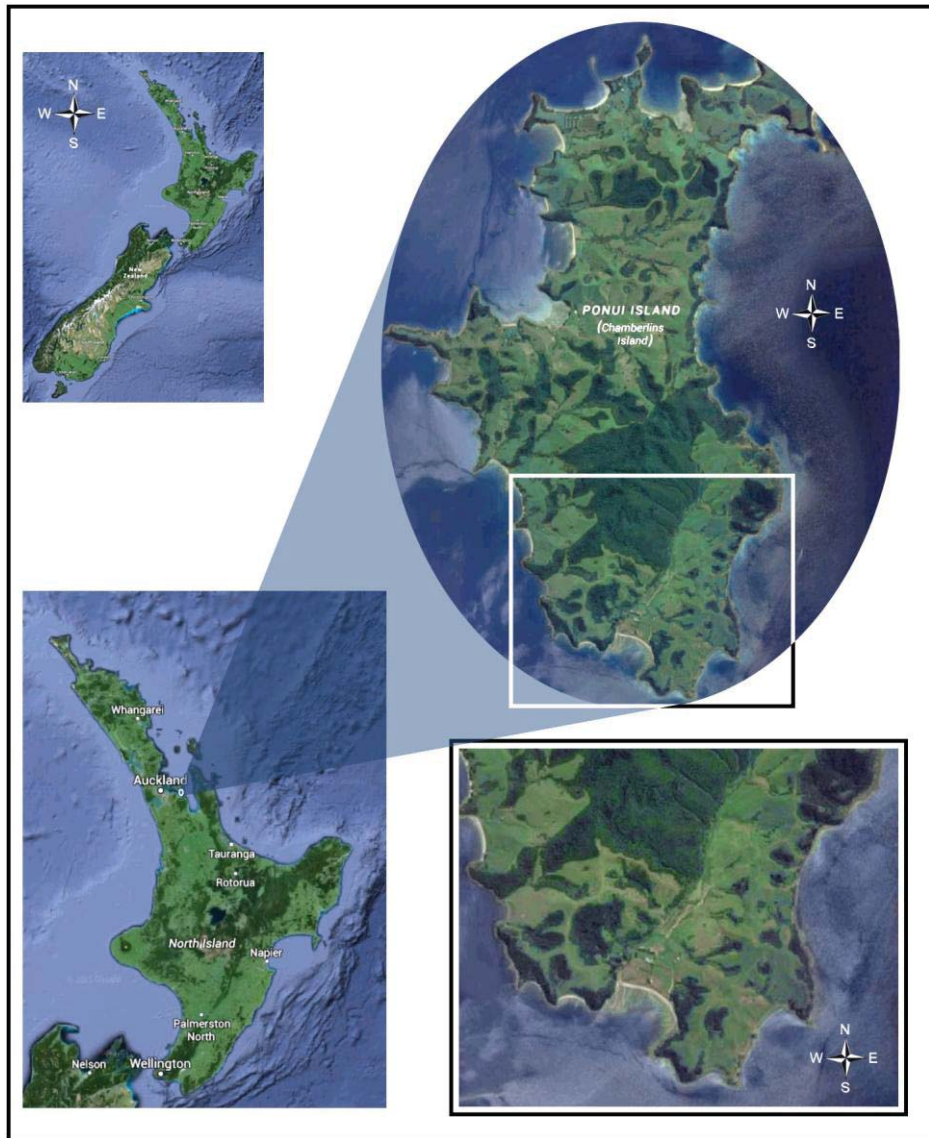


Figure 1.3 Map of New Zealand (top left), the North Island (bottom left), Ponui Island (top right) and detail of the study site of South Ponui (bottom right) (Google Maps).

For a private island, Ponui has been the site of many scientific studies, including ground-breaking discoveries about New Zealand's national bird, the kiwi. A large population of North Island Brown Kiwi (*Apteryx mantelli*) inhabit the island and have been studied for over a decade by Dr Isabel Castro and her colleagues and students. This is not the first time some of the resident morepork of the island have been followed and studied as Kirsty Denny studied their diet, prey availability, and roost site characteristics (2009). Other study subjects on the island besides morepork and kiwi include rats, parasites such as avian malaria, ticks (*Ixodes anatis*) and other kiwi

ectoparasites and the pathogens they transmit, and feral cats, all made possible by the generosity and enthusiasm of the Chamberlin family.

While the majority of this study was conducted on Ponui Island, the sound recordings in captivity were conducted in the wildlife parks of Wingspan Birds of Prey Centre, Rotorua; Nga Manu Nature Reserve, Waikanae; and Owlcatraz Native Bird and Wildlife Park, Shannon.

Thesis Overview

The thesis was structured to begin with an introduction and literature review chapter followed by three research chapters – outlined below – which were written to both stand alone and link to each other, therefore some repetition may occur. Finally a fifth chapter, the general discussion, aims to bring together the key findings of the research chapters and discuss the implications of the project.

Chapter 2: Characterising the different morepork calls from recordings of individual birds.

Fundamental to understanding the vocal communication system of an animal is knowledge of what sounds it uses and this requires comprehensive description of these vocalisations. Spectral and temporal structures are two important characteristics of vocalisations. This chapter aimed to fill the gap in knowledge about the details of morepork calls by characterising calls through matching qualitative descriptions with quantitative measurements taken from vocalisation recordings of individual wild morepork and captive morepork.

Chapter 3: Investigating temporal variation in wild morepork vocalisations.

Investigating how vocal behaviour varies over time is not only useful to building an understanding of the communication behaviour of a vocal species, but can also assist inferences about hunting, habitat bioacoustics, vocalisation functions, and seasonal behaviour, such as reproductive season and territoriality. A robust knowledge-base of the acoustic ecology and behaviour of a nocturnal, cryptic species has applications in both population monitoring and conservation, whereby more effective and efficient

methods of monitoring can be designed using that knowledge base. This project aimed to investigate whether morepork calling showed temporal variation both across a night (per hour) and across a year (per month).

Chapter 4: Study of the behavioural responses of wild morepork to audio playback.

Not only repertoire, but an understanding of the behaviour and function behind each call type of a species gives valuable knowledge to further studies. Most commonly this is studied with behavioural experiments involving the study of individuals' responses to playbacks of pre-recorded calls broadcast to them in the field or laboratory. This project aimed to investigate the responses of New Zealand morepork to different call types broadcast in playback experiments. With this information we hope that the context and function of certain call types can be better described in this owl.



Chapter 2 - What does the Ruru say?

Characterising morepork calls and associated behaviour



When you go owling

You don't need words

Or warm

Or anything but hope.

(Yolen, 1992)

Abstract

The New Zealand morepork (*Ninox novaeseelandiae*) is an owl that is highly vocal throughout the year. Both sexes call and their call structure and calling behaviour have not yet been quantified. Knowledge of call repertoires and vocal behaviour can be useful to gain insight into the ecology of cryptic or nocturnal animals. This study aimed to characterise and describe morepork vocalisations. Morepork calls were recorded at high quality with a digital sound recorder and directional microphone. Only calls of seven known morepork were analysed. These were birds that had been captured and fitted with radio-transmitters and reflective leg bands. Qualitative descriptions were matched with quantitative measurements taken from recordings of individual birds.

Eleven different calls were identified in this study which I named: *more-pork*, *trill*, *rororo*, *more-more-pork*, *weow*, *low trill*, *copulation squeal*, *single hoot*, *distress squeak*, *chicketting call*, and *chick trill*. Both sexes were heard to use the main morepork call types: *more-pork*, *trill*, *rororo*, *more-more-pork*, and *weow*. Morepork also combined different call types in single bouts of calling which for simplicity I termed 'combinations', for example, *weow-pork*, and *rororo-more-pork*. Also, while not strictly a vocalisation, morepork were heard to make a 'bill clap' noise when captured but also on one occasion of dispute between two individuals. I analysed the spectral and temporal characteristics of three of the most common calls: *more-pork*, *rororo* and *trill*. Individual variation was found in these three calls, but a lack of evidence for sexual variation in the frequency (pitch) and duration of their calls could not confirm previous suggestions of sexual dimorphism, however, sample sizes were small and this included a sex ratio bias male to female of 2:7. This suggests that while it may not be possible to identify the sex of a morepork by these temporal and spectral characteristics of their calls, it may be possible to identify individuals by their calls.

Introduction

Vocalisations are important to the survival and behavioural ecology of most bird species, so understanding their communication systems is crucial to gaining insight into their overall ecology (Corfield et al., 2008). An understanding of vocalisations and their variation has applications for further research on a species and for future management and conservation, including population monitoring both by direct call surveys and playback and automated sound recorder surveys (Odom & Mennill, 2010). Fundamental to understanding the vocal communication system of an animal is knowledge of what sounds it uses, and this requires comprehensive description of these vocalisations. Spectral and temporal structures are the two most important characteristics of vocalisations that researchers are interested in when taking the first step towards this understanding.

Significance of Call Structure

The spectral and temporal structural characteristics of a call have been shown to encode a wide range of important information, including identity at species and individual level, resource quality and ownership, territory, and potential mate suitability in terms of body size and fitness (Galeotti & Pavan, 1991; Corfield et al., 2008). Morton (1977) described a convergence in many animal sounds of the use of similar context-dependent call structural characteristics, for example, friendly versus hostile call types. He also noted an apparent relationship between call structure and call function.

The physics of the acoustic structure of a call affects how it travels. Lower pitch (frequency) calls carry further than higher pitch calls (Marler & Slabbekoorn, 2004). However, background noise can obscure some frequencies. Similarly, lower frequency calls, if uttered close to the ground, can be cancelled out by hitting the ground and being absorbed. Habitat is a significant selecting factor on avian call structures due to the varying propagation abilities of different sounds across different habitat types (Morton, 1975). Natural environments are dynamic and not constant, therefore affecting how sound travels with a mixture of sound energy reduction and redirection. This is particularly true in forest habitats where there are many vegetation obstacles

that can absorb, reflect, and diffract sound (Morton, 1975). The frequency of the sound itself also influences how quickly it attenuates, or loses power, as it travels through an environment. Higher frequency sounds have shorter wavelengths than lower frequency sounds and attenuate faster because their short wavelengths are less able to travel around obstacles that reflect the sound and cause it to lose energy (Morton, 1975). Thus, lower frequency sounds can travel further than higher frequency sounds in an obstructed environment. Interestingly - and converse to the general rule of the lower the frequency, the lower the attenuation rate - Morton (1975) found that in forest environments, there was lower excess attenuation of pure tones of frequencies between 1,585 and 2,500 Hz than tones of both higher and lower frequencies. As expected, however, frequencies over 2,500 Hz attenuated much faster. It is not only vegetation that causes sound to attenuate faster compared to an obstacle-free environment. The ground also absorbs sound energy, and hence increases attenuation rates. Morton (1975) found that with sounds produced closer to the forest floor, the sound attenuation was greater than for sounds produced at a higher level above ground. Conversely, the forest canopy appeared to act as a ceiling which allowed the sound to propagate further by reflection, attenuating less in the forest environment when compared to the edge or grassland environment where sound energy was lost upwards.

Individual Variation in Bird Calls

There is often more to a call than simply to announce presence. Animal vocalisations, particularly bird calls and song, can convey a wide range of encoded information, including the identity of the caller via individual call variation. This has been found in a diverse range of bird species including: Eastern Phoebes (*Sayornis phoebe*) (Foote et al., 2013); *Aptenodytes* spp. Penguins (Robisson, 1990); Tawny Owls (*Strix aluco*) (Galeotti & Pavan, 1991); Northern Saw-whet Owls (*Aegolius acadicus*) (Otter, 1996); Christmas Island Hawk-owls (*Ninox natalis*) (Hill & Lill, 1998); North Island Brown Kiwi (*Apteryx mantelli*) (Corfield, 2005; Hojem, 2006); and Little Spotted Kiwi (*Apteryx Owenii*) (Digby et al., 2014), and has been suggested to exist in Wilson's Storm Petrels (*Oceanites oceanicus*) (Bretagnolle, 1989) and in Marbled Frogmouths *Podargus ocellatus* (Smith & Jones, 1997). Given the challenges of communicating in the dark,

vocal identity can be expected to be important to a nocturnal vocal bird's ecology, so these birds are well represented in the literature. Vocal identity has applications in behavioural studies, population monitoring, and conservation, as reviewed by Terry et al. (2005).

Morphology and Call Frequency

Body condition, particularly body mass can affect the frequency of avian vocalisations (Morton, 1977). Studies of owls found that frequency was often negatively correlated with increasing body mass in a single sex, for example, male Tawny Owls (Appleby & Redpath, 1997) and male Scops Owls (Hardouin et al., 2007). Generally owls display reversed sexual dimorphism in body size whereby females are larger than males. In bioacoustics a larger body size often corresponds to the ability to produce lower frequency vocalisations. However, sexual links to differences in call frequencies are often difficult to pin down. Some studies have found frequency differences between the sexes, but few have related this to body size differences, and evidence in owls can be contradictory. Herting and Belthoff (2001) found male Western Screech Owls to have 30% lower pitched calls than females despite the species displaying body size RSD and the males being the smaller sex. Herting and Belthoff cite studies that have found Eastern Screech Owls to also differ from the general pattern of larger body size correlating with a lower pitch call. In Falconiformes, which display reversed sexual dimorphism, female White-Tailed Hawks (*Buteo albicaudatus*) have deeper calls than males (Farquhar, 1993 as cited in Herting & Belthoff, 2001) but in the Verreaux Eagle (*Aquila verreaux*) in which the female is larger, the females have higher pitched calls than the males (Rowe, 1947 as cited in Herting & Belthoff, 2001).

Herting and Belthoff (2001) suggest a link between sexual variation in calls and the ability of territory holders to assess intruder identity by their calls. Hardouin et al. (2007) suggested that response to territorial intruders was affected by the body mass of the intruder, perceived through the frequency of the intruder's calls. Hardouin et al. (2007) tested the responses of territorial male Scops Owls to playback re-synthesized calls of $\pm 5\%$ and $\pm 20\%$ average frequency calls and found that the intensity of territorial response was positively correlated to the frequency of rival calls. This suggested that Scops Owls had the ability to perceive an intruder's body mass via the

frequency of their calls. Hardouin et al. (2007) found that the responder's own mass did not affect the intensity of their response, but the perceived body mass of the intruder did, with stronger responses (quicker, closer, longer responses with more approaches) elicited by higher frequency calls simulating lower-weight intruders. Hardouin et al. (2007) also showed that Scops Owls appeared to be able to alter the frequency of their response to a small extent depending on the pitch of the intruder's call.

Appleby and Redpath (1997) found a positive correlation between call frequency and parasitic load in Tawny Owls, suggesting a mechanism for how the frequency of calls may encode information on body condition given the energy cost of lower pitch calls. Hardouin et al. (2007) built on this idea and, using body mass as an index of body condition, concluded that better body condition was correlated to lower frequency calls.

Most of the 22 species of *Ninox* owls exhibit reversed sexual size dimorphism, a trait common to nocturnal and diurnal raptors (McDonald et al., 2005; Pavey, 2008), and there have been many hypotheses proposed as to why this occurs in birds of prey. Wing length and body mass are common measurements used to study reversed sexual dimorphism. Of the 12 *Ninox* species studied by Pavey (2008), the majority were found to be monomorphic for wing length with the exceptions of *Ninox novaeseelandiae undulata*, *N. natalis* and *N. j. Jaquinoti*, which showed strong reversed sexual dimorphism. Also three of the largest *Ninox* species, *N. c. connivens*, *N. Strenua*, and *N. r. Rufa*, showed non-reversed sexual dimorphism in wing length. *N. c. connivens*, *N. strenua*, *N. boobook* and *N. leucopsis* - the latter two close relatives of the New Zealand morepork - showed strong non-reversed sexual dimorphism in body mass. No data were presented for *N. n. novaeseelandiae*, the morepork, however. This is interesting as it is often suggested that reverse sexual size dimorphism is displayed by morepork and boobook whereby studies often describe females being larger than males. To my knowledge no study has looked at call frequency and body size of *Ninox* owls specifically.

Morepork Calls

The New Zealand morepork (*Ninox novaeseelandiae*) has a range of calls from a long series of short, harsh, low pitch, staccato syllables to drawn out bouts of higher pitched, wavering trill calls and even a high pitched, extended, wavering squeal. However, as there are inconsistencies in the nomenclature used to describe vocalisations, so too are there inconsistencies in the naming of morepork calls.

Previous Studies

Most research on bird calls has been conducted on passerines or songbirds given the prominence of their calls. Other less vocal groups, including nocturnal species, have been much less studied. For example, call types have not featured comprehensively in the literature surrounding owls, and in particular, morepork or its close relative the Australian Southern boobook (*Ninox boobook*); rather some studies have dealt with the subject mainly as part of wider ecological studies. One of the earliest studies regarding calls, Fleay (1968), described the 'cree' call in Southern boobook as a contact call given during the breeding season with sub-adult calls heard five to six months post-hatching. O'Donnell (1980) cited Fleay's (1968) observations that boobook do not leave their roosts in poor weather and that the female incubates while only the male calls, and suggested that this information might be useful to interpreting the calling and behaviour of the NZ morepork.

Olsen et al. (2002a) studied and confirmed the occurrence of ten different calls uttered by the Southern boobook, named in Higgins (1999) as: *boobook* call, *single hoot*, *por* (croak), *squeal*, *bray*, *trill*, *yelp*, *growl*, *scream* and the *squeak*. Olsen et al. (2002a) determined that both sexes use most calls. They categorised the calls as either territorial or contact and found that call frequency varied the most according to season, social context and individual differences.

There has been little study of the New Zealand morepork's calling behaviour directly, with the focus being on call surveying. Consequently, much of what is known about morepork calling is often inferred from anecdotal studies, or studies of its more widely researched close relative the Australian Southern boobook. The most detailed description to date of the calls of the New Zealand morepork is part of a larger

ecological study of morepork by Stephenson (1998) who described the different calls and associated behaviours on Mokoia Island, Rotorua. He identified seven different calls: *More-pork* (location call); *More* (agitated location call); *Purr* (contact call); *Peow* (series location call); *Pew* (alarm call); *Chitter* (chick alarm call); and a juvenile begging call.

Stephenson (1998) reported both pair duetting and rival duelling calling behaviours, with the use of playback calls in the field successfully eliciting responses. He also found the pitch of calls varied greatly and suggested this was related to the sex of the bird calling, with certain call types uttered more frequently by one sex than the other. Debus (1996) and Olsen and Trost (1997) also suggested a link between call pitch and sex, but Stephenson (1998) concluded that it was not possible to reliably identify the sex of a calling bird in the field with any certainty.

On the other hand, Fleay (1968, as cited in O'Donnell, 1980) described the calls of the boobook as sexually dimorphic; males had shorter, clearer calls than females which were hoarser and lower pitch. In a more recent study, however, Olsen et al. (2002a) agreed with Stephenson's observations of morepork (1998) and suggested that while reliable sexing was also difficult in boobook, perhaps some individuals may be identified by voice. Olsen et al. (2002a) were able to identify a particular male boobook by a recognisably low-pitched call. Even with apparent individual variation in call pitch, Olsen et al. (2002a) reported this would be difficult to do consistently. It is therefore unclear whether morepork calls are sexually dimorphic, and more investigation is necessary to determine whether morepork calls show detectable individuality.

Few studies of Australian Southern boobook (Olsen & Trost, 1997; Olsen et al., 2002a; Olsen et al., 2002b; Olsen et al., 2010a; Olsen et al., 2011), an analogous species used to draw inferences into morepork calling, provided visual representations of the calls, or used measurable spectral characteristics to describe or compare the various calls, focussing on behaviour and using call counts to study temporal and environmental variation in calling. The following studies included spectrograms: a comparative study of the Sumba boobook (*Ninox rudolfi*), Little Sumba Hawk-owl (*N. sumbaensis*) and Southern boobook ("*Ninox novaeseelandiae*") (Olsen et al., 2009); a study on short

vocal descriptions of the Togian boobook (*N. burhani*) with comparisons to boobook of Sulawesi, Indonesia (King, 2008) and Northern boobook (*N. japonica*) (King & Icaragnal, 2008); and a study of the Philippine Hawk-owl complex (*N. philippensis*) (Rasmussen et al., 2012). Higgins (1999) included spectrograms in describing the calls of the Southern boobook and morepork and Stephenson (1998) included a spectrogram of the morepork's disyllabic call.

Aims

A standardised vocal repertoire is useful for simple field identifications to more complex contextual behavioural ecology. Before such studies can take place, the underlying ethology and repertoires must be described and agreed upon. This foundation is not yet in place for the morepork, whose vocalisations have not been studied in much detail.

This chapter aims to fill this gap, characterising the calls of the morepork by matching qualitative call descriptions with quantitative measurements taken from recordings of individual birds, coupled with behavioural context where possible. This chapter offers the beginning of a characterised morepork call *repertoire* by aiming to characterise both quantitatively and qualitatively the calls uttered by the morepork on Ponui Island. My observations were made in one or two weeks each month for twelve months. In this chapter, I provide a detailed description of each call using verbal descriptions together with spectrograms and details of the associated behaviour, and I compare fundamental frequencies and the durations of each of three main call types from seven known individual morepork. I discuss ways in which the data may be used in future for further study of morepork behaviour, ecology, and conservation.

Methods

Marked Study Population

In July 2013, eight wild morepork were captured (under New Zealand Banding Office Permit No. 2012/014, Department of Conservation Permit No. 36228-FAU, and Massey University Animal Ethics 13/21) using mist nets (60.5 mm spaced netting, four-tier, 6 m or 9 m long). The necessary considerations surrounding marking birds highlighted by Silvy et al. (2005) and Varland et al. (2007) were taken into account. Following

standard techniques (Melville, 2011), the birds were banded with uniquely numbered, size-E metal leg bands, provided by the New Zealand Banding Office, and fitted with backpack-harnessed, single-stage, radio-transmitters (V1H 116A ULTIMATE LITE HARNESS™ from SirTrack, Hawke's Bay, New Zealand) (Figure 2.1).

These harnesses were fitted with a weak link designed to break should the harness become entangled (Karl & Clout, 1987). The transmitter and harness had a combined weight of 5.5 g, approximately 3% of the bird's body weight. Adhesive reflective tape pre-cut to size was attached to the leg bands using a dab of superglue. This tape assisted identification of study birds by torch-light from a distance in the dark. The morepork were measured (weight by Pesola™ balance; bill length, depth, width and tarsus length with Vernier callipers; and wing cord with a wing ruler), and a feather sample taken for DNA sexing at Massey University's Equine Parentage and Animal Genetic Services Centre, Palmerston North, New Zealand. For identification purposes these morepork were named: Kahlua, Flat White, Macchiato, Calypso, Espresso, Perico and Ristretto, and their roosting areas are plotted in Figure 2.3. The eighth bird, Affogato, died early on in the study most likely from predation, however, only a small number of feathers and transmitter were recovered which impaired determination of cause of death.

Prior to the capture effort, a day was spent at Wingspan Birds of Prey Centre in Rotorua learning and refreshing appropriate morepork handling and transmitter attachment techniques. During the capture effort I was supervised by Andrew Thomas (MSc) (Level 3 NZ Raptor bander) from Wingspan, Dr. Isabel Castro (Level 2 NZ Raptor bander) of Massey University who are both experienced, qualified New Zealand bird handlers and banders. I was also advised by David Izquierdo, an experienced raptor biologist from the Research Institute for Wildlife Ecology (FIWI, Vetmeduni, Vienna).



Figure 2.1 Morepork transmitter attachment, gear and technique. From top left: working on and handling morepork with white falconer's hood (top left and centre); transmitter and weak-link backpack harness alone (top right) and transmitter once fitted on the morepork before securing the backpack harness (top far right); transmitter attached to morepork once harness was secured with metal bands and excess harness removed (bottom left); morepork measuring equipment (Vernier callipers and wing rule by notebook), transmitter and harness (by scissors) and brown falconer's hood (bottom centre); and morepork with finished transmitter (bottom right).

The initial capture effort spanned eight days, during New Zealand's winter, with capture missions in the early evening (setting up around 4 pm, an hour prior to sunset), and early morning (setting up by 5 am). A total effort of 22.5 hours was spent mist-netting with evening effort lasting from two to as long four and three quarter hours, and morning sessions lasting from two hours or until sunrise. This was time until a bird was captured, not including processing time.

Team size varied from two to four people and numbers did not seem to impact capture success with successful captures occurring with various numbers of people present, including a team of just two people which had two successful captures, one at dusk and one at dawn. Sitting directly under the net, or very close to it, did not seem to be a hindrance and allowed for a quick response to a bird flying into the net.

Mist-netting methods were similar to Denny's (2009); nets were opened shortly before dusk in areas investigated as potential catch sites earlier in the study (Figure 2.4), then checked regularly, and left open for a period of time dependent on interest shown by

morepork in the area. We set up three mist nets (two six-metre and one nine-metre) in varying orientations and proximities to each other in both sheltered and more open areas of forest (Figure 2.2). There was not a clearly defined optimum capture time, but based on previous studies we focussed on the period surrounding dusk and dawn. This resulted in the successful capture of eight morepork within ten days, with seven out of eight birds captured in the evening within a three-hour period following dusk (between 6pm and 9pm). The earliest capture occurred at 6pm (sunset at 5.45pm) and the latest at 8.45pm. There was potential for captures later in the evening, however, we observed a marked reduction in investigation of the net areas in response to playback calls the later the time of evening. We ensured at every stage that stress and potential for injury to the bird was kept to a minimum, including the use of a falconer's hood. Two hoods (Figure 2.1) sourced from Wingspan Birds of Prey Centre, Rotorua, and although they were intended for use on harrier hawks, they were effective at keeping the birds relatively calm in the absence of a hood designed specifically for morepork.



Figure 2.2 Mist-netting set up. From top left: Placement of speakers behind nets (top left two); net in foreground (pole at far right) with speakers in background ponga (top right); net at dusk with plush morepork silhouette (bottom left); improvised branch net-pole repair (bottom centre); net in dense scrub forest (bottom right).

Non-living lures were used to entice morepork into the net area, and methods were adapted from Stephenson (1998) and Denny (2009). The use of playback calls was a highly successful strategy in luring and capturing morepork; multiple, high quality recordings made locally in April and June 2013 were broadcast from high quality, portable Sony speakers hidden beneath the nets. The use of a long auxiliary cable enabled the operator to sit away from the net. In addition to the calls, we trialled various items to invoke interest in the net area with varying success. These included an 'Original Mockingbird™ Audubon' bird caller to mimic a distressed small-bird call; egg-carton cut-outs of moths and bugs; two plush morepork (one small, one large), or saddleback, placed in a net pocket or perched nearby; and a plush bat on fishing twine strung over a nearby branch and manipulated from a distance. While a systematic study into the most effective lure type was not conducted, some types were observed to have more success than others. From number of successful captures, the best lures were the egg-carton decoy insects and the playback calls, which were involved in 8/8 and 6/8 captures respectively. Figure 2.3 shows the successful capture of a morepork where playbacks and an egg-carton moth (white blob) were used. The Audubon bird caller was used intermittently, so its effectiveness is difficult to estimate. The plush birds each featured once or twice in successful captures and the effectiveness of each were also difficult to comment on. On one occasion however, the plush morepork was physically attacked and knocked from its perch.



Figure 2.3 Capture of a morepork in a mist net where a decoy moth was used (bright white shape). Screen shots taken from Sony HandyCam infra-red video.

Having a marked study population enabled identification of individual birds in the field in the dark at night and their sex to be known with certainty, as any sexual dimorphism in morepork is very subtle (Stephenson, 1999). Care was taken during the capture effort to ensure that individuals came from different gullies to reduce the potential to record two marked birds at once. With the small number of transmitters available, it

was decided that placing a transmitter on both birds in a pair or on neighbouring birds was not an efficient use of transmitters, so I marked one bird in a pair. There was a sex bias in the study population with six females to two males caught and marked. One male was found dead early in the study, leaving a female: male ratio of 6:1.

Definitions

Variation exists between studies in the terminology used to describe vocalisations, so the following are the key terms used in this chapter. Given the definitions of ***calls*** and ***song*** presented in Marler and Slabbekoorn (2004) (Chapter One), and despite discrepancies between owl vocalisation researchers as to whether owl vocalisations are ***calls*** or ***song***, I will refer to morepork vocalisations as ***calls***. As outlined in Chapter One, calls and song can be split into smaller units of sound. However, as calls often lack the structural complexity of bird song, the smallest unit is usually referred to as a ***syllable*** and I will use this term here. I will use ***call bout*** to define a collection of syllables of the same call-type. Finally, a ***repertoire*** encompasses all the vocalisations that both sexes of a bird species make over their lifetime (Baker, 2001).

Call Types

Different calls have different functions, and these functions can often be inferred from the call's auditory qualities, but more importantly from the context in which they are uttered. Both observation and experiment-based studies are used to confirm this, but there is some general theory surrounding call types and their function. Call-types can be grouped by function and include calls used for contact, alarm, submission, begging, aggression, separation, and food sharing. A factor which potentially affects what type of call is used and the acoustic characteristic of the call used is known as the audience effect. The call type depends on who is listening or present (Marler et al., 1991, as cited in Marler & Slabbekoorn, 2004).

Contact calls function to establish and maintain contact if the birds are out of visual or close contact. Marler and Slabbekoorn (2004) describe these as brief, softer calls which range in frequency depending on the species. A variant of this type of call is the ***separation contact*** call which is often more individualised, louder and at a higher rate.

Alarm call is a name given to encompass a wide range of calls given in situations of varying degrees of alarm or excitement. Alarm calls are diverse in structure and delivery, and some even double as contact and separation calls (Marler & Slabbekoorn, 2004). Again, the audience effect dictated what type of call is used depending on whether the call is aimed at friend or foe. Depending on the species and the distance the call needs to travel, alarm calls can vary across frequencies, from low to high. Conversely, for very vocal birds, a cease in calling can be a stronger signal of alarm than a call, and resuming calling can indicate an all-clear (Marler & Slabbekoorn, 2004).

Food sharing calls are an altruistic display of inclusive fitness in announcing the presence of food and the willingness to share it. This is most commonly seen in group-foraging birds and has benefits in social-bonding and mate attraction, with the best examples seen in *Galliforms* from the domestic rooster (*Gallus gallus*) to the California quail (*Callipepla californica*) (Williams, 1969; Stokes & Williams, 1972 as cited in Marler & Slabbekoorn, 2004).

Begging calls are crucial in the early life stage of the majority of birds, and in many instances they are critical to their survival. In nidicolous (nest-inhabiting) birds, begging rate is often correlated to hunger, however, the conspicuousness of calls is limited by the risk of predation (Marler & Slabbekoorn, 2004).

Aggressive calls tend to be harsh and low-pitched and are made up of single, relatively long notes (Marler & Slabbekoorn, 2004). The theory is that the larger the animal's body size, the lower the pitch of their calls, which has significance to settling aggressive interactions by calling. This is because a larger body size encoded in the call pitch could serve to win out against an animal of smaller body size by call alone, thus avoiding direct combat. This is an honest signal as body size generally limits the ability to produce a low pitch call (Marler & Slabbekoorn, 2004).

Data Acquisition

Study Site

Recordings were conducted on Ponui Island (described in Chapter One) during monthly trips between August 2013 and March 2014. The study area included mature kauri (*Agathis australis*) and podocarp-broadleaf forest; manuka (*Leptospermum scoparium*)

and kanuka (*Kunzea ericodes*) scrub; and stock-grazed pasture (Figure 2.4). The seven radio-tagged morepork comprised the study population which were tracked with radio-telemetry to confirm their identity when they vocalised.



Figure 2.4 Locations of roosting areas of the seven radio-tagged morepork on Ponui Island, Hauraki Gulf, North Island, New Zealand (Full map in Chapter One). (White line from Espresso shows his relocation during the breeding season 2014). Plotted using Google Earth.

Manual Sound Recording

Equipment

Manual digital sound recorders (Marantz professional solid state recorder - PMD661, DC 5V, 1.4 A) with user-operated directional hand-held 'shotgun' microphones (Sennheiser MKH 60 948), were used to obtain clearer, closer (<20 m approach distance) recordings of individual morepork vocalisations (Figure 2.5). Recordings were made with a sampling rate of 44.1 kHz, 24-bit and saved as WAV format audio files. Radio telemetry was used alongside recording to track and record vocalisations of

known birds using a Wildlife Telonics TR4 receiver coupled to a Yagi three-element antenna. Videos of behaviour accompanying the vocalisations were recorded where possible using a Sony Handycam Digital video-camera (DCR-SR45 Hybrid HDD) and an infrared light source (Model IRLamp 6, Wildlife Engineering) (Figure 2.5), due to the light constraints of filming at night.

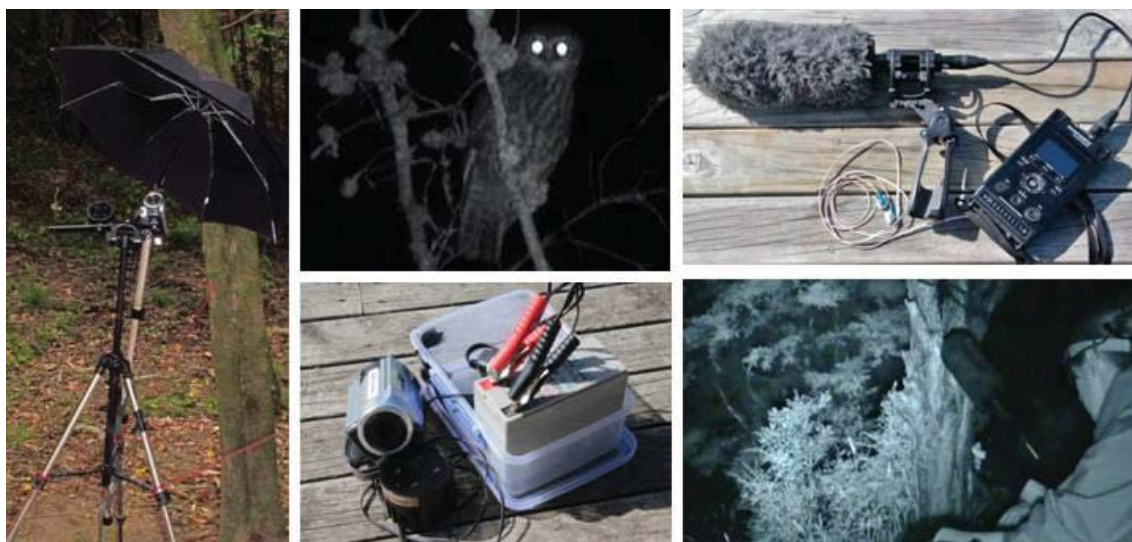


Figure 2.5 Manual sound and video recording equipment. From left: Video set up with tripod and umbrella; Top centre: Infra-red video screen shot of a morepork; Top right: Sound recorder and shotgun microphone; Bottom centre: Infra-red video camera and black IR light with 12V battery and connectors; Bottom right: the author recording sound at night (IR video shot).

Night work

Trips to the island to track and record morepork usually lasted for 10-14 days each month from August 2013 to March 2014, mostly in single trips, but in four of the months there were two shorter trips.

Manual recording sessions were organised into 4-5 hour shifts to sample data from all times of the night as follows: 18:00-23:00; 22:00-02:00; and 02:00-06:00 hours. For the most part, these sessions were conducted by one person. In retrospect, two people would have been ideal, one to record sound and operate the telemetry gear and the other to operate the video camera, although with practice it was possible, albeit clumsily, to do this by myself. This was a trade-off between the reduced noise disturbances of a single operator versus increased ease of operation with two operators. When weather permitted, a recording session was conducted each night of the monthly trips to the study site. To ensure the best quality recordings possible,

recording sessions were not conducted on nights with moderate or heavy rain and wind because of interference noise.

Recordings were made of spontaneous call bouts, focussing on the marked study population, but also including unmarked morepork call bouts. Two females nested in summer 2014 and calls from these two pairs of chicks were also recorded. Playback calls were not used to elicit calling as it was deemed unnecessary. Morepork calling was relatively frequent and playback experiments were planned later in the study, necessitating that the population be kept naive of exposure to pre-recorded playback calls, with the exception of the few calls played in the capture effort.

Captive Recordings

An automated sound recorder (Wildlife Acoustics Inc., Song Meter 2+) was left in the enclosures of captive birds for up to a week at a time. Captive recordings were conducted at Wingspan Birds of Prey Centre, Rotorua; Nga Manu Nature Reserve, Waikanae; and Owlcatraz, Shannon. There were some limitations to the recordings made in captivity, namely the noise from air-conditioning units and human voice, which made the data less useful. The only recordings useful to a characterisation study, where calls from an individual bird were important, were those from two birds living in separate enclosures (and therefore individually identifiable) at Wingspan Birds of Prey Centre - a female, Whisper, and a male, Frodo. The recordings from the other enclosures will provide useful data for future investigations however.

Data Processing and Analysis

Processing

A sample size of nine birds was used which included the seven marked wild birds of Ponui Island and two captive birds, a male and a female, from separate enclosures at Wingspan. This gave a male:female ratio of 2:7. The raw sound files were processed manually using RavenPro v1.4, (Cornell Laboratory of Ornithology 2011, Ithaca, NY, U.S.A), to isolate and classify each call bout from each of the 200+ individual usable recording files. Each call bout was cut from the original recording file and saved as a sound file bearing the call name, location, date, time, and origin sound file number in

its new file name for ease of subsequent retrieval for analysis. Calls were named based on phonetic and English words as descriptors.

Analysis

Structural Characteristics

After initially classifying each call bout, the classified files were again opened in Raven Pro and each individual call was isolated by using the manual selection tool to draw a rectangular border delimiting time (in seconds) on the vertical edges and frequency (kHz) on the horizontal edges of the selection rectangle (Figure 2.6). Predefined measurements were selected from a list in Raven which, on committing each selection, automatically measured, calculated and added to a selections table each parameter for each selected individual call. Only the three most common call types were used for further spectral and temporal analysis due to the time constraints of manually selecting each syllable; these call types were *more-pork*, *trill*, and *rororo*. The number of good examples of syllables per individual bird in the study varied and so sample size for the three calls varied (Table 2.1).

Table 2.1 Sample sizes for each syllable type and measurement in this study. FF = Fundamental Frequency; FD = Fundamental Duration; IS = Inter-Syllable Duration. The total number of individual birds was 9.

Syllable	Total n FF & FD	How sampled (FF & FD)	Total n (IS)	How sampled (IS)
More	155	20 syllables per bird, except: Kahlua (n =11) Frodo (n = 4)	155	20 Is durations per bird
Pork	155	20 syllables per bird, except: Kahlua (n =11) Frodo (n = 4)	155	20 IS durations per bird
Ro	270	30 syllables per bird	240	30 IS syllables per bird except: Kahlua, Espresso, Whisper n = 27; Fdub, Mac, Perico n = 29; Calypso, Ristretto n = 28; Frodo n = 16
Trill	135	15 syllables per bird	125	15 IS syllables per bird except: Mac, Perico n = 13; Calypso, Whisper n = 14; Frodo n = 11;

When calls consisted of multiple syllable types (such as the disyllabic *more-pork* call which was comprised of *more* and *pork* syllables; Figure 2.6i) then five main selection borders were drawn, one for each of the two syllable types, a third to encompass both syllables (for the purpose of call duration calculation). The fourth spanned the duration between each syllable (inter-syllable duration) and the fifth measured the duration between calls in a bout. If there were harmonics present the two further selections encompassed these (Figure 2.6i). For the *trill* and *rororo* calls, only four selections were made: one to encompass the fundamental syllable, the next to measure the interval between syllables, the third to measure the duration of the syllable, and the fourth to encompass any harmonics above the fundamental (Figure 2.6 ii and iii). A fifth selection was attempted, where possible, to measure the interval between call bouts, however, this was not always possible if another bout from the same bird did not occur. Not all of the selections were eventually used as the fundamental harmonic was chosen for spectral analysis which avoids the problem of the harmonics above the fundamental (higher pitched) often overlapping with other noise such as crickets and kiwi.

Parameters Analysed

The parameters analysed in Raven for the *more-pork* call were: F1 (the fundamental frequency (Hz) of syllable 1 Figure 2.6 i) a)); F2 (the fundamental frequency (Hz) of syllable 2 Figure 2.6 i) b)); D1 (the duration (s) of syllable 1; Figure 2.6 i) a)); D2 (the duration (s) of syllable 2; Figure 2.6 i) b)); TD (the total duration of call; Figure 2.6 i) e)); IS (the inter-syllable duration; Figure 2.6 i) f)); and IC (the inter-call duration; Figure 2.6 i) g)). For the *trill* and *rororo* calls, which only had one syllable type, only F1, D1, TD, IS, and where possible IC were measured. Parameter definitions can be found under 'Measurements' in Chapter 6 of the Raven Pro 1.4 User Manual (Charif et al., 2010).

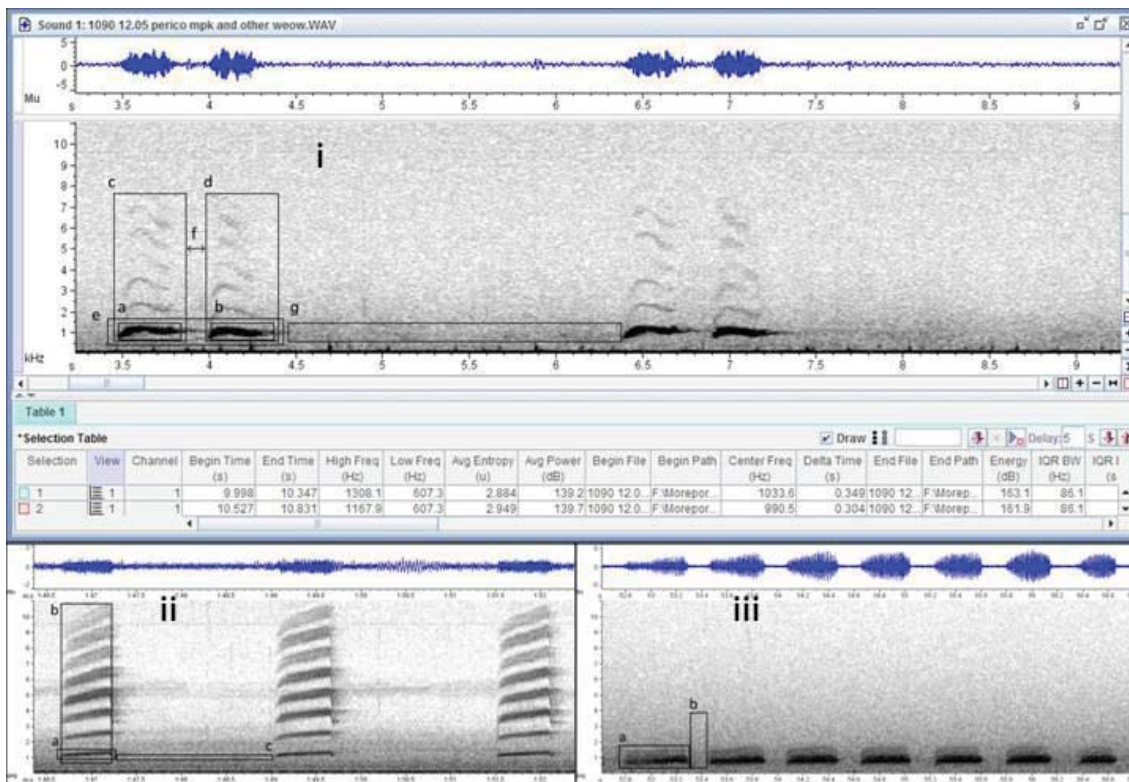


Figure 2.6 Example of the selections made on spectrograms of three morepork call types : i) the *more-pork* call showing a) the fundamental *more* syllable for F1 and D1 measurements, b) the fundamental *pork* syllable for F2 and D2 measurements, c) and d) which each encompass the harmonics of the *more* and *pork* syllable respectively, e) the whole *more-pork* call for TD measurement, f) the inter-syllable gap between *more* and *pork* syllables to measure IS, and g) the gap between *more-pork* calls for IC measurement; 2.6 ii) the *trill* call showing a) the fundamental *trill* syllable, b) the harmonics of the *trill* syllable, and c) the IS between the *trill* syllables; and 2.6 iii) the *rororo* call showing a) the fundamental *ro* syllable and b) the IS between *ro* syllables. Spectrograms produced using RavenPro.

Statistical Analyses

The data were exported from the Raven selection table to a Microsoft Excel spreadsheet where they were graphed and further explored in both Microsoft Excel and SPSS v.22 (IBM, 2013). On investigation, the data for many of the parameters were not normally distributed (Shapiro-Wilks test), so I used a Kruskal-Wallis test to examine the effect of two single factors - individual morepork and call type - on the response variables of fundamental frequency, fundamental duration, and inter-syllable duration. To account for the multiple comparisons, I used the Benjamini-Hochberg Procedure (Benjamini & Hochberg, 1995). This procedure is recommended when carrying out many comparisons where the expectation is that a large number of them may be significant and, for example, as corrections such as Bonferroni may result in false negatives. I followed Thissen et al. (2002) to conduct the Benjamini-Hochberg procedure using Microsoft Excel.

Results

Call Repertoire

Morepork varied in pitch; some birds could be loud or quiet, soft and smooth, or staccato and harsh. Their calls ranged from 0.5 kHz to 11 kHz (including harmonics), or to about 4 kHz when considering only the fundamental frequencies (excluding harmonics). Interestingly, despite previous reports that morepork call only at night, morepork on Ponui were heard to vocalise during the day on a number of occasions, but never when they were within sight of the observer. Calls during the day were heard when approaching a roosting area, whilst leaving and when stood nearby, but out of line-of-sight to a roost. This is possibly a diurnal response to disturbance, or simply as a form of diurnal contact. Morepork call throughout the year and show temporal variation in amount of calling by month and per hour of the night (Chapter Three). I identified eleven distinct calls uttered by the study morepork which I named as follows: *more-pork*, *more-more-pork*, *rororo*, *trill*, *low trill*, *weow*, *copulation squeal*, *juvenile chicketting call*, *chick trill*, *distress squeak* and *single hoot* (Figure 2.7).

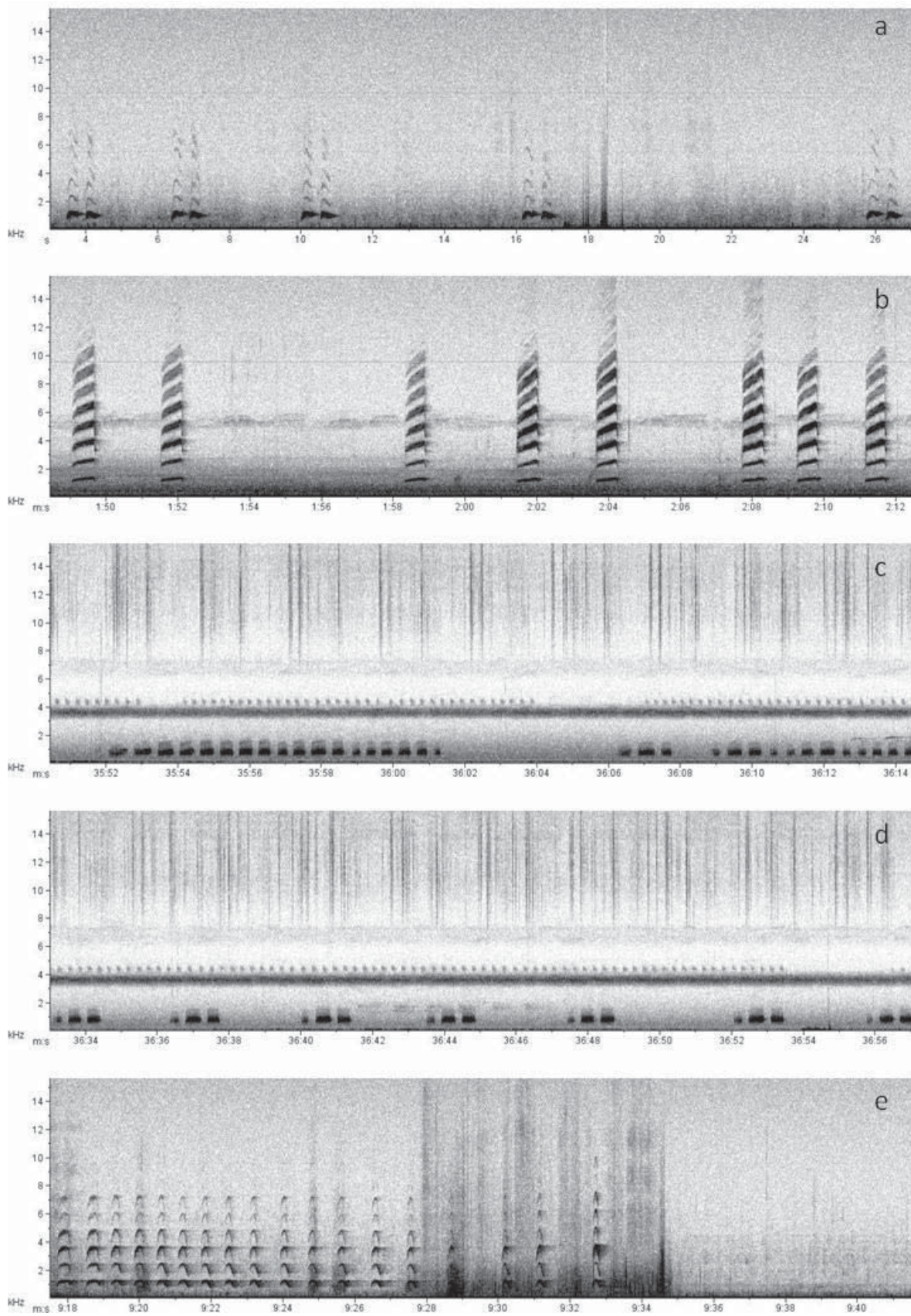
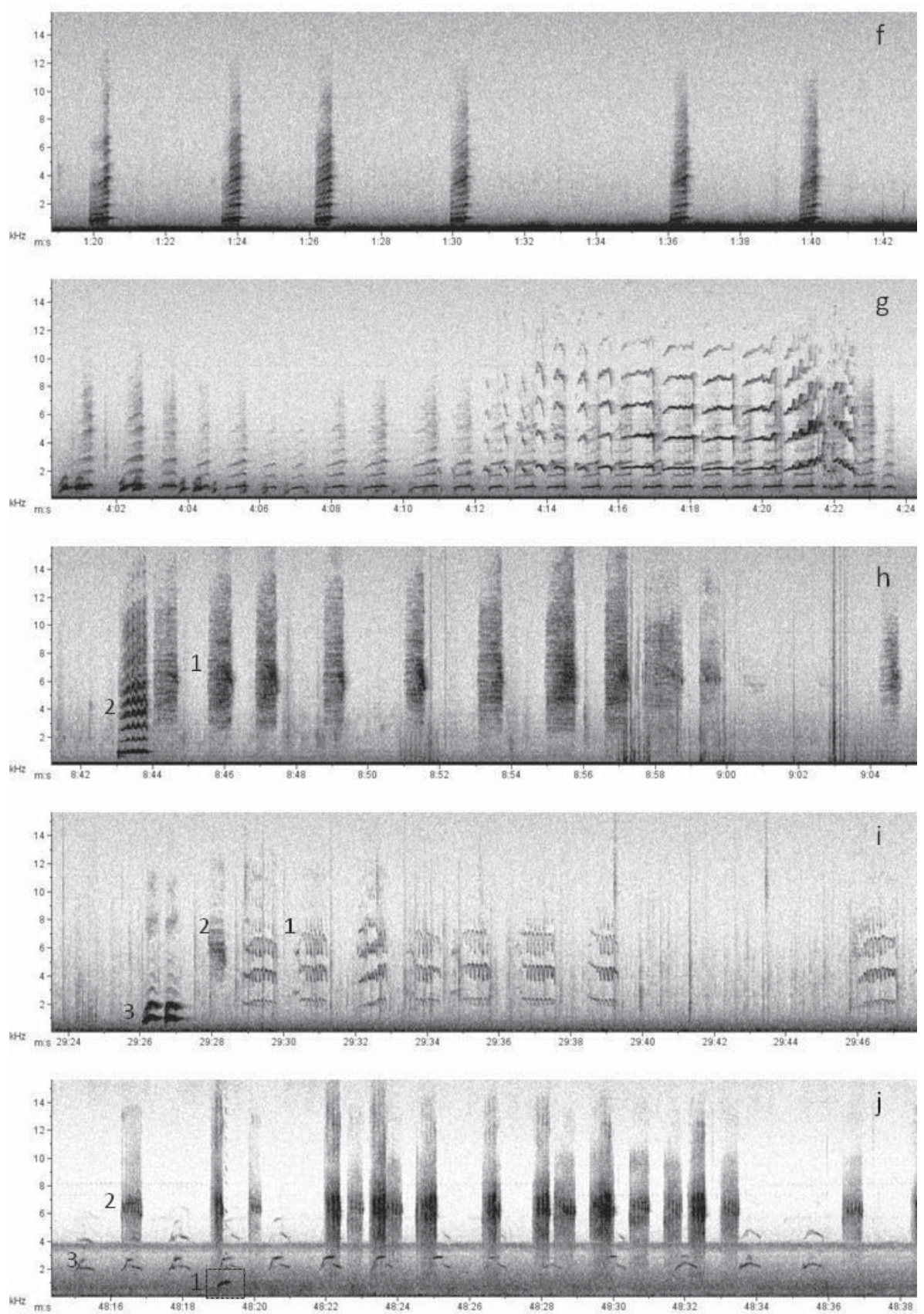


Figure 2.7 Spectrograms of each morepork call type where y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds) : a) *more-pork* b) *trill* c) *rororo*; d) *more-more-pork* (in c. and d. the horizontal line and dots around 4kHz are field cricket noises and the vertical lines are rain drops); e) *weow* call (the darker smudging after 9:28 is where I moved to track the bird in flight);



f) low trill (the thick dark line below 1kHz is an aeroplane); g) copulation squeal (beginning at 4:12 with build-up more-pork and trill calls); h) chicketting calls (h.1) (preceded by a parent's trill (h.2); i) chick begging trill (i.1) (preceded by a parent's more-pork call (i.3) and a chick's chicketting call (i.2); j) single hoot (j.1: black selection box) with chicketting calls (j.2) and male kiwi calls (j.3) in background. Spectrograms produced using RavenPro.

More-pork Call

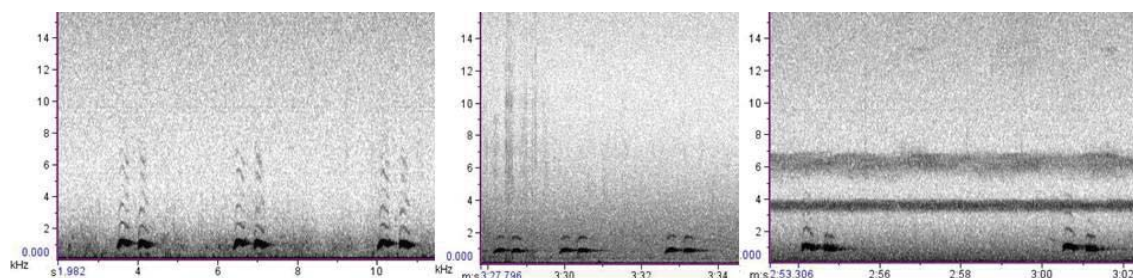


Figure 2.8 Spectrograms of three examples of different *more-pork* calls from three different birds used in this study. The y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds). The two lines in the far right spectrogram around 4 and 6 kHz are cricket noises.

The *more-pork* call (Figure 2.7 a) and Figure 2.8) is the disyllabic call most easily recognised in the morepork's repertoire and is the reason for the owl's name. The Maori name, Ruru, which refers to the bird's call, also fits its disyllabic nature, and can be used interchangeably to name the owl and its call. I shall use *more-pork* for the call as it more clearly denotes the two separate syllables which will be discussed; *more* and *pork*. It is the most common of the morepork's calls and has been hypothesised as its territorial advertisement call (Stephenson, 1998; Higgins, 1999).

All the birds in this study uttered the *more-pork* call (i.e both unbanded birds and those fitted with transmitters), demonstrating that this call is used by both sexes. The call was uttered both when the caller appeared to be alone, and when there were birds present or close by. I observed the call being uttered from a single perch location in extended bouts where the bird remained perched, but also in shorter bouts as the bird moved about. It was used when the bird was alone, and also together with either its mate, or in a duel with distant neighbours. I observed bouts to be variable in length, appearing to be situation and audience dependent and lasting from 10 seconds to close to an hour. These bouts may comprise just a single disyllabic call, or over one hundred calls and therefore 200 syllables.

The first syllable '*more*' displayed varying degrees of frequency modulation (a change in frequency), some appearing relatively flat on the spectrogram (Figure 2.8), and others showing more of a shallow inverted 'V' shape (Figure 2.8). The second syllable '*pork*' was often less frequency modulated and flatter. This call carried well across

distance particularly on clear, calm nights. Across flat pasture, a calling morepork could be heard at a distance of approximately just under a kilometre (Pers. obs.).

While *more-pork* was the most common call, the birds often combined and split the syllables into variations. One of these – *more-more-pork* (Figure 2.7 d) – I believe could be classified as a call in its own right. Other combinations were less frequent and I have left them as variants of the *more-pork* call. These include: *more-pork-more*; *weow-pork*; *more-more-pork-more*; *more-weow* and *rororo-more-pork*. During the *more-pork* call, the bird adopted what I interpreted to be an aggressive stance, sitting low to a branch, spreading its feathers and slightly lifting its wings away from its body so that it appeared larger. The owl's body moved with each syllable, most noticeably causing its head to bob down while uttering each syllable. The *more-pork* call occurred throughout the year; however, its occurrence varied between nights, months and weather types (Chapter Three).

Across all study birds (seven wild marked and two captive) the fundamental frequency of the *more* syllable ranged from 710.6 Hz to 1098.2 Hz and the fundamental frequency of the *pork* syllable ranged from 710.6 Hz to 1033.6 Hz. The syllable durations of the *more* and *pork* syllables ranged from 0.22 to 0.54 seconds and 0.24 to 0.50 seconds respectively. The interval between *more* and *pork* syllables ranged from 0.08 to 0.26 seconds and the duration of the whole disyllabic call itself ranged from 0.66 s to 1.11 s. The interval between calls varied greatly from 0.40 s to 12.23 s with a median of 3.34 s (Figure 2.9 a-c). Each of the seven measurements differed significantly between individuals (Table 2.2).

The median fundamental frequencies of both the *more* and *pork* syllables varied significantly between study birds (Kruskal-Wallis *more*: $\chi^2 = 87.45$; df: 8; $p \leq 0.001$; *pork*: $\chi^2 = 84.77$; df: 8; $p \leq 0.001$, Table 2.2; Figure 2.9 a and Figure 2.9 b). Most of the difference between individuals in *more* syllable frequencies was due to Macchiato, Perico and Ristretto being significantly different from other morepork (Figure 2.9 a, and pairwise tests in Table Appendix 1.01). Macchiato's *more* syllables had a lower frequency than many of the other birds while Ristretto and Perico had higher

frequency *more* syllables. There was also variation within each bird's *more* syllable frequencies (Figure 2.9 a).

The median fundamental frequencies of the *pork* syllable were lower than those of the *more* syllable for each bird (Figure 2.9 b) and this difference was significant (Pairwise Kruskal-Wallis: *pork-more* $\chi^2 = 103.69$; $p \leq 0.001$). While more pronounced with the *more* syllables, there was also individual variation about the median frequency for all birds' *pork* syllables (Figure 2.9 b). The difference between birds (Table 2.2) was due to Perico and Macchiato being significantly different from other birds with higher and lower fundamental frequencies respectively (Table A1.02).

The median duration of each bird's *more* syllables (Figure 2.9 c) ranged from 0.30 seconds to 0.46 seconds, but six of the wild birds' medians lay between 0.30 s and 0.36 s with only one just above 0.40 s; the captive female had the highest median duration of 0.46 s. Differences between birds were significant (Table 2.2), but most of the differences were due to two birds, Whisper and Calypso being significantly different to five and four other birds respectively (Table A1.03), both birds having longer syllable durations.

The *pork* syllable median durations (Figure 2.9 d) showed less individual variation as all the birds had median durations within a range of 0.1 seconds and this was less than the variation seen in the *more* syllable. Almost all *pork* syllables had a median duration shorter than the *more* syllable. There was individual variation (Table 2.2), however this was spread across four birds each being different to three others (Table A1.04).

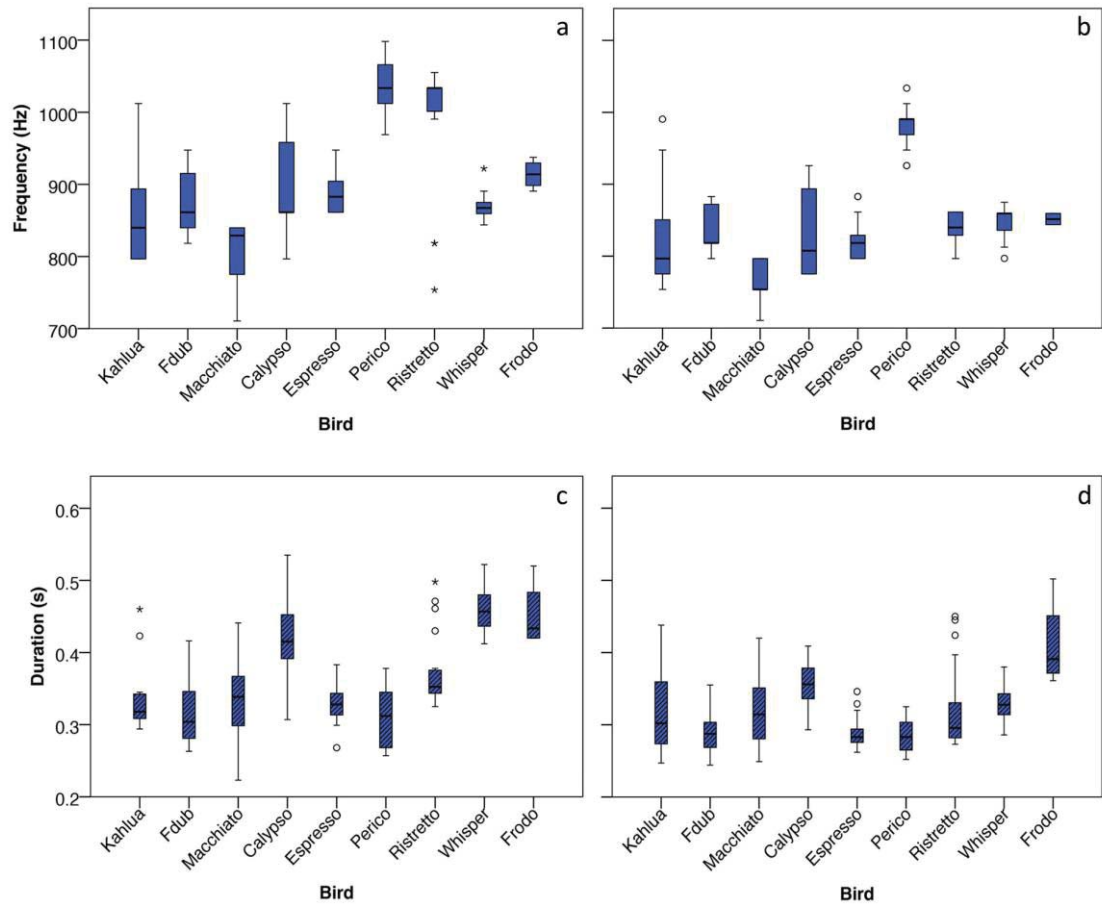


Figure 2.9 a-d: Box plots comparing the median values for a) *more* syllable fundamental frequency (Hz); b) *pork* syllable fundamental frequency (Hz); c) *more* syllable fundamental duration (s) and d) *pork* syllable fundamental duration (s) per individual morepork in the study. The first seven bird names are the wild birds and the last two (Whisper and Frodo) are the captive birds. The line within each box is the median and the upper and lower short edges of the box are upper and lower 25% quartiles. The whiskers (lines extending from the box) extend to the largest and smallest unbooked values (neither outlier nor extreme) and the open circles are outlying values whilst the asterisks are extreme outlying values.

The total duration of the whole disyllabic *more-pork* call varied between birds from 0.74 s to just under one second (Figure 2.9 e), which was significant (Table 2.2) and due to Whisper and Calypso's calls being significantly longer than most, and Fdub's being significantly shorter (Table A1.05).

While the ranges of each individual bird showed overlap in inter-syllable duration (Figure 2.9 f), there was significant difference between the birds (Table 2.2), with Calypso, Perico and Ristretto having longer inter-syllable durations than the other birds (Table A1.06).

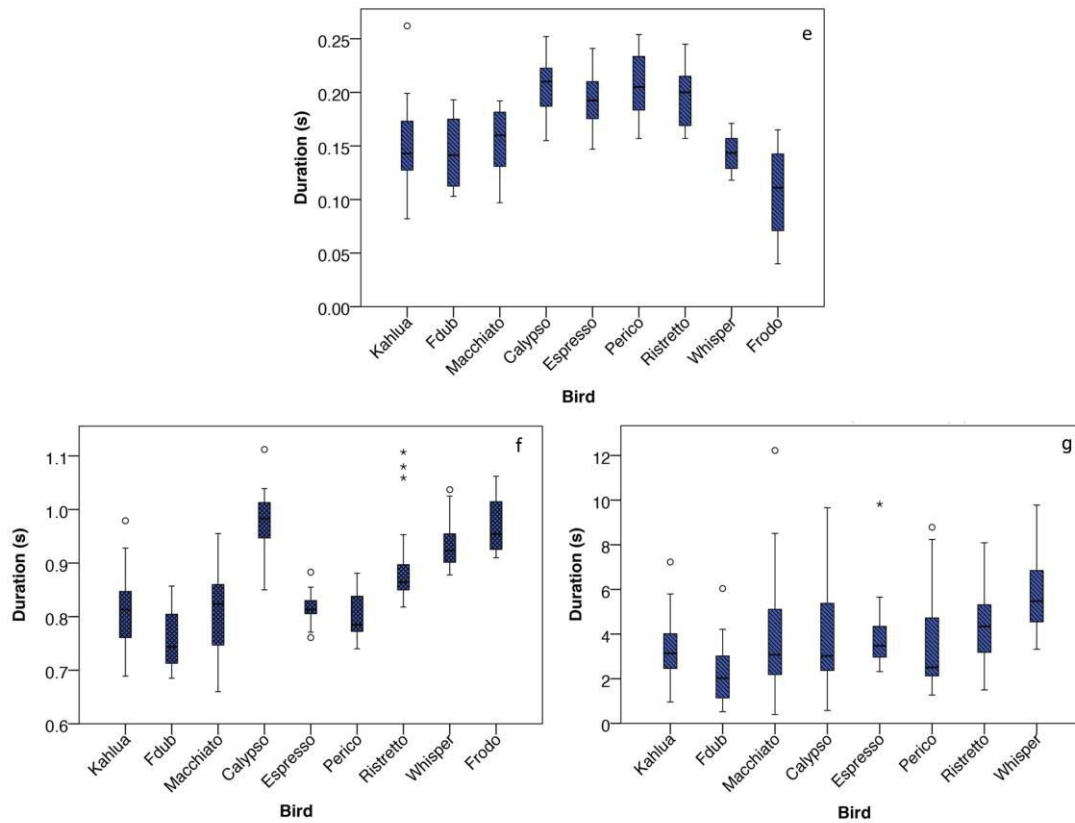


Figure 2.9 e – g: Box plots comparing the median values for e) total *more-pork* call duration (s); f) inter-syllable duration (s); and g) inter-call duration (s) per individual morepork in the study. The first seven bird names are the wild birds and the last two (Whisper and Frodo) are the captive birds. Frodo is absent from box plot g as the only calls found were single, separate *more-pork* calls, not call bouts. The line within each box is the median and the upper and lower short edges of the box are upper and lower 25% quartiles. The whiskers (lines extending from the box) extend to the largest and smallest unbooked values (neither outlier nor extreme) and the open circles are outlying values whilst the asterisks are extreme outlying values.

Table 2.2 Results of Kruskal-Wallis tests examining the effect of individual on the following call characteristics of individual birds: fundamental frequency of the *more* (F1) syllable; fundamental frequency of the *pork* (F2) syllable; duration of the *more* (D1) syllable; duration of the *pork* (D2) syllable; total duration of the whole *more-pork* call (TD); inter-syllable duration (IS) and inter-call duration (IC). Figures 2 a-e give a visual representation of the variation between individuals.

Parameter	Chi-square	df	p	n
F1	87.45	8	≤ 0.001	155
F2	84.77	8	≤ 0.001	155
D1	86.50	8	≤ 0.001	155
D2	57.84	8	≤ 0.001	155
TD	102.89	8	≤ 0.001	155
IS	79.74	8	≤ 0.001	155
IC	37.04	7	≤ 0.001	149

More-more-pork Call

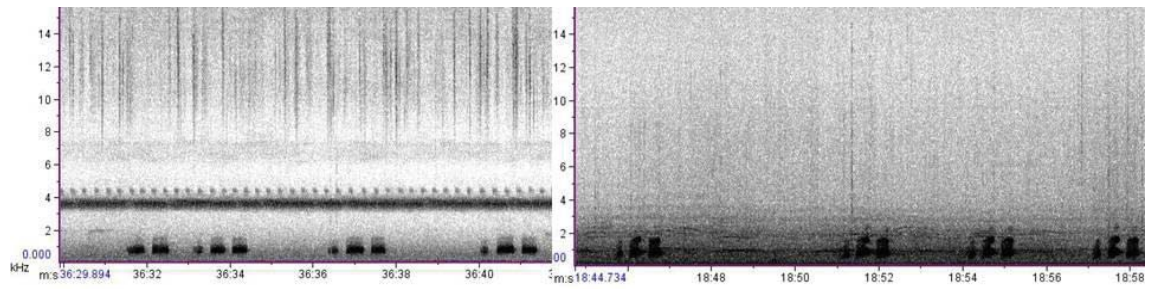


Figure 2.10 Spectrograms of two different *more-more-pork* calls from two different birds. The y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds). The dark line and dots above in the spectrogram on the right are the noise of field crickets.

This call appeared to be a more urgent version of the *more-pork* call and in my observations it sounded to be uttered with more force (Pers. obs., 2014), possibly conveying more aggression. It often followed short bouts of *rororo* or was interspersed within long bouts of either *rororo* or *more-pork* calls. The added syllable gave the call extra emphasis over the disyllabic *more-pork* call as if building up to a more powerful *more-pork* call. This added power can be seen in the waveform of the call when compared to the *more-pork* call (Figure 2.11). Unlike the aforementioned multiple variants of the *more-pork* call, the *more-more-pork* call (Figure 2.7 d and 2.10) was far more prevalent than any of the other combinations suggesting that this perhaps has a different meaning to the *more-pork* call and can be elevated to the status of a call type in its own right.

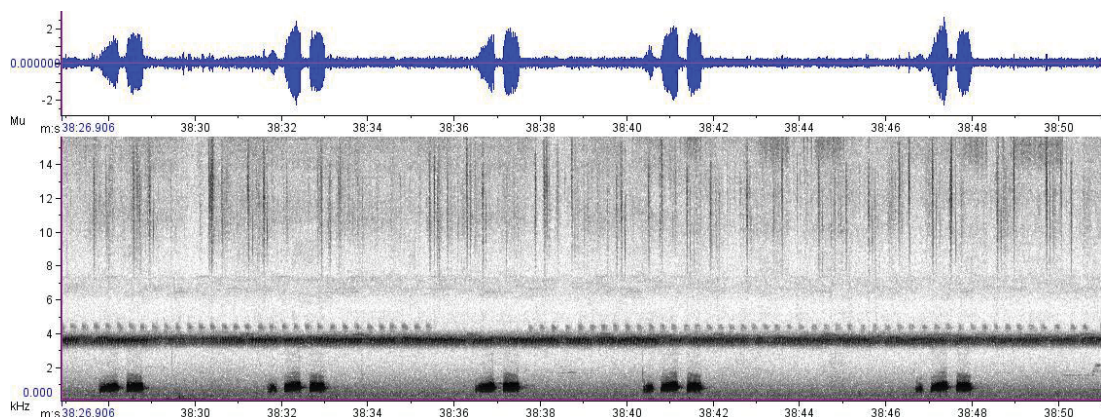


Figure 2.11 Waveform (top) and spectrogram (bottom) of a call bout by one bird (Ristretto, female, 20/02/2014; 23:29) containing both disyllabic *more-pork* (first and third calls at 1 kHz on spectrogram) and trisyllabic *more-more-pork* (second, fourth and fifth calls around 1 kHz on spectrogram) showing difference in waveform and apparent emphasis on each syllable. The y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds). The line and dots around 4 kHz are crickets.

Rororo Call

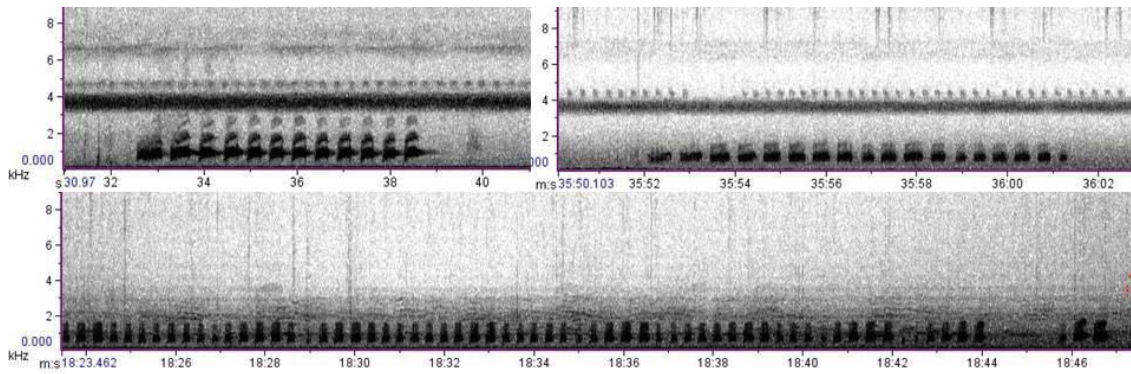


Figure 2.12 Spectrograms of three different *rororo* bouts showing difference in bout length. The y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds). In the two top spectrograms, the line and dots around the frequency of 4kHz are sounds of field crickets.

The *rororo* call (Figure 2.7 c and 2.12) was composed of one syllable which we termed ‘ro’ repeated many times. The fundamental frequency of this call syllable ranged from 468.8 Hz to 904.4 Hz with a median of 732.1 Hz. The duration of this call syllable ranged from 0.14 s to 0.60 s with a median of 0.26 s. The duration between syllables was low, ranging from 0.08 s to 0.36 s with a median of 0.16 s. There was significant variation found between individuals for all three measurements (Table 2.3).

Table 2.3 Kruskal-Wallis test of the effect of individual bird on the three response variables: fundamental frequency, fundamental duration and inter-syllable duration of the *rororo* call.

	Chi-square	df	p	N
Fundamental Frequency	142.31	8	≤ 0.001	270
Fundamental Duration	59.63	8	≤ 0.001	270
Inter-Syllable Duration	114.76	8	≤ 0.001	240

The median fundamental frequency for the nine individuals’ (seven wild and two captive) *ro* syllables ranged from 573.8 Hz to 861.3 Hz (Figure 2.13 a). There appeared to be a grouping of the wild birds because both captive birds (Whisper and Frodo) had lower median frequencies than all the wild birds. There was, however, a fair degree of variation in the ranges of the wild birds, which showed overlap with the captive birds’ frequencies, so it was just the medians which differed. The differences between individuals were significant (Table 2.3.). The wild birds seemed to show more variation than the captive individuals (Figure 2.13 a). The differences were found in pairwise

comparisons mostly due to Whisper, Kahlua and Calypso being significantly different to the other birds (Table A1.07). Whisper was significantly different to all other birds and had the lowest frequency *ro* syllable. Calypso and Kahlua were different to five others with both these two birds having quite high *ro* syllable frequencies (Figure 2.13 a).

Each birds' median *ro* syllable duration did not seem to vary much with a range of 0.21 s to 0.36 s, though there were significant differences found between individual bird's syllable durations (Table 2.3), mostly due to Ristretto and Frodo (Table A1.08) with both birds having relatively long *ro* syllables (Figure 2.13 b).

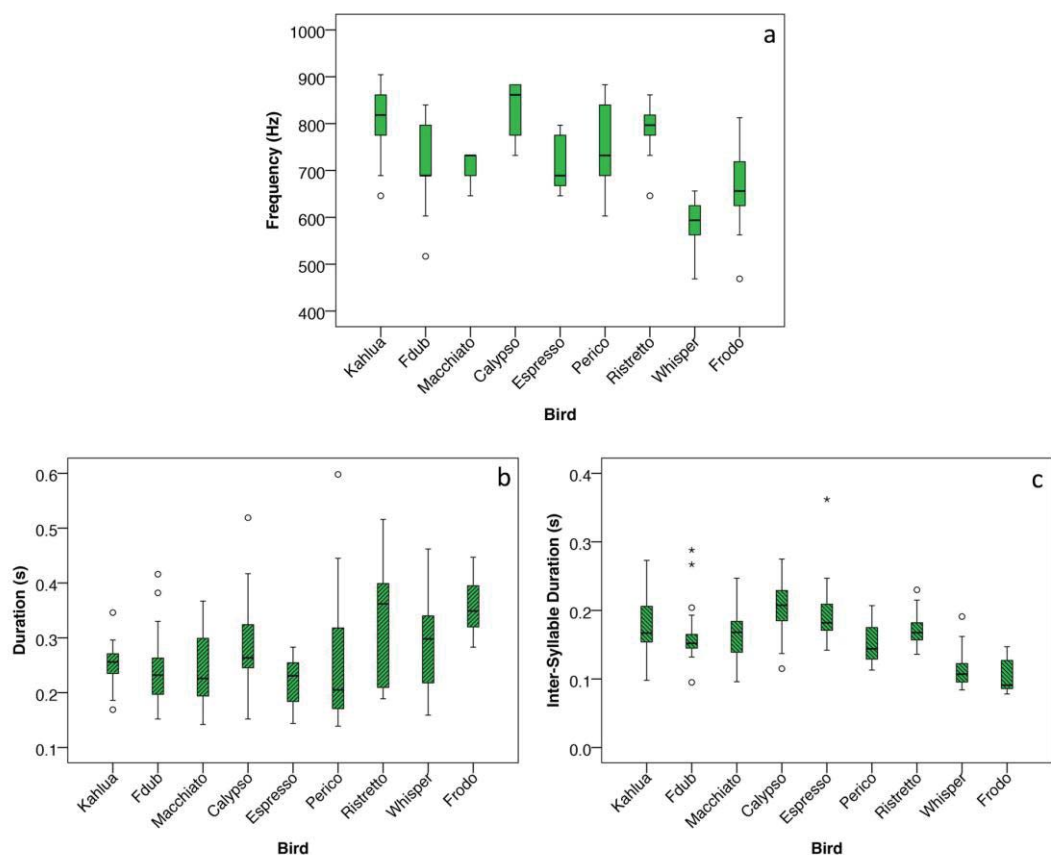


Figure 2.13 Box plots comparing the median values for a) *ro* syllable fundamental frequency (Hz); b) *ro* syllable fundamental duration (s) c) inter-syllable duration (s) between *ro* syllables per individual morepork in the study. The first seven bird names are the wild birds and the last two (Whisper and Frodo) are the captive birds. The line within each box is the median and the upper and lower short edges of the box are upper and lower 25% quartiles. The whiskers (lines extending from the box) extend to the largest and smallest unbooked values (neither outlier nor extreme) and the open circles are outlying values whilst the asterisks are extreme outlying values.

Inter-syllable duration medians ranged from 0.09 s to 0.21 s with only three of the nine individuals showing much range about the median (Figure 2.13 c). Again, differences between individuals were significant (Table 2.3), which is accounted for by both the captive birds – Whisper and Frodo - being different from all the wild birds, but not each other (Table A1.09), in having shorter inter-syllable durations between *ro* syllables (Figure 2.13 c).

The number of syllables per bout was highly varied as the *rororo* call was used as a shorter stand-alone call, either in prefix to a bout of *more-pork* calls or as an extended bout of *rororo* calls. The number of syllables then was seen to range from five to over 150 in a single bout. Like the *more-pork* call, from my field observations, the length of the *rororo* bout appeared to be situation and audience dependent. Bout lengths varied greatly from five seconds to many minutes.

Each syllable was monotonous at a single pitch (however, this may vary slightly between bouts given by the same bird), and they displayed no frequency modulation (Figure 2.12). It was not a highly common call, but nor was it rare, and seemed to be strongly associated with aggressive or excited situations where two birds interacted, or where a bird responded to playback (Chapter Four). The call often was given with aggressive posturing, such as sitting low to their perch with slightly drooped wings. It was most common in close range situations where the birds were very close to each other, or to the playback speakers, and both sexes seemed to use this call. I observed the single study male Espresso and a female Calypso sat in neighbouring trees engaging in a long bout of overlapping *rororo* calls. I hypothesised that Calypso may have been either Espresso's ex-mate or mother because I found them roosting together for a while until the breeding season when they separated. It was very difficult to discern each bird from the other and syllables seemed to be similar between individuals (Figure 2.14a).

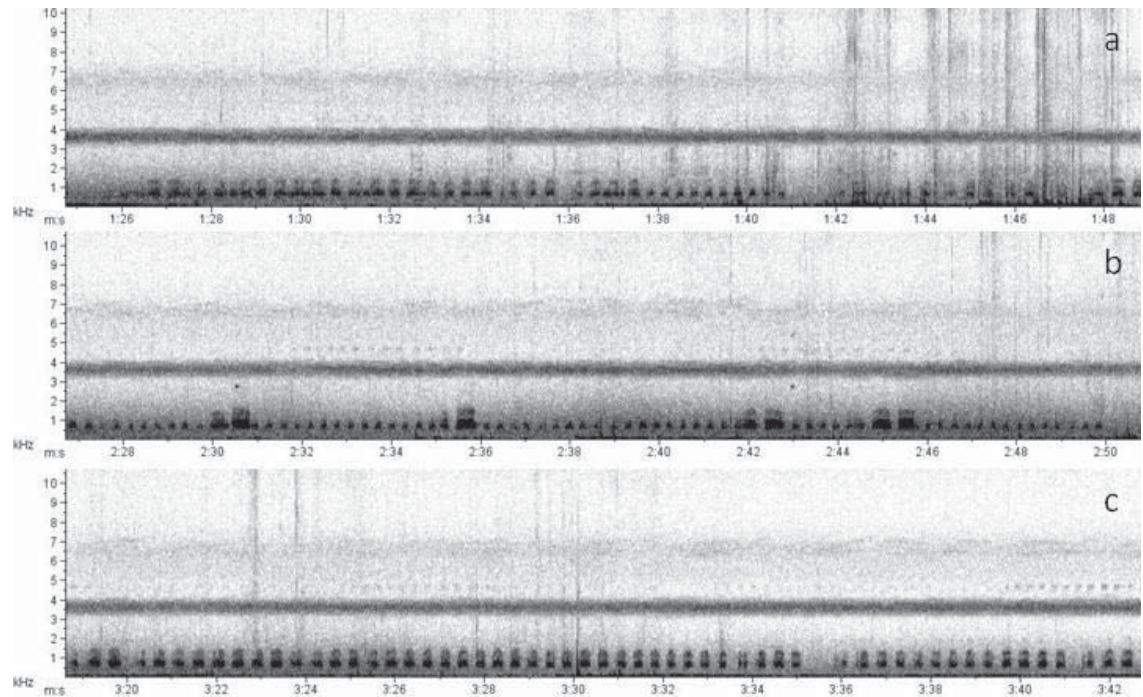


Figure 2.14 Three spectrograms of a vocal interaction between two morepork: Calypso and Espresso: a) Both birds utter *rororo* and the call bouts overlap making identity difficult to discern; b) One bird (Espresso) changes to a *more-pork* call (bolder, thicker syllables visible on spectrogram b) while the other bird (Calypso) continues with *rororo*; c) One bird is silent whilst the other continues a *rororo* bout. The y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds). The band lines around 4 kHz are cricket calls.

Trill

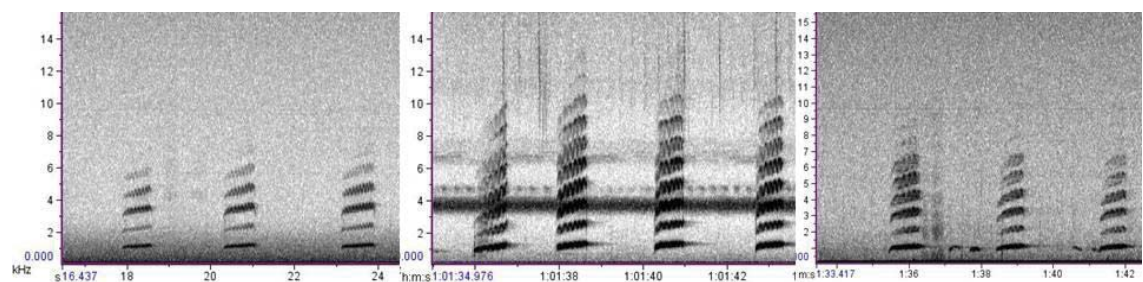


Figure 2.15 Spectrograms of three different *trill* calls from three different birds. The y-axis is frequency (kHz) and x-axis is time since sound recording started in 2 second intervals (m:s = minutes:seconds). The line and dots at 4 kHz in the middle spectrogram is cricket noise and in the far right spectrogram there is another morepork giving more-pork calls in the background.

Trill may be a broad term, however, this was found to be the morepork's most frequency modulated call and the name '*trill*' was deemed appropriate to describe it. The *trill* call (Figure 2.7 b and 2.15) was composed of one syllable which increased in frequency, rising upwards in pitch at varying degrees. This increase seemed to depend

on the bird, but an effect of situation is also likely as variation between a single bird's trills was observed on spectrograms (Figure 2.15).

Overall the fundamental frequency of this call syllable showed a wide range with a median of 1055.1 Hz; this variation was due to significant individual variation (Table 2.4). The *trill* call had the highest number of harmonics, most often having seven to nine, but having as many as ten and as few (in lesser quality recordings) as four in addition to the fundamental harmonic. The call duration ranged from under half a second to over one second with a median of 0.69 s. The time interval between syllables had a median of 0.17 s and both fundamental duration and inter-syllable duration contained significant variation (Table 2.4).

Table 2.4 Kruskal-Wallis test of the effect of individual bird on the three response variables: fundamental frequency, fundamental duration and inter-syllable duration of the *trill* call.

	Chi-square	df	p	n
Fundamental Frequency	87.30	8	≤ 0.001	135
Fundamental Duration	70.84	8	≤ 0.001	135
Inter-Syllable Duration	20.28	8	0.009	125

The median fundamental frequencies of each of the nine morepork varied from 937.5 Hz to 1270.5 Hz without showing signs of a grouping pattern (Figure 2.16 a). Differences between each bird's *trill* frequencies were significant (Table 2.4). Both males (one wild, one captive) showed that calls could not be sexed by frequency; the wild male (Espresso) had one of the highest median frequencies (1162.8 Hz), where the other captive male (Frodo) had the lowest median frequency (937.5 Hz). Significant differences were found between individuals in fundamental frequency (Table A1.10) with most of the differences involving Frodo, Fdub, and Perico. Frodo and Fdub both had the lowest frequency trills, whereas Perico's had the highest (Figure 2.16 a).

Fundamental durations of the *trill* syllable also showed variation between individual, ranging from 0.52 s to 0.92 s, and like the fundamental frequencies (Figure 2.16 a) showed no sign of grouping (Figure 2.16 b). Significant differences between the individual bird's syllable durations were found (Table 2.4) and these were mostly due to Fdub and Whisper being different to others (Table A1.11). Whisper's *trill* syllable length was long, whereas Fdub had the shortest *trill* syllable duration (Figure 2.16 b).

The inter-syllable durations showed little variation when medians were compared (Figure 2.16 c). The median inter-syllable durations centred around 1.20 s to 1.50 s with only two exceptions (Macchiato: 3.82 s and Calypso: 2.00 s). There did not appear to be the variation in ranges about the medians seen in other measurements. While there was an effect of bird on inter-syllable duration (Table 2.5), there was only one significantly different pairwise comparison and this was between Perico and Macchiato (Kruskal-Wallis: $\chi^2 = 53.39$; df: 8, $p = 0.006$; Table A.1.12).

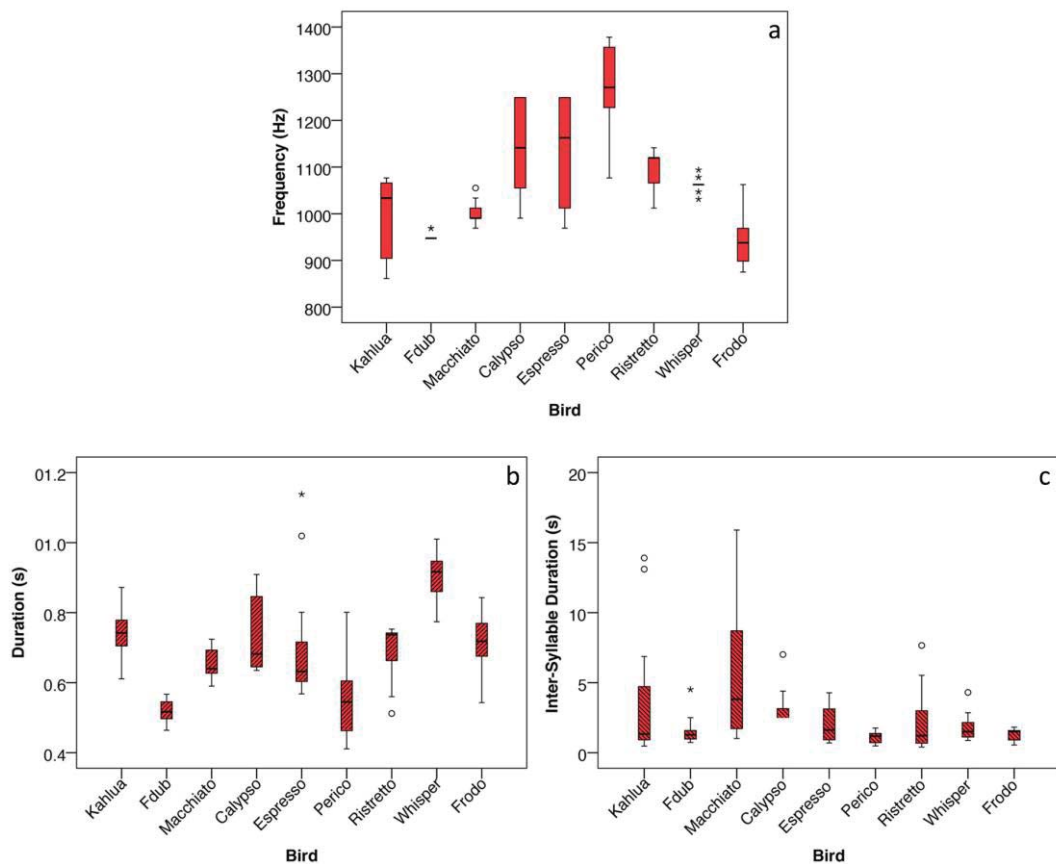


Figure 2.16 Box plots comparing the median values for a) *trill* syllable fundamental frequency (Hz); b) *trill* syllable fundamental duration (s) c) inter-syllable duration (s) between *trill* syllables per individual morepork in the study. The first seven bird names are the wild birds and the last two (Whisper and Frodo) are the captive birds. The line within each box is the median and the upper and lower short edges of the box are upper and lower 25% quartiles. The whiskers (lines extending from the box) extend to the largest and smallest unbooked values (neither outlier nor extreme) and the open circles are outlying values whilst the asterisks are extreme outlying values.

The *trill* call was highly frequency modulated giving each syllable a vibrato (vibrating) quality which was visible in high quality spectrograms (Figure 2.6 b; 2.15). Each syllable ranged from highly uniform to varying in pitch change-rate and time-interval spacing.

In addition, the morepork sometimes combined *trill*, *weow* and *pork* syllable into a bout of trills ended by 'weows' and finally 'weow-pork' (Figure 2.26 b and c).

Distance between birds did not appear to influence the utterance of this call (as seen with the *rororo* call) as morepork were observed to give the call when birds were close, but also when the calling morepork appeared to be alone. A video recording of a bird giving this call showed that it is given with an open beak. They did not appear to favour a location from which to give this call suggesting that this is a call more involved in contact and current location than territoriality or advertisement. Often a trilling bird would call from one tree for some time then move to another tree to resume its calling. It was not heard to be uttered by a bird that was on the wing, which would have been easily heard to decrease in volume as distance from the observer increased (see *Weow*) as the bird changed location, or got nearer or further away from the observer. As the single male morepork in this study was heard to utter the *trill* call I have assumed that the call is not sex specific.

Low Trill

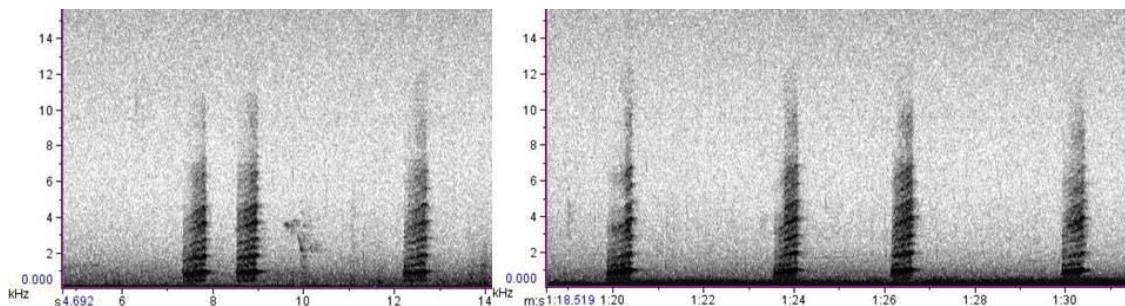


Figure 2.17 Spectrograms of two *low trill* call bouts, dark shadowing at the base of the second spectrogram is the noise of an aeroplane. Spectrograms show: a) more harmonics than the *trill* call and b) harmonics which are less defined and have a 'smudgy' quality when compared to the *trill* calls. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes:seconds) since sound recording started in 2 second intervals.

The morepork gave a call which although similar to the *trill* call sounded distinctively different and could be differentiated by ear in the field. It had a rumbling, harsher quality to it than the clearer sounding *trill* call. This I named '*low trill*' (Figure 2.7 f and 2.17).

Low trill differed to the *trill* call in that it was a lower pitch and quieter call suggesting that it might have a different function. The same birds were heard to give loud, clearer, high pitched *trill* calls, but also quieter low-pitch trills. To investigate whether there was a difference, these calls were isolated as *low trill* when sorting manual sound recordings, and analysed separately to see if it was different to the other *trill* calls. While quality recorded examples of the *low trill* were limited, spectrographically, the call appeared to have less well defined harmonics and a more smudged appearance (Figure 2.18 b) than the *trill* call (Figure 2.18 a). While these harmonics appear to line up with those of the *trill*, they are more numerous (almost twice the number that *trills* have) as there are overtones scattered between the expected *trill* harmonics in the *low trill* (N. Carlson, Pers. comm., 2014) (Figure 2.18).

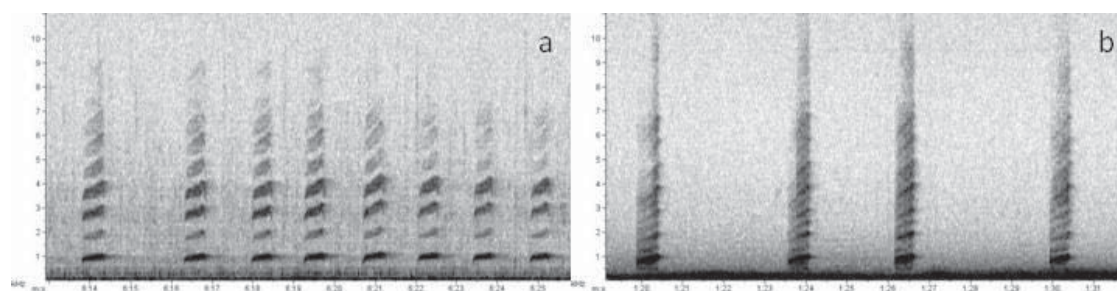


Figure 2.18 Spectrograms of a) the *trill* call and b) *low trill* call of the same bird (Fdub). Note the smudging which only occurs as the *low trill* call is uttered which is indicative of being part of the call and not a recorder fault. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes:seconds) since sound recording started in 2 second intervals.

The fundamental frequency of the *low trill* ranged from 796.7 Hz to 1012.1 Hz with a median of 904.4 Hz. A sub-sample of *trill* calls from the same three birds for which *low trills* were recorded was analysed to compare with the *low trills*, and these normal *trill* calls had a *trill* call fundamental frequency which ranged from 861.3 Hz to 1076.7 Hz with a median of 969.0 Hz (Figure 2.19 a). The duration of the *low trill* call ranged from 0.45 s to 0.81 s with a median of 0.55 s where the *trill* ranged from 0.46 s to 0.87 s with a median of 0.64 s (Figure 2.19 b).

The *low trill* was found to be significantly different to the *trill* in pitch with a lower median fundamental frequency (Mann-Whitney: $N = 62$; $U = 620.5$; $p \leq 0.001$) (Figure 2.19 a). No significant difference was found in either the median fundamental duration or inter-syllable duration of the two calls. There were individual differences between the three birds. Fundamental frequency and duration were significantly different

between birds for *trill* (Table 2.5), but only fundamental frequency was significantly different between birds for *low trill* (Kruskal-Wallis test: $N = 17$; $\chi^2 = 11.57$; $df = 2$; $p = 0.003$).

Table 2.5 Kruskal-Wallis test of the effect of individual bird on the three response variables: fundamental frequency, fundamental duration and inter-syllable duration of the *trill* call.

	Test Statistic	df	p	n
Fundamental Frequency	8.545	2	0.014	45
Fundamental Duration	34.015	2	≤ 0.001	45
Inter-Syllable Duration	7.233	2	0.027	45

Unlike the higher pitched *trill*, *low trill* was often heard being uttered when another morepork was nearby having announced its presence with a short *more-pork* call. The *low trill* seemed to elicit feeding by the other bird because on two occasions the *low trill* was garbled as if eating mid-call, so perhaps this call functions as an adult begging call.

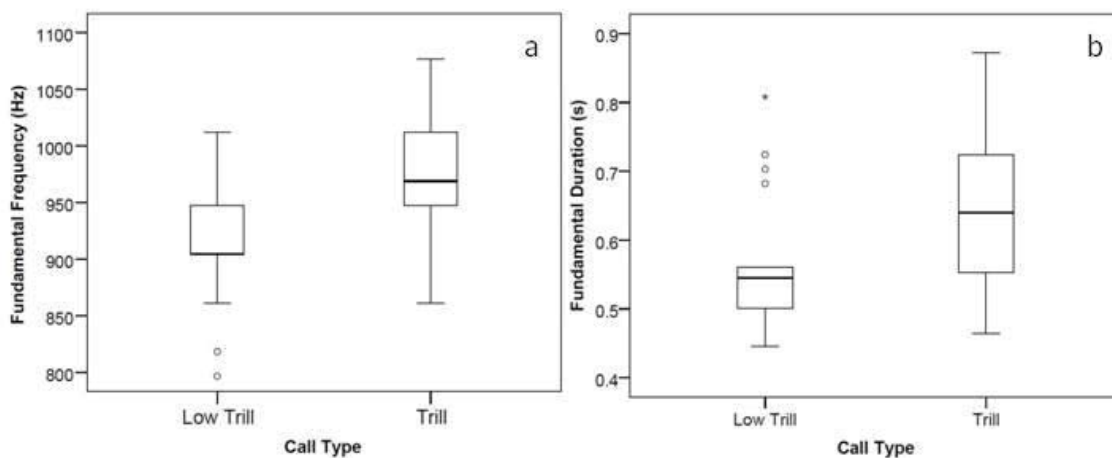


Figure 2.19 Box plots comparing median values for a) fundamental frequency and b) fundamental duration between two calls: *trill* and *low trill*. The line within each box is the median and the upper and lower short edges of the box are upper and lower 25% quartiles. The whiskers (lines extending from the box) extend to the largest and smallest unbooked values (neither outlier nor extreme) and the open circles are outlying values while the asterisks are extreme outlying values.

Weow

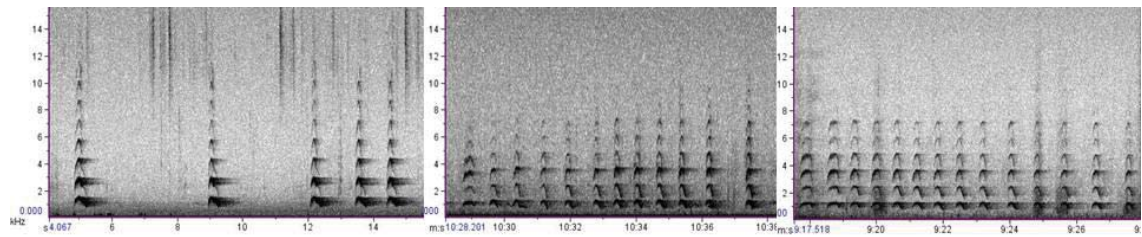


Figure 2.20 Spectrograms of three different *weow* calls from different birds showing difference in syllable spacing. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes:seconds) since sound recording started in 2 second intervals. The smudging to the left of each syllable is due to echo.

The *weow* call (Figure 2.7 e and 2.20) was less commonly heard than the main three calls (*more-pork*, *rororo*, *trill*), but was by no means a rare call. It was a staccato call of quickly rising and falling, high-pitched syllables and was often given in a short bout of calls in quick succession. On the spectrogram, these calls formed a steep-sided chevron with harmonics similar to the number seen in the *trill* call with a very short inter-syllable gap, however, this was varied (Figure 2.20). It was not heard to be used in interactions with other birds and was only heard from a single bird at a time. It appears to be an alarm and movement call because it was often heard when a bird was startled and took flight as observers walked through the bush. The movement of the calling bird could often be seen on the spectrogram as a fading of the sound print as the bird moved further from the microphone (Figure 2.21) and this can often be heard when the sound is played back as the call gets progressively fainter.

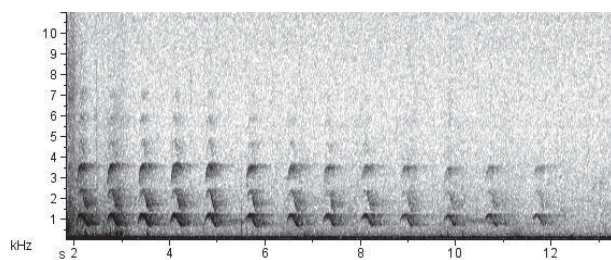


Figure 2.21 Spectrogram of a *weow* call given by a retreating bird showing how the sound print fades as distance from the microphone increases. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes: seconds) since sound recording started in 2 second intervals.

The *weow* call was not difficult to record, however, it was often difficult to see or know the caller's identity for certain because the call was often made as a bird retreated at speed. It was not possible to approach a bird giving this call. For this reason it was difficult to be certain how many of the recorded *weow* calls were from each target individual. For this reason no further analysis was conducted.

Copulation Squeal

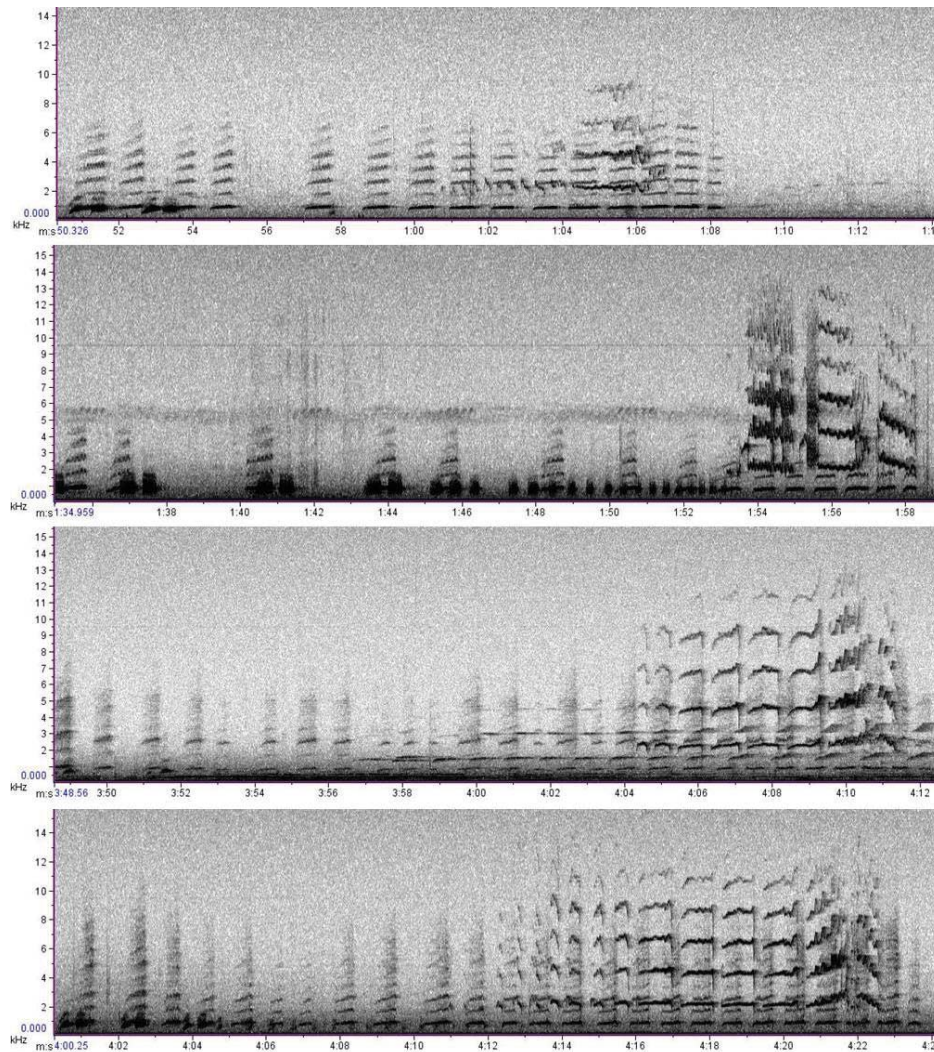


Figure 2.22 Spectrograms of four different *copulation squeals* from four different morepork pairs showing the difference in length and structure of different squeals. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes:seconds) since sound recording started in 2 second intervals.

This call was unlike any other of the morepork's calls. In fact, on first encounter both I. C. Castro and I thought an animal had been killed (Pers. obs., 2013). It was a shrill, wavering squeal and if heard out of context, without visual reference, it can be rather alarming and perplexing. Visual confirmation of the accompanying copulation behaviour to this call did not occur until late in this study. It was never heard as a single call without a second bird being vocally involved, and because it was confirmed to be associated with copulation and in concurrence with other reports, I suggest that the squeal occurs most commonly in, although not limited to, the breeding season. In this study the *copulation squeal* was heard mostly from September to December, but it

was not often easy to acquire recordings of the interaction. What was very interesting about this call, once confirmed to be uttered during copulation, was that it was heard outside the accepted breeding season of September to March. The first recording of this call was made on 27th April 2013, the end of the breeding season. I obtained seven recordings of this call type, four of which involved my study birds: Macchiato, Ristretto, Kahlua, and Calypso.

The *copulation squeal* was precluded by one bird emitting a progressive series of *more-pork* calls; *more-more-pork* calls and then *rororo* calls leading up to a climactic squeal. Simultaneously, a second bird emitted *low trills* which got progressively shorter. The squeal itself consisted of varying numbers of long, high-pitched, wavering, highly frequency modulated syllables (Figure 2.7 g and 2.22). There was variation in the whole squeal's length, which in this study ranged from 1.9 to 12.4 seconds in the seven recordings I made, and in which the number and length of each syllable varied. Of the seven recorded squeals, the median fundamental frequency was 2282.5 Hz. The length of entire copulation vocal events, including the *more-pork* calls and trills as the two birds vocalised to each other, lasted from 5.03 s to 37.75 s. I hypothesise that the trills were made by the female as I often heard females uttering *low trills* in the presence of the male, most likely to elicit cooperation from their mate. However, I have not managed to confirm which bird of the pair makes the squeal with any of my study birds.

“Chicketting” Call – juvenile begging call

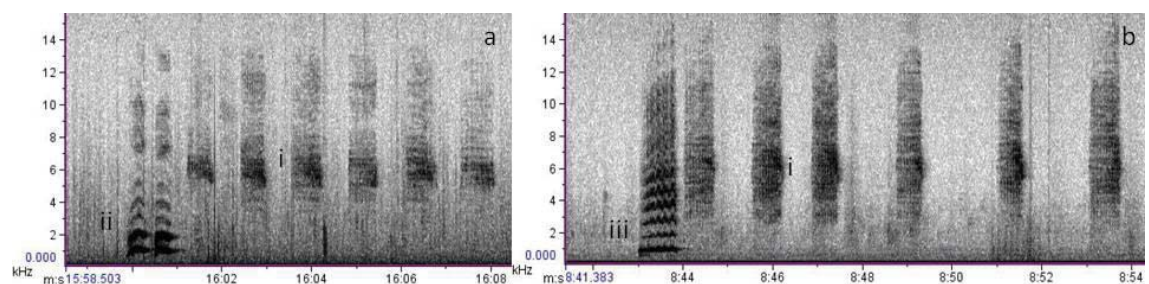


Figure 2.23 Spectrograms of two different bouts of the *chicketting* call (i), the first bout (a) is given in response to a parent morepork's *more-pork* call (ii), the second bout (b) is given in response to the parent's *trill* call (iii). The vertical lines are noises of movement by the arriving parents and the chicks. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes:seconds) since sound recording started in 2 second intervals.

To the observer's ear, the chicketting call sounded very similar to the noise made by field crickets (*Teleogryllus commodus*), but, as can be seen from the spectrograms, the form of the sound is very different (Figure 2.23 – chicketting call versus Figures 2.7 c and d which have prominent cricket-noise bands) It was a call uttered by morepork chicks and so I named it the “*chicketting*” call (Figure 2.7 h and 2.23). It was heard more or less continuously while the chicks were in the nest, and after leaving the nest, up to and slightly after fledging. It could be heard throughout observation periods from the middle to the end of the breeding season, and is presumably the juvenile begging call as it only ceased briefly when a food item was delivered by a parent bird, recommencing almost immediately. Even after fledging, this call was still observed while the chicks perched, preened in new feathers, tested their vision, and practiced pouncing on passing insects. This call was never heard from adult birds.

In the forest, this call made locating the chicks a challenge because it was not a sound that could be pin-pointed to location among dense trees and foliage. In outcrops of trees in open pasture, chicks were much easier to find by following this call.

Chick Trill

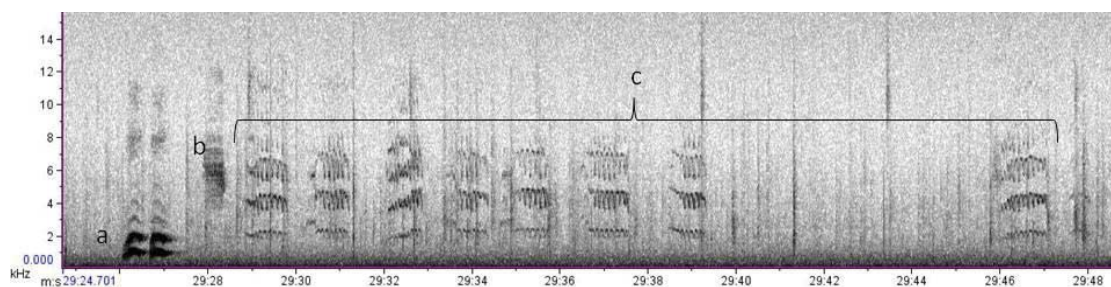


Figure 2.24 Spectrogram showing structural differences between bouts of the *chicketting* and the *chick trill* calls where a) is the parent's *more-pork* call to which the chicks are responding; b) is a *chicketting* call and c) are the *chick trill* calls. The y-axis is frequency (kHz) and x-axis is time (m:s = minutes:seconds) since sound recording started in 2 second intervals.

The *chick trill* (Figure 2.7 i and 2.24) appeared to more closely resemble adult trills in spectral structure, but were higher pitched. Discrete harmonics were visible on the spectrograms and while still more broadband in frequency than the adult *trill*, this was less so than the *chicketting* call. This call was mostly heard when the chicks were still in the nest. Spectrographically, the *chick trill* had more pronounced harmonics and frequency modulation than the *chicketting* call. It resembled the *copulation squeal* in

spectral appearance, but was a very soft, wavering trill sound quite unlike the loud *copulation squeal*.

Distress squeak

This sound, like a peep or high-pitched grunt, was only heard occasionally when a morepork was captured and struggling in the hand. It was not recorded nor heard out elsewhere in the field. It was unlike any other call the morepork made, suggesting that this call only occurs in a distress situation, such as capture.

Single hoot

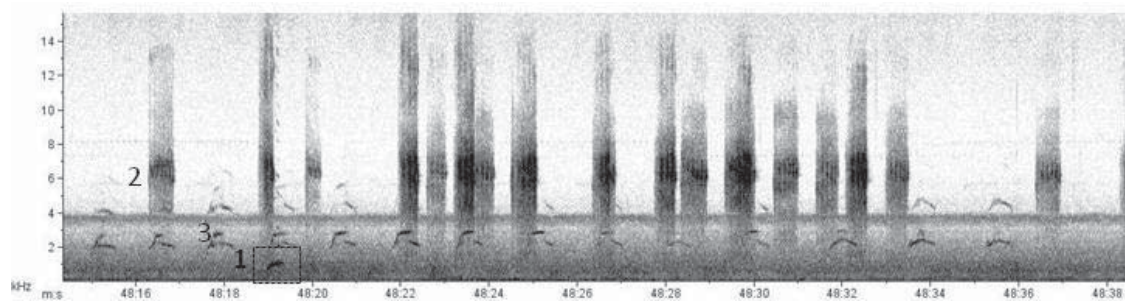


Figure 2.25 Spectrogram of the *single hoot* call (dashed box, number 1). Few instances of this call were heard or recorded and this best example occurs amongst interference from both a male kiwi call (thin lines, number 3) and the *chicketting* calls (dark smudges, number 2).

The *single hoot* was only heard twice and recorded once (Figure 2.7 j and 2.25). Both instances occurred in the breeding season and were uttered by the same male as he approached his chicks to deliver food.

Bill clap

The *bill clap* is worth mentioning here despite not being strictly a vocalisation. It is a clap sound produced by the bill being snapped shut. Potentially an aggressive display, this behaviour was seen when using playbacks in the re-capture mission to remove transmitters, whereby a morepork would clap its bill once or twice each time it landed after flying over and around the net. It was also observed when a morepork had been caught and was being handled or extracted from the net, often followed by an attempt to bite. It was heard once without human interference in a dispute between two birds, but was not commonly heard.

Combinations

Morepork also combined different call types in single bouts of calling, which I simply termed combinations (Figure 2.26). These included some calls which were common enough to warrant naming by combining my call names such as *weow-pork* (Figure 2.26 a – c) and *rororo-more-pork* (Figure 2.26 f).

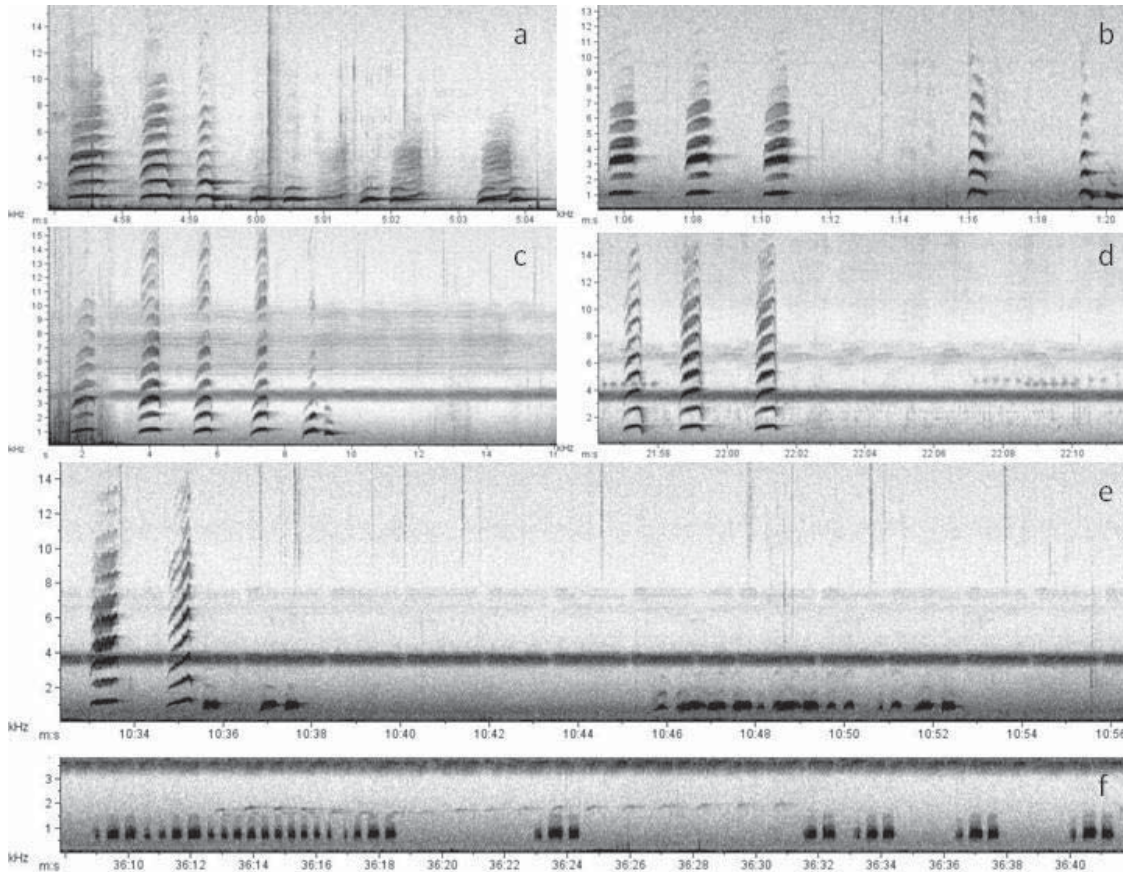


Figure 2.26 Examples of morepork combining call types in on call or call bout including a) *trill, trill, weow, weow-pork, more-pork, more-pork*; b) *three trills, weow and weow-pork*; c) *two trills, two weow calls and weow-pork*; d) *weow, trill, trill*; e) *trill, trill-weow-pork, more-pork* and a bout of *more-more-pork*; f) *more-more-pork, rororo* bout, *more-more-pork*, and *more-pork* then three *more-more-porks*. The lines around 4kHz on spectrograms c, d, e, and f are cricket noises. The horizontal dashes in spectrogram f, around 2 kHz, is the call of a male kiwi.

Call Comparisons

Fundamental Frequency

On average the *trill* had the highest median fundamental frequency of the three calls (Figure 2.27 a) with *rororo* having the lowest median frequency. The two syllables of the *more-pork* call were slightly different with *pork* having a lower median frequency than *more* (Table 2.6; Figure 2.27 a).

Fundamental Duration

Both syllables from the *morepork* call were similar in length with the second syllable (*pork*) having a median slightly less than the first syllable (*more*). Each *ro* syllable was shorter still than either the *more* or *pork* syllables. A *trill* syllable had a median duration around twice as long as any of the other three syllables, but when the *more-pork* call was measured as a whole call, it had the longest duration (Table 2.6).

Table 2.6 Summary statistics for spectral and temporal parameters measured from the calls of 7 wild and 2 captive morepork. Data is listed as medians, Inter-quartile range (in brackets) and range below. FundFreq is the fundamental frequency of the syllable and FundDur is the duration of the fundamental syllable. IS is the Inter-syllable duration. TD is the total duration of the two *more* and *pork* syllables which form the morepork call.

Call type	n (ruru)	n (syllables)	FundFreq (Hz)	FundDur (s)	IS (s)	TD (s)
<i>More</i>	9	155	861.3 (150.7) 710.6-1098.2	0.35 (0.10) 0.22-0.54	0.17 (0.06) 0.04-0.26	0.85 (0.14) 0.66-1.11
<i>Pork</i>	9	155	839.8 (78.3) 710.6-1033.6	0.30 (0.06) 0.22-0.50	0.17 (0.06) 0.04-0.26	
<i>Rororo</i>	9	270	732.1 (172.3) 437.5-904.4	0.26 (0.12) 0.09-0.60	0.16 (0.55) 0.08-0.36	N/A
<i>Trill</i>	9	135	1055.1 (150.7) 861.3-1378.1	0.69 (0.15) 0.41-1.14	1.49 (1.81) 0.40-15.90	N/A

Inter-Syllable Duration

Both *more-pork* and *rororo* calls had very similar short durations between syllables; the inter-syllable duration for the *trill* was much longer (Figure 2.27 c). However, the time duration between *more-pork* calls (which include both syllables) could vary from short to longer periods of time depending on the bout. In this analysis, only the duration between the *more* and *pork* syllable was included. The duration between the *trill*

syllables showed large variation, although it was difficult to determine when a bout finished and another began. All three parameters were found to be significantly different between call types (Table 2.7).

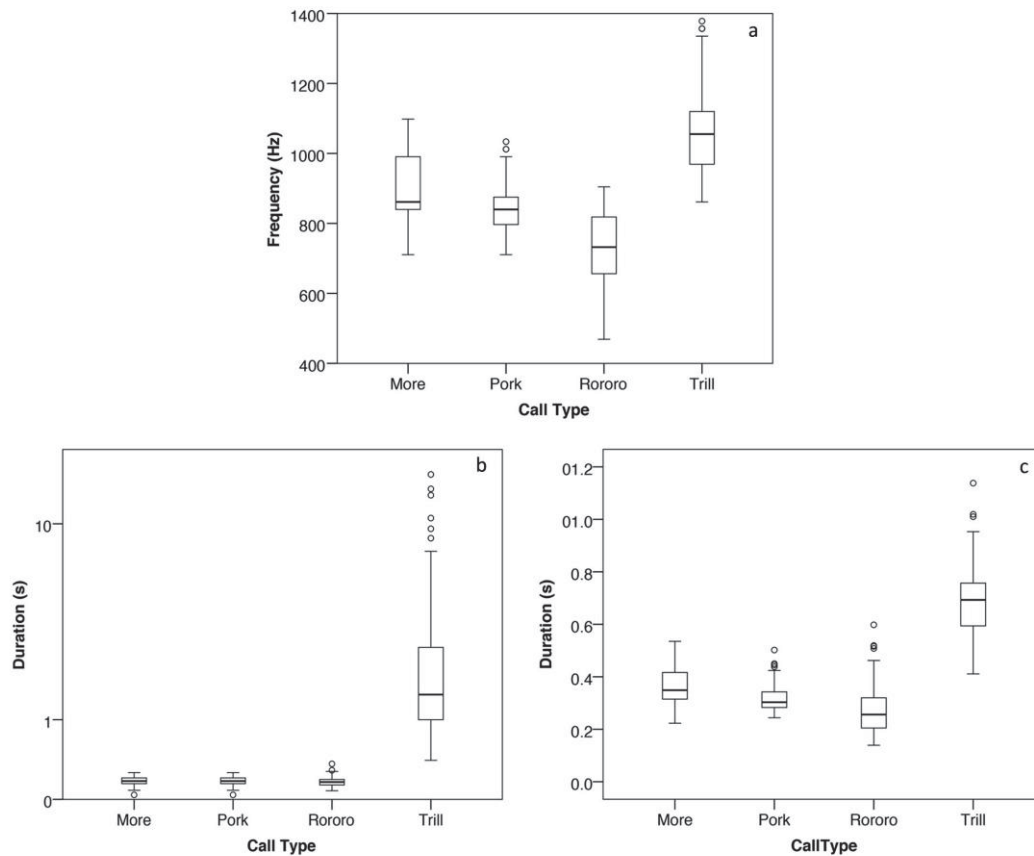


Figure 2.27 Box plots comparing the median values for a) syllable fundamental frequency (Hz); b) syllable fundamental duration (s); and c) inter-syllable duration (s) between syllables. For each of the three call types (four syllable types: *more*, *pork*, *trill* and *ro*). The line within each box is the median and the upper and lower short edges of the box are upper and lower 25% quartiles. The whiskers (lines extending from the box) extend to the largest and smallest unbooked values (neither outlier nor extreme) and the open circles are outlying values.

Table 2.7 Kruskal-Wallis test of the effect of call syllable type on the three response variables: fundamental frequency, fundamental duration and inter-syllable duration.

	Test Statistic	df	p	n
Fundamental Frequency	411.89	3	≤ 0.001	715
Fundamental Duration	423.62	3	≤ 0.001	715
Inter-Syllable Duration	313.06	3	≤ 0.001	675

In pairwise comparisons for each parameter of each call between each individual bird (Table Appendix (A) 1.13) the variation in number of significant differences for each bird appeared to be fairly even across individuals. Although some showed higher

variation in certain call-type's parameters, such as Whisper being different to all eight other birds for *ro* fundamental frequency, when the total number of significantly different pairwise comparisons for each bird was compared, the numbers were fairly similar.

Regarding the syllable types themselves, *ro* seemed to have the highest degree of individual variation (number of significant differences) in median fundamental frequency with over half of the pairwise comparisons being significantly different. Frequency of the *pork* syllable had the lowest variation between individuals.

Individual Variation

The body size of the wild birds did not show strong correlation with the median fundamental frequencies of their four call syllables. Birds with relatively high body-size indices had low frequency calls. However, Macchiato had low median fundamental frequencies for all four syllable types yet had the lowest body-size index (Figure 2.28).

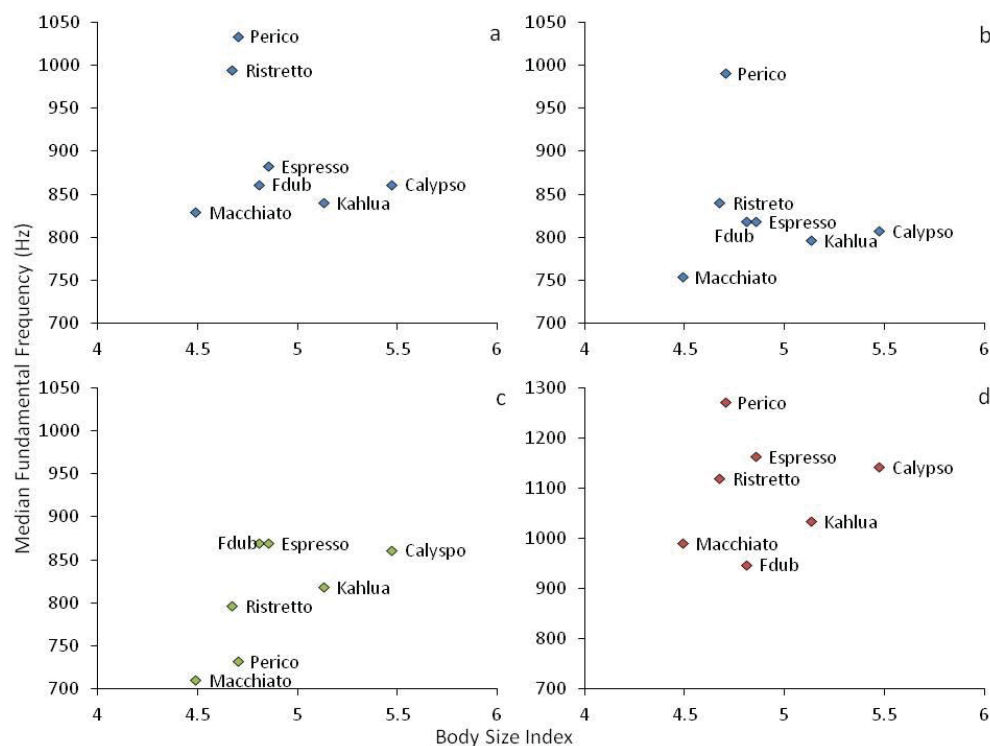


Figure 2.28 Scatter graphs of the body size index (body weight (g) divided by tarsus length (mm)) versus frequency (Hz) of each of the four syllable types per individual morepork a) *more* syllable; b) *pork* syllable; c) *ro* syllable; d) *trill* syllable.

The frequency of each call syllable type per bird was not strongly correlated to body weight either (Figure 2.29) with birds with low weights, for example Fdub and

Espresso, having low frequency syllables, but birds with larger body weights having low frequency syllables too.

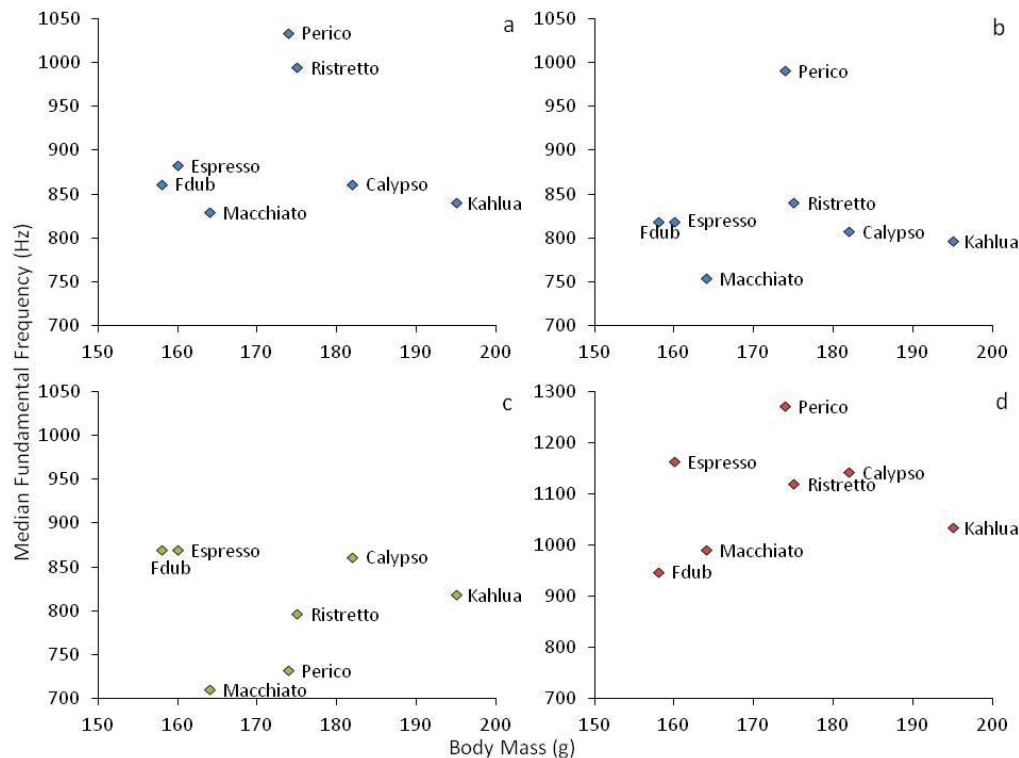


Figure 2.29 Scatter graphs of the body weight (g) versus frequency (Hz) of each of the four syllable types per individual morepork a) *more* syllable; b) *pork* syllable; c) *ro* syllable; d) *trill* syllable.

Discussion

The most important findings in this chapter are that there was a high degree of variation in the temporal and spectral parameters analysed both between call types and between individual birds. These findings suggest that individual morepork may be identifiable by their call characteristics. This was also found in Christmas Island Hawk-owls (*Ninox natalis*) (Hill & Lill, 1998). While no difference was found between the sexes in the spectral and temporal call parameters analysed in this study, the small sample sizes and sex ratio of 2:7 (male:female) do not allow robust conclusions to be made about sexual variation in morepork calls.

The repertoire of the morepork studied on Ponui Island was found to contain eleven call types. This is higher than reported for many other *Ninox* owls, but there is also a distinct lack of repertoire-quantifying studies into *Ninox* owl species. The vocalisations of one *Ninox* owl, the Australian southern boobook, have been studied in more detail than in other *Ninox* species and was found by Olsen et al. (2002a) to have a repertoire

of ten call types. Previous studies on the morepork have reported repertoires of ten and seven calls (Higgins (1999) and Stephenson (1998) respectively). In *N. natalis*, Hill and Lill (1998) identified at least six different call types.

Call Comparisons

The three call types chosen for further analysis were quite different from each other both in terms of what they sound like in the field and their ethology. The fundamental frequencies, duration and inter-syllable durations varied between call types, and also within call types between individual birds.

Individual Variation and Sexual Dimorphism

The individual variation found between birds both within a single call type and across all calls was interesting. My results suggest that individual identification may be possible from both spectral (frequency) and temporal (durations) characteristics of their calls. An owl's call has been compared to a DNA fingerprint because it is inherited and shows little geographic variation across an owl's range (Olsen et al. 2010).

In the spectrograms, individual differences could be seen in the frequency modulation of some of the call types, for example in the *more* syllable. This was also noted in Christmas Island Hawk-owls (Hill & Lill, 1998).

Not only were the different call types spectrally and temporally different from each other, but so too were each bird's calls of each type between individuals. My results suggest that each bird's call fundamental frequency is different depending on the bird, because the bird with the lowest pitched *more* and *pork* syllable (Macchiato) did not also utter the lowest pitch *trill* or *rororo*. Likewise, Perico who had the highest pitch *more*, *pork* and *trill* syllables did not have the highest pitch *ro* syllable.

Previous authors have commented on the potential for sexual dimorphism in the calls of morepork, but I found no evidence of this in my small wild population of Ponui Island birds. Neither was this clear when the two captive individuals (one male, one female) were included in the data set. In comparing the calls of birds within a mated pair, Hill and Lill (1998), however, reported that four of their radio-tracked male birds

gave higher pitched advertisement calls than the female of the pair. What is more apparent though is the individual variation between birds.

A larger sample of males would have provided information regarding the extent of male frequency variations and further, marking both members of a mated pair would have allowed investigation into whether there were pitch differences within pairs. However, my male morepork's calls had frequencies which regularly fell within the females' range suggesting that there may not be pronounced sexual dimorphism in morepork calls. I think that a study with reduced sex bias would be useful, looking in depth at how each sex uses the main call types and the frequency each call is used. This was beyond the scope of my study, but sexual identification may be possible from the way each bird uses certain call types.

Body size, and particularly the common correlation of lower frequency sounds to larger body sizes, has often been discussed as a factor influencing call frequency. My study population – whose weights I measured on capture – did not seem to follow a strong pattern of frequency related to neither body size index nor weight.

If further study (perhaps by discriminant function analysis (Hill & Lill, 1998)) confirms that vocal variation of individual birds permits identification of individuals in the field, future morepork population census efforts could benefit. Census of cryptic birds by individual identification has been suggested by many authors including Otter (1996) whose study of Northern Saw-Whet Owls (*Aegolius acadicus*) found significant variation both spectrally and temporally in male advertisement calls.

Call Repertoire

Morton (1977) outlined a set of motivation-structural rules for calls which can be applied to many bird and mammal sounds. These rules dealt with the expected frequencies and degree of frequency modulation and emphasis which a call structure contained relative to its function, and may enable some inferences into the function of morepork calls when temporal and spectral structures are considered.

Morton (1975) found upper forest birds (n: 17 species) produce sounds with a mean frequency of 2.71 (\pm 5.52 SD) kHz which was higher than lower-forest birds (n: 68),

whose frequency averaged around 1.48 ± 1.39 kHz, but was lower than those of forest edge (n: 71) and grassland birds (n: 21), which averaged 3.69 ± 6.25 kHz and 3.45 ± 5.65 kHz respectively. Morton defined lower forest birds as those which inhabit tree-foliage strata of 6-12 meters and upper forest birds as those which inhabited the tree-foliage strata of 22 to 30 m (Morton, 1975). From this we can expect the morepork calls to be predominantly low frequency, short and simple in order to communicate in a forest environment. I will now explore each of the call types found in this study and how they fit with Morton's ideas.

More-pork

The literature and field observations from this project suggest that the *more-pork* call is primarily a territorial announcement. Morton's (1977) description of longer-distance calls adds evidence to support the longer-ranging territorial function of the *more-pork* call as he described long-distance calls as being harsh, low frequency sounds. While his motivational-structural rules are less applicable to long-distance calls, being more applicable to those used in close contact where sender motivation is influenced by an immediate situation, his description of long-distance territorial calls is closely mirrored by the characteristics of the *more-pork* call.

Lower frequency calls attenuate slower than higher pitched calls (Marler & Slabbekoorn, 2004), so it is reasonable to expect that territorial announcement calls may be optimised to travel further distances than contact calls. Certainly, the *more-pork* call carries well across distance, particularly on clear, calm nights. Across flat pasture, a calling morepork could be heard a kilometre away (Pers. obs., 2014), however, this may be limited in dense bush or forest. Stephenson (1998) reported that the *more-pork* call carried at least 500 metres and this study agrees, however, it will depend on the topography.

The *more-pork* call occurred throughout the year, agreeing with Stephenson's (1998) observations, but its frequency varied between nights, months, and weather types. An investigation into the calling frequency is presented in Chapter Three and found both nightly and monthly variation in calling.

Hill and Lill (1998) described what they termed a *boo-book* call in Christmas Island Hawk-owls which has a high similarity in description to the *more-pork* call of morepork. They state how the second syllable was often lower pitch than the first, which is also similar to the *more-pork* call and that it occurred year-round.

More-more-pork

Stephenson (1998) also defined it as a '*more-more-pork*' call, but only as a variant of the *more-pork* call and not as its own call. Unlike Stephenson, I believe this call has a different function to the territorial *more-pork* call and might be a call used in more aggressive situations. However, the emphasis that the extra *more* syllable adds to the call could also serve as a longer-travelling territorial call. The call has more power and is longer than the disyllabic *more-pork* call. Perhaps these two functions convey urgency and aggression that the *more-pork* call lacks. Hill and Lill (1998) describe how the *boo-book* call in *N. natalis* was often preceded by a quieter hoot, but that these owls could give up to four hoots in a call. This is suggestive of the *more-more-pork* call given by morepork, but like Stephenson (1998) Hill and Lill (1998) seem to class this as a variation of the *boo-book* or *more-pork* call itself. Further investigation into the use of this call would be useful to confirm whether this *more-more-pork* call deserves a call-type of its own.

Rororo

The *rororo* call, has mostly been described in morepork by other authors as a succession of 'more' calls (Stephenson, 1998; Heather & Robertson, 2005), 'por' calls (Higgins, 1999), a 'grumble' call (Fraser & Hauber, 2008), and also 'quork-quork' (Seaton & Hyde, 2013). In Southern boobook it has been called 'croaking' (Olsen & Trost, 1997), and in Christmas Island Hawk-owls it has been named 'por-por' (Hill & Lill, 1998). It is apparent that there are discrepancies between authors as to how this call should be named. I find these names slightly misleading and propose '*ro*' as the syllable and '*rororo*' as the call name. Not only because '*ro*' gives a more staccato quality to the call syllable, but also because of the difference to the *more* syllable spectrographically. Each *ro* syllable is slightly different to each *more* syllable from the *more-pork* call in that the *ro* syllable is often shorter, harsher, less frequency

modulated and often more broadband in its frequency range. Naming it '*more*' implies a longer call than often is the case with the *ro* syllable.

Rororo was not a very common call, but nor was it rare, and it seemed to be strongly associated with aggressive or excited situations where two birds interacted, or where a bird responded to playback (Chapter Four); this concurs with Stephenson's (1998) observations.

As well as the aggressive posturing accompanying the *rororo* call observed in the field, the structural characteristics of the call also hint at its function. Morton (1977) described hostile calls as commonly consisting of low and harsh sounds and the *rororo* call conforms to this rule. He also stated that the harsher the sound, the more aggressively motivated the sender is likely to be. Morton's (1977) reasoning is that these sounds are often proportional to body size and commonly, therefore, dominance. The *rororo* call could play a part in close aggressive interactions between morepork in territorial disputes. My study birds however, did not show strong correlation between body size and frequency of calls, so perhaps body size is less important to aggression of calls in morepork.

The characteristics of the *rororo* call – particularly its rapid repetition and narrow frequency band - can be used to infer that it is a close range call. This inference is supported by Wiley and Richards (1982) findings that sounds with these qualities are not only associated with aggression, but cannot travel far in a forest due to sound degradation.

Trill

This call, or one very similar, has been named many things and without consistency in nomenclature, it is often difficult to know what call type each researcher who uses a different name is referring to. Other names for this call in morepork and boobook are 'purr' (Stephenson, 1998; Olsen et al., 2002a); 'bray' (Olsen & Trost, 1997; Higgins, 1999); 'cree' (O'Donnell, 1980; Heather & Robertson, 2005; Fraser & Hauber, 2008) and 'quee' (Seaton & Hyde, 2013).

Early, and also some more recent, literature reported this call to be a 'hunting call' (Heather & Robertson, 2005), but to my knowledge no explanation has been given in the literature as to how this assists hunting, or why it is associated with hunting. During field observations here, it was difficult to tie this behaviour to the call and further investigation would be necessary to confirm it as a hunting call. O'Donnell (1980) reported only hearing this call in August, September, November, December, February and April, but in this study this call was heard throughout the year (Chapter Three). More recent studies suggest this is a contact call in morepork (Stephenson, 1998) and in Southern boobook (Olsen et al., 2002a).

Regarding activity, it is plausible that this call could be given while hunting, but I propose that it functions more to maintain contact and give location information. Often a trilling bird would call from one tree for some time then move to another tree to resume its calling. It was not heard to be uttered by a bird that was on the wing, which would have been easily heard to decrease in volume as distance from the observer increased (see *Weow*) as the bird changed location, or got nearer or further away from the observer. That is not to say that it is a call never given on the wing as direct observation of the calling bird itself was often difficult.

Due to the sex bias in the study population, it is difficult to comment on whether this call is used more by females than males, as had been reported in some studies. The single, wild, study male, Espresso, was heard to give this call occasionally, which implies that both sexes use it. However, he was not heard to utter it frequently, although this bird was very difficult to track, shifting territories twice (Figure 2.3: white line). This is further compounded by the two observational hypotheses that Espresso may have been either a juvenile still roosting with his mother, Calypso, for half the study period, or that he was Calypso's mate who was deposed by another male in the second half of the study.

In terms of *trill* call context, literature on call structure can be used to back up field observations of this call being used for contact. Morton (1977) described the structure of calls used when animals are near to each other as having a higher frequency and therefore attenuation rate, and being more frequency modulated, two characteristics

not suited to long distance communication. The *trill* certainly is higher frequency and more frequency modulated than *more-pork* and *rororo*, suggesting that it is used for closer range contact between individuals. From Morton (1977) the rising frequency structure (upward slope of the spectrogram) of *trill* calls indicates a call lacking in aggression or fear.

Low Trill

Higgins (1999) reported that females give a low rumbling trill and this is the only call in this review that garnered the name ‘trill’. I feel that while this call could be described as a variant of the higher pitched, more common *trill* call, its less common occurrence and seemingly singular function also means it could be characterised as a call in its own right. I have therefore termed it ‘*low trill*’. Hill and Lill (1998) also describe a female-begging call, ‘chirring’ which had a “bleating” quality and the description of which bears resemblance to what I call the *low trill*. The spectrogram presented by Hill and Lill (1998) only showed a single harmonic, making comparisons with the spectrograms of the morepork *trill* and *low trill* difficult and suggesting that this call was different to the morepork’s *low trill* I describe.

There are names for variations of this call (see Olsen et al. (2002a) in particular). As well as variation between individuals in call frequency, speed, and length, there is also variation in the calls of an individual. This suggests that there may well be individuality or situational context factors causing the calls to vary. Olsen et al. (2002a) classed trills into at least four types: *Purr*, *Bray*, *Trill* and *Growl*. In this project, time was restrictive and it was not easy to observe all behaviours which accompanied many of the calls, or to study a single call in particular detail. I cannot confidently identify differences between *trills*, except for the *low trill* I have described. The *low trill* was distinctively different to the *trill* and could be differentiated by ear in the field. It was not easy to record in the field and consequently I acquired only a very small sample size of *low trill* recordings.

Comparing the three parameters for the two call types, *low trill* and *trill*, using a small sample size, I found that there was a significant difference in both frequency and duration of the fundamental syllable, and also differences in both calls between

individual birds. The small sample size means that further investigation by sampling a larger number of recordings of the *low trill* call would be necessary to establish more confidently whether the *low trill* can be termed a separate call to the *trill*.

Weow

In his analysis of how motivation-structural rules influence animal sounds, Morton (1977) noted that higher frequency, tonal sounds often indicate submission or fear. The application of this rule holds true for the morepork's *weow* call which I commonly heard when a bird was startled and retreating or moving elsewhere. Morton's (1977) list included a rule that the higher the frequency of the call the more submissive or friendly the sender might be. I found a degree of variation between *weow* calls, which suggests pitch may encode more detail about the situation depending on how high-pitched each *weow* call is. The observation of movement away from a stimulus whilst uttering the *weow* call is consistent with Morton's (1977) list that an alarm sound is often accompanied by the individual withdrawing from the stimulus. Morton also describes sounds which have a chevron structure (as seen in the *weow* call, Figure 2.6 e and 2.18), very common in avian call repertoires, indicating a middle ground between hostility and fear, but often associated with indecision.

The alarm or "wek" call of the Stellar Jay (*Cyanocitta stelleri*) is used to signal an intruder and alarming events with a short, sharp, loud succession of calls of a rising and falling chevron spectrographic shape, a structure noted by Morton (1977) as being common in alarm calls of many mammal and bird species. This call is much like the morepork's *weow* call in sound and structure. Marler and Slabbekoorn (2004) discussed how the number and speed of the 'weks' in a Stellar Jay's alarm call vary depending on context, and this is also true of the morepork. On the spectrogram, the *weow* call also forms a steep-sided chevron shape and occurs in quick succession (Figure 2.18). The number of *weow* calls in a bout could vary from a short bout of seven syllables to longer bouts of over 50 syllables, although this was much less common.

The *weow* call has been defined as an alarm call by Stephenson (1998) and Higgins (1999), but the names they used are different. In using *weow*, I have used the closest

phonetic word I could fit to the call. Other names include ‘pew’, however, ‘P’ is a harsh consonant sound that does not appear in the call itself and the verbal emphasis becomes the ‘p’ sound where it should be on the ‘e’. Naming the call ‘weow’ implies the brevity of the call as the ‘w’ creates a boundary around the “eo” sound. A synonym exists in the literature too: ‘whio’ has been used by some authors such as Fraser and Hauber (2008), as well as ‘yeo’, a phonetic version of the call described in Southern boobook as a ‘yelp’ call by Olsen et al. (2002a) which they heard once as a bird left the area.

Copulation Squeal

Higgins (1999) fittingly described this call as a “rabbit-like wavering whistle”. A *copulation squeal* has also been described in Christmas Island Hawk-owls by Hill and Lill (1998). It was difficult to confirm which bird of the pair made the squeal and since not many authors have described this call it is difficult to draw inferences from other *Ninox* owls. Olsen et al. (2002a) suggested that it is the female which makes the squeal in their study of *N. Boobook*, whereas Hill and Lill (1998) also could not confirm which bird, or the pair, made the squeal in *N. natalis*.

In my study, the first recording of this call was on April 29th, 2013, when copulation should, in theory, no longer be happening for breeding purposes because autumn is the start of the non-breeding season. A potential explanation for this occurrence is that the call also doubles as pair-bond maintenance; especially as the call was elicited using a playback call to sample calls of unmarked birds at the beginning of this study. This has been reported by Debus (1996, 1997) as cited by Olsen et al. (2002b), and described as a duet and mating squeal in response to playback, but the time of year of the response was not mentioned. We suggest that this *copulation squeal* could have been a pair-bond affirmation behaviour in response to a foreign morepork calling in that pair’s territory, a behaviour not often reported in birds. It was a response to playback, but not an immediate one. Straight after the playback, the pair engaged in a bout of *rororo* calls interspersed with *more-pork* calls. In my playback experiments (Chapter Four), however, a *copulation squeal* was never heard as a response. This could be due to the different time of year of the playback experiments (November/December 2013 and March 2014), or that the experimental playbacks

were shorter and potentially less offensive. The call used in April 2013 was a 30-second *more-pork* call bout. Other potential reasons for the squeal response in April 2013 could be that extra-pair copulations occur in this population of morepork, this pair was breeding very late, it was juveniles practising copulation behaviour, or that strong selection starts in the non-breeding season and that this population of morepork are only seasonally monogamous.

Juvenile calls: “Chicketting” call and juvenile begging call

Fleay (1968) first described this call as a cricket-like trill and it was also described by Olsen and Trost (1997) as a juvenile begging call with a suggestion the call might develop into what they called the ‘bray’, or the *low trill* I have described. Stephenson et al. (1998) reported a call recorded when handling morepork chicks, which they named as a ‘chick alarm call’ and described as it as a high-pitched trilling which occurred when the chicks were handled. I did not hear a call which I could associate with alarm as the begging trill I heard seemed to occur when a parent arrived at the nest, but not wanting to disturb the nest, this call may also have occurred without the presence of a parent. In Christmas Island Hawk-owls, Hill and Lill (1998) also describe a shrill, trilling juvenile begging call which occurred continuously while young were in the nest and which increased in intensity when a parent bird arrived. This agrees with my observations and those of other studies of morepork and Southern boobook, suggesting that this call is common to most *Ninox* owls.

Single hoot

This is in keeping with Olsen et al. (2002a) who also describe a single hoot given by parent birds when approaching or defending their chicks. Hill and Lill (1998) however, describe a repeated series of *kar-kar* (Figure 1.1 d) in *N. natalis* given by a male delivering food to the nest which more closely resembles the *rororo* call of this study.

Limitations of this study

Night Work

Working alone was a trade-off between only having a single pair of hands, but being able to control disturbance noise, versus working as a pair and making more noise, but being able to simultaneously record high-quality sound, record video, operate the

telemetry gear, and write notes. Perhaps for future field studies a mixture of the two methods would increase the efficiency of sound recording, but still maintain recording quality.

Obtaining a clear observation was often challenging in the dense bush, as described above, due to dense foliage, bird movement, and trying to minimise light and noise disturbance. This needs consideration if future tracking studies into morepork behaviour are to be undertaken. In his telemetry study in 1975, Imboden reported that morepork were highly mobile during the night and that following them on foot proved to be a challenge; birds often traversed the extent of their home range and back several times within an hour, rendering hourly location data of little use. Imboden (1975) also commented on the birds appearing to be disturbed and moving more frequently when followed too intensely. These observations were also made in my study, so future studies may benefit from the use of a transmitter type, such as those used by Stephenson (1998) with an activity sensor to add data where observation is difficult. Also, for behavioural studies, obtaining video was highly challenging for all of the above reasons. The focus of this study was to record the vocalisations and while the original aim was to video behaviour simultaneously, the limitations of working alone often made this impractical.

Analysis

A parameter that was measured but not analysed further was the inter-call duration. It was very challenging to delimit call bouts without a better understanding of call bout duration. It was often unclear whether an extended pause was a pause between bouts, or simply a pause between calls of the same bout. More time would need to be spent in the field focussing on bout lengths. It also appeared to me that inter-call duration seemed to vary depending on situation and may have been influenced by other factors such as audience – the presence or absence of other birds, the motivational state of the bird, and also researcher presence. Often recordings would miss the first part of a bout, or a bout may be cut short due to the arrival or presence of a researcher.

Future study

I was limited by sample size in making inferences into the calling behaviour of morepork as a whole species, as well as by the nature of New Zealand bush where density combined with the cryptic nature of morepork often impeded visual observations. In addition, visual identification was often difficult. With the study depending on quality sound recordings, disturbance of a calling bird had to be minimised. Reliance on a single telemetry receiver without often achieving visual confirmation reduced the certainty of individual identification. While the results of my study suggest there is individual variation between individual's calls and that there is a lack of sexual dimorphism, further study to confirm this at other sites using more birds would increase the confidence of these conclusions. Also, given the challenges of sound recording in dense bush, further studies into vocal identity and sexual dimorphism should consider using more than one researcher and triangulation methods with two radio-telemetry sets to enable higher certainty of caller-identity.

While my study provides a base on which to build, defining a complete repertoire for morepork would require a considerably longer study time. In addition, confirmation that the calls heard in this study all occur elsewhere in New Zealand would be required, and the inclusion of any calls which occur elsewhere, but not on the island from multiple study sites. A very important outcome of this study is the production of spectrograms of all but one of the morepork's calls on the island. From a comparative view point, spectrograms produced via sound recordings of calls from which spectral and temporal characteristics can be measured constitutes one of the only methods with which to compare calls between individuals, regions and species.



Chapter 3 - Temporal Variation in Calling Behaviour of Morepork

Investigating temporal (annual and diel) variation in morepork calling behaviour via automated sound-recorder surveys and sound-analysis software.



If you go owling

You have to be quiet

(Yolen, 1992)

Abstract

Automated recordings were made for 12 months from April 2013 to April 2014 to detect temporal variation in morepork calling both across the night and over a year. A subsample of the large number of recordings was analysed comprising one night of 14 hours for each of the 12 months at five different sites. Number of calls varied significantly across months. A low amount of calling in winter compared to summer appeared to coincide with the morepork breeding cycle that runs from September to February. Call number peaked from November to January and was lowest in February when some of the study birds still had dependent chicks.

The number of calls per hour after sunset varied significantly with peaks around the middle of the night and in the last hour of darkness. The number of calls heard in the first two hours after sunset were significantly lower than during the rest of the night. Information on temporal variation in calling behaviour provides useful knowledge on the behavioural ecology of morepork, and may also be of use in the planning of bioacoustic surveys of morepork by providing information on the optimal time of night and year to sample morepork calls.

Introduction

Types of Temporal Variation

Bird vocalisations are one of the more common behaviours investigated for temporal variation. Temporal variation in a biological context refers to patterns in behaviour that are related to the passage of time or a specified time period. This chapter focuses on two types of temporal variation: nightly (diel) and monthly (annual).

Monthly (annual) Variation

The information encoded in bird calls plays key roles in important aspects of the bird's life, territoriality and breeding in particular. Calling behaviour may change across a year due to both physiological and environmental factors that vary seasonally.

Nightly (diel) Variation

Variation in calling behaviour of nocturnal species on a nightly basis not only shows whether calling variation has a pattern or is random, but also offers insight into the less easily studied behaviours of cryptic species. For example, time budgets, feeding, and interactions between individuals. Calling behaviour across the hours of the night is influenced by ambient conditions such as temperature, moonlight, and weather.

Factors Influencing Calling Behaviour

Numerous factors can influence calling behaviour of both diurnal and nocturnal species and include motivational states, foraging efficiency, breeding stage, social context such as age or dominance, population structure and density, prey availability, weather, temperature, and microclimatic factors. Many studies have investigated the influence of these factors on calling behaviour, both in diurnal and nocturnal species. Examples of studies on nocturnal species include owls (Ritchison et al., 1988; Morrell et al., 1991; Clark & Anderson, 1997; Martinez & Zuberogoitia, 2003; Penteriani et al., 2011; Mori et al., 2014), and kiwi (Corfield, 2005; Hojem, 2006; Digby et al., 2014). One factor that is specific to nocturnal species is the light variation across a night from the moon, and also anthropogenic sources of light which may influence variation in behaviour.

Moonlight affects predator-prey interactions and can make it difficult to decipher reasons for some activity patterns. For example, an increase in moonlight may cause increased shelter-seeking and vigilance in prey species, so while prey is more easily spotted in increased light, predators must spend more time hunting due to the lunar-phobic behaviour of many prey species (Penteriani et al., 2011). In this way, the amount of time predators spend calling may be reduced. Moonlight may also increase predator activity directly because the increase in ambient light may assist foraging, again reducing the amount of time that a predator spends calling. Interestingly, some owls use visual communication despite being mostly active in darkness, for example breeding Eagle Owls (*Bubo bubo*) use their bright white neck feathers to visually enhance vocal displays (Penteriani et al., 2010).

Weather can also strongly influence vocal displays. Morrell et al. (1991) found that Great Horned Owls (*Bubo virginianus*) called most in the early morning when temperatures were coolest and when there was the least wind, probably because their calls would attenuate less. The breeding season also had an effect on the calling activity of Great Horned Owls (Morrell et al., 1991).

Territoriality is often one of the key motivators behind announcement calls. Territorial calling is a trade-off of costs and benefits to the individual. It requires time and energy to give advertising call bouts which can be long, taking time away from hunting and feeding. Conversely, advertisement calls are important for maintaining territory boundaries and forming and maintaining pair bonds. Because of these costs and benefits, Martinez and Zuberogitia (2003) suggested that in Eurasian Eagle Owls (*Bubo bubo*) energy input into territorial calling depends on the presence of conspecifics. This could result in monthly temporal variation in calling behaviour depending on when in the year conspecifics are more likely to be looking to dispute a territory or find a mate; for example, during the breeding season. Calling rate of Eagle Owls was also found to be influenced by age, sex, and density of Eagle Owls as well as prey-density (Martinez & Zuberogitia, 2003)

Digby et al. (2014) found that Little Spotted (LS) Kiwi (*Apteryx owenii*) calling rate varied over the year and across a night (with sex-specific variation), correlating with

the onset of the breeding season in males (increased) and the end of the breeding season in females (increased). The nightly calling rates were found to peak in the first third of the night for both sexes. They also found LS kiwi calling rate was influenced by weather of all types, with call rates decreasing when temperature, pressure, cloud, wind, and rain increased and increasing when humidity and ground moisture increased. Unlike the study by Penteriani et al. (2011) of Eagle Owl vocal activity which found a strong influence of moonlight, Digby et al. (2014) found no influence of moonlight on Little Spotted Kiwi vocalisations.

Changes in season, micro-climatic factors such as weather and humidity, and moon-phase can all influence the behaviour of nocturnal animals across the year. Patterns within a night can also occur and Clark and Anderson (1997) stated that most owl species show a biphasic pattern in calling behaviour that peaks once within three hours of sunset and once more closer to dawn.

This chapter investigates temporal influences on the vocalisation behaviour of morepork both at annual and diel levels.

Morepork Calls

The New Zealand morepork (*Ninox novaeseelandiae*), like most *Ninox* owls, has a disyllabic call. The morepork's call is one of the most recognisable nocturnal bird sounds in New Zealand and accounts for its common name. The morepork's call repertoire extends beyond the well-known "*more-pork*" call to include at least six other call-types (not including its two juvenile calls), namely a *trill*, *low trill*, *rororo*, *weow*, *more-more-pork* and a *copulation squeal*. The detailed descriptions and spectrograms of these are presented in Chapter Two.

Both territoriality and breeding cycle are likely to be key influences of morepork calling behaviour. Morepork are nocturnal, territorial and non-migratory (Stephenson, 1998; Konig et al., 1999; Higgins, 1999; Haw et al., 2001). They are territorial throughout the year, favouring specific parts of their home-range and defending their territories with vocalisations and aggressive behaviours (Stephenson, 1998). The morepork breeding season lasts from September to February with egg-laying occurring around the beginning of October (Stephenson, 1998; Higgins, 1999). Imboden (1975) reported an

increase in calling just before the beginning of the breeding season, around the end of August and early September, as well as calling episodes during late afternoon before dark early in the breeding season.

With no published studies to date focussing in detail on the calling behaviour of the New Zealand morepork, much of the knowledge about their vocalisations is inferred from studies of their close relative the Australasian Southern boobook (*Ninox boobook*) (Olsen & Trost, 1997, 2007; Higgins, 1999; Olsen et al., 2002a, 2002b, 2010, 2011; Olsen, 2011), mostly from extensive listening and observational surveys.

Studying Temporal Variation

Two common methods used to study calling behaviour and aspects of it, such as temporal variation in calling, involve either manual listening call surveys or monitoring using automated sound recorders. The former is a well-established, widely used method whereas the latter has, until recently, been less used.

Manual Call Surveys

Manual call surveys involve researchers or volunteers listening to and writing down the calling behaviour of the target species. This method is well established as an owl survey technique which can involve: actively following the owl using radio-telemetry techniques (in Eastern Screech Owls (*Otus asio*), Ritchison et al. (1988), and Eagle Owls, Penteriani et al. (2010, 2011)), passively observing at listening stations; or moving along transects (with Long Eared Owls (*Asio otus*), Boreal Owls (*Aegolius funerus*) and Northern Saw-whet Owls (*A. acadicus*) Clark & Anderson, 1997, and Eagle Owls, Martinez & Zuberogoita, 2003). In New Zealand, call surveying is a key monitoring technique used in the conservation of many elusive bird species, including the five species of Kiwi (*Apteryx* spp.) (Digby et al., 2014), Australasian bitterns (*Botaurus poiciloptilus*) (O'Donnell et al., 2013), and Weka (*Gallirallus australis grey*) (Castro et al., 2000). It has also been used in a study of morepork abundance in urban areas (Morgan & Styche, 2012).

Automated Sound Recorders

Automated sound recorders remotely record and store sound in the field and can be programmed to record at certain times and for certain durations (Rognan et al., 2012).

They can greatly increase effective field survey effort and site coverage due to the ability to operate automatically (Steer, 2010), but have not yet been used extensively due to the relatively young nature of the technology. Until recently, the use of such machines was limited by the cost, battery life and file storage capabilities. With specific reference to New Zealand, Steer (2010) identified a lack of personal computers capable of handling large data files and the difficulty inherent in analysing such files as additional reasons for the slow uptake of the automated recorder technology. Recent technological advancements have made automated sound recorders far more accessible and they now offer a powerful monitoring tool to both academia and biodiversity monitoring. Rognan et al. (2012) reported that the low-frequency and far-carrying characteristics of many owl vocalisations make them ideal for studying and monitoring using automated sound recorders. This technology has been used to study the calling behaviour, including temporal variation, of a range of bird species including Little Spotted Kiwi (Digby et al., 2014), Brown-throated Wrens (*Troglodytes brunneicollis*) (Sosa-Lopez & Mennill, 2014), and Great Gray Owls (*Strix nebulosa*) (Rognan et al., 2012).

Sound Identification Software

Automated sound recorders can produce a large volume of raw data in the form of long sound recordings. While the recorder reduces the time the researcher spends in the field, a new challenge arises in how to process the large data sets. There has been an increase recently in the development of software to automatically process, analyse sounds, and count calls from large sound recording files and there are many complex methods by which this is achieved (reviewed in Brandes, 2008).

Applications of Vocal Temporal Variation Knowledge

Investigating how vocal behaviour varies over time not only increases our understanding of the communication behaviour of vocal species, but can also inform us about hunting, habitat bioacoustics, vocalisation functions, and seasonal behaviour, such as reproductive season and territoriality. Hypotheses into call function, for example, can be facilitated by knowledge of timing. If one call is more often heard within the breeding season than at other times of year, it likely has a role in the breeding ecology of the animal. Ritchison et al. (1988) found that Eastern Screech Owls

displayed seasonal variation in spontaneous vocalisation and they used this variation to infer call function. In addition, Penteriani (2002) discussed how seasonal and diel variation in calling can also be useful to infer temporal patterns in behaviours other than communication, such as feeding, reproduction and territoriality which may otherwise be difficult to study in cryptic species. In song-birds, in particular those in temperate regions, the seasonal correlations of increased singing occurred with the onset of the breeding season, with increased territoriality, and mate attraction is a well-studied phenomenon, reviewed by Catchpole and Slater (2008).

Behavioural knowledge of how vocalisations vary by time of year or night can inform the development of conservation strategies. Marler and Slabbekoorn (2004) discussed how the acoustic ecology of a species can be important to conservation of that species, other species and ecosystems as a whole. Some of these applications are also true of temporal variation studies. Many owl populations, given the challenges of surveying nocturnal cryptic birds, are estimated and monitored using call surveys (Mori et al., 2014). The relationship between time of night or time of year and owl calling behaviour can be critical to the accuracy of such surveys (Clark & Anderson, 1997). For example, if call surveys are used to investigate the abundance and density of a species, and if there is temporal variation in calling behaviour in that species, this might have an effect on detect-ability. Depending on when in the year the surveys are conducted, temporal variation could be a source of bias in estimates of numbers and would need to be considered. The better the knowledge of the calling behaviour of a species, the more effective the conservation strategies stand to be. Knowledge of whether and how their vocal behaviour varies temporally is fundamental to further study the environmental factors that may affect calling behaviour; surveys can then be planned accordingly to avoid estimation errors (Clark & Anderson, 1997). Data and knowledge from studies of temporal variation in calling can be used for improved census techniques as well as monitoring habitat health by using vocal species as biodiversity indicators. Techniques used in these studies, such as automated sound recordings and automated species call recognition, also have important conservation applications in population monitoring (Marler & Slabbekoorn, 2004).

Aims

The aim of this study was to ascertain whether the occurrence of the three main calls of the morepork (*more-pork*, *trill* and *rororo*) show temporal variation both across a night (per hour) and across a year (per month).

Hypotheses

Based on our knowledge of the calling behaviour of the morepork's closest relative, the Southern boobook, I hypothesised that:

1. Calling behaviour in morepork would show variation between months over a year.
2. Calls would have a reproductive function and an increase in calling would be correlated to the onset of the breeding season.
3. Calling would vary according to time of night.

Methods

Study Site

Automated sound recorders were used to collect a monthly sample of whole-night recordings from which to study the number of calls of morepork. This was conducted in the southern half of Ponui Island (36° 55' S, 175° 11' E) in the Hauraki Gulf of the North Island of New Zealand for 12 months from late April 2013 to April 2014. This included the breeding season (September to February) and non-breeding season (March to August). Nine recording sites (Figure 3.1, Table 3.1) were used: sites 1-5 were located in three forested gully systems (Pipe Gully, Red Stony Hill Gully (RSHG), Kauri Gully, and Pohutukawa (PK) Gully) on the island; and sites 6-9 were out in pasture and wooded outcrops of the farmed area of the island. These sites covered varying habitats, including dense forest, scrub, swamp and open pasture, in an effort to representatively sample the whole study site.



Figure 3.1 Automatic Sound Recorder (SR) locations on South Ponui Island, Hauraki Gulf, New Zealand. Plotted using Google Earth.

Table 3.1. Automatic sound recorder sites, habitat and GPS coordinates (S;E).

Site	Site Name	Habitat	GPS (S;E)
1	Pipe Swamp	Scrub and Raupo swamp	36°53'01.0"; 175°11'28.8"
2	Pipe Forest	Podocarp-broadleaf forest	36°52'57.3"; 175°11'12.2"
3	RSHG Swamp	Manuka scrub and swamp	36°53'11.4"; 175°11'16.5"
4	RSHG Forest	Podocarp-broadleaf forest	36°53'05.6"; 175°11'04.1"
5	Kauri Forest	Kauri-broadleaf forest	36°53'07.5"; 175°10'47.6"
6	PK Gully	Pohutukawa outcrop	36°53'13.3"; 175°11'1.6"
7	Woolshed Hill	Manuka and Kanuka scrub over Raupo swamp	36°53'29.2"; 175°11'10.9"
8	Orchard/Camp Hill	Kanuka scrub surrounded by pasture	36°53'43.0"; 175°11'23.4"
9	Cottage Paddock	Pasture, box-thorn and pine trees	36°53'37.8"; 175°11'13.6"

Automated Sound Recordings

Three automated sound recording devices (Song Meter 2+, Wildlife Acoustics Inc., Concord, Massachusetts; Figure 3.2) were deployed in the field to record sound across whole nights for nine nights in each month (three nights at each of three sites) in positions close to known morepork territories (Figure 3.1). The length of each night's recording session was 14 hours, from 17:00 through to 07:00, and this stayed constant throughout the 12-month study. A reconnaissance trip to the study site to investigate optimal recording sites took place early in 2013 and involved walkthroughs at night of suspected appropriate sites to survey for morepork presence.



Figure 3.2 Automated Sound Recorders (ASR) (Song Meter 2+, Wildlife Acoustics), set up and data downloading procedure. From far left: Field laptop and internal view of ASR; second from left: close-ups of ASR; second from right: ASR deployed on tree; far right: netting and rope securing ASR to tree and information on flagging tape.

The Song Meter 2+ (Figure 3.2) comprises of a weatherproof plastic box housing the recording device's circuit board, four D batteries, and SD memory card slots with two weather-proof stereo microphones attached externally in opposite directions. This was secured to a tree with elasticised rope around 2 m above the ground during the day of the first night of the three nights at each site. The time of placement varied from morning to just before dark en-route to a manual recording session (Chapter Two). When possible, the devices were collected at the end of each three night period and the data transferred to an external hard drive. The capability of the devices to store up to a month's worth of nightly recordings (four memory card slots able to support a 32 Gigabyte (GB) SD card each), and with 14-hour recordings totalling 3 GB per night, allowed for one 32 GB card to be put in each device. Sound recordings were saved as two 16-bit .WAV files per night, one of 2 GB and the other of 1 GB, as 2 GB was the maximum file size the machine saved.

Data processing

The sampling rate gave a cumulative total of over 4,000 recording hours and made manual analysis of the recordings impractical. This meant that automated software which could process and analyse large amounts of sound data at a time needed to be investigated. It was decided, with advice from a sound engineer (N. Priyadarshani, Pers. comm., 2014), that SoundID (Boucher et al., 2003) would be the most effective automated sound recognition software to use.

Even with automated software, processing such a data load would have been very time consuming, with more active involvement with the software required than was anticipated. I therefore sub-sampled the data. During data collection it became apparent that certain sites suffered from more interference – weather, human, and farm animal noise – than others, so the five best sites for recording quality of the nine used were selected for analysis with SoundID, which corresponds to the first five sites listed in Table 1.

Adobe Audition (Version 2014.2, Adobe Systems Inc., 2014) on a Mac computer was used to stitch together sound recording segments from each night. This addressed the problem that the sound recorder cut off a recording once it had filled a 2 GB file, but this occurred at an arbitrary time of the night (02:19:20 most often), resulting in two recording files – one from 17:00 to 02:19 and the other from 02:19 to 07:00. Nineteen minutes were cut from the first recording and attached to the second recording to yield two recording files that could easily be cut into hour-long chunks. This file size was deemed both the most manageable size for SoundID and for further analysis as the call recognition output data would already be split per hour of the night. SoundID has a module whereby large sound files can be cut into specified lengths. These files from Audition were split by SoundID's 'File Cutter' module into hour-long files.

Night-length Correction

Since recording time (14 hours) remained unchanged throughout the 12 months of sampling with recording beginning at 17:00 each night, recordings began in daylight during the months of summer. To correct for night length, any hour of a recording that

occurred in daylight was removed using sunset times to the nearest hour. This changed the data set to hours after sunset instead of clock hours.

Call Identification Software

Sound ID Software

SoundID has a professional version that is capable of running batches of recordings i.e. processing many sound files one after the other in one go. Unfortunately, running so many sound files as a batch on one computer requires a large amount of RAM (Random-access Memory) which many personal computers lack. SoundID was therefore installed onto 12 computers in Massey University's AHC1.04 computer laboratory and these were used to run a whole month's worth of recordings each. Each month's worth (5 sites x 14 hours = 70 files) of sound recordings took five hours for SoundID to process on these computers with 8GB RAM. By using one computer per month, a 60-hour job for a single computer was reduced to five hours with 12 computers.

SoundID requires optimisation before it can be used to run its recognition module on sound files to count calls. SoundID works by using a set of pre-isolated call examples, "references", which it tries to match via algorithms to sounds within a given file. These references were isolated from both manual sound recording files (see Chapter Two for methodology) and automatic sound recordings. The references were very small sound files of individual syllables, with 50% of the syllable length of silence either side of the syllable, which were cut from their original sound file using RavenPro and saved as 16-bit .WAV files. Only the three main call types (four syllable types); *more-pork* (divided into the two component syllables), *rororo* and *trill* were used as references. Training of SoundID for the purposes of this chapter was conducted by Nirosha Priyadarshani, an engineer pursuing a PhD in automated avian song recognition at Massey University.

Raven Pro Software

RavenPro (Version 1.4, Cornell Laboratory of Ornithology 2011, Ithaca, NY, USA) sound analysis software was used to verify some of the results produced by SoundID. The hour-long recordings were opened in Raven and scanned visually to count the number of syllables that occurred that hour. Once a call was found, parameters such as call

type, number of syllables, bout start and finish times (according to sound recorder), length, quality 1-3, distance, and comments were recorded.

Data Analysis

Microsoft Excel (Microsoft Corporation, 2007) and the statistical software SPSS (Version.22, IBM, 2013) were used to process and analyse the data. The raw data were copied from the SoundID output .txt file into an Excel spreadsheet and macros were written to remove the text prefixing each output value. As well as an output file for each hour, by organising the 5 sites' recordings from each month to run in the same batch on SoundID, an index file containing a summary of each hour's recording at each site was produced for each month. This meant that only 12 .txt files needed to be pasted and processed into Excel.

Statistical Analysis

To gain a representative sample of calling behaviour from the study site, it was necessary to use different sites as well as habitats. The sites of each sound recorder (Figure 3.1) were unlikely to have sampled the same individuals due to the topography, vegetation obstacles and distance between the sites, so each site was assumed to be independent. The data from the five sampling sites were investigated and site was found to have an effect. The sum of the data from each site was used there-after to investigate the effect of month and hour after sunset without the influence of site. This was because the focus was to obtain a representative sample of the study site as a whole; investigation into the effect of habitat at each site was beyond the scope of this thesis.

The data were not normally distributed and so were analysed using a generalised linear model (GLM) that took account of this. The GLM was constructed using the summed data for the five sites (giving a single value per hour after sunset each month) using SPSS. As the data were count data, we used a Poisson distribution with a Log-link function. Given the difference in night length between the months of autumn-winter (Apr/May 2013 to Sep 2013 and Apr/May 2014) and spring-summer (Oct 2013 to Mar 2014) months, the data were split and GLM constructed for each sub-set of six months to investigate any effect. The dependent variable was the total number of syllables,

and month and hour after sunset were the factors. The factorial model was selected to include interactions between factors and pairwise comparisons between month ($n = 12$) and hour after sunset ($n = 14$); both factors were conducted using sequential Sidak adjusted tests (SPSS output can be found in Appendix 2). When the more conservative sequential Bonferroni adjustment was made to the GLM, the results were identical to those of the model constructed with the sequential Sidak adjustment, so the results of the latter are presented.

The graphs were plotted using the unweighted means (Estimated Marginal Means in SPSS) (Appendix 2) calculated by each of the GLMs. The Estimated Marginal Means of a GLM in SPSS display the mean response for each factor, adjusted for any other variables in the model including unequal sample sizes and covariates. These means therefore reflect the model rather than the raw data.

Results

Monthly (Annual) Variation

Morepork called in almost every night sampled throughout the year and there were significant differences in the number of syllables between the months (Figure 3.3; Wald Chi-square 1493, df: 11, 156, $p \leq 0.001$). All months except August 2013 and December 2013 were significantly different from the others (Table 3.2). The mean number of syllables from the beginning of the study in April-May 2013 through to October 2013 stood between 100 and 150 per month (Figure 3.3). The most striking change in syllable numbers occurred in November 2013 when the number of syllables rose to an average of $226.3 (\pm 4.3)$. Calling dipped slightly in December 2013 (158.1 ± 3.8), rising in January 2014 (171.7 ± 3.8) which saw the second highest mean number of syllables. Calling dropped off sharply into February 2014 (60.3 ± 2.3) which had the lowest number of syllables. Calling then rose again towards April-May 2014 to similar levels to the previous year (Table 3.2.).

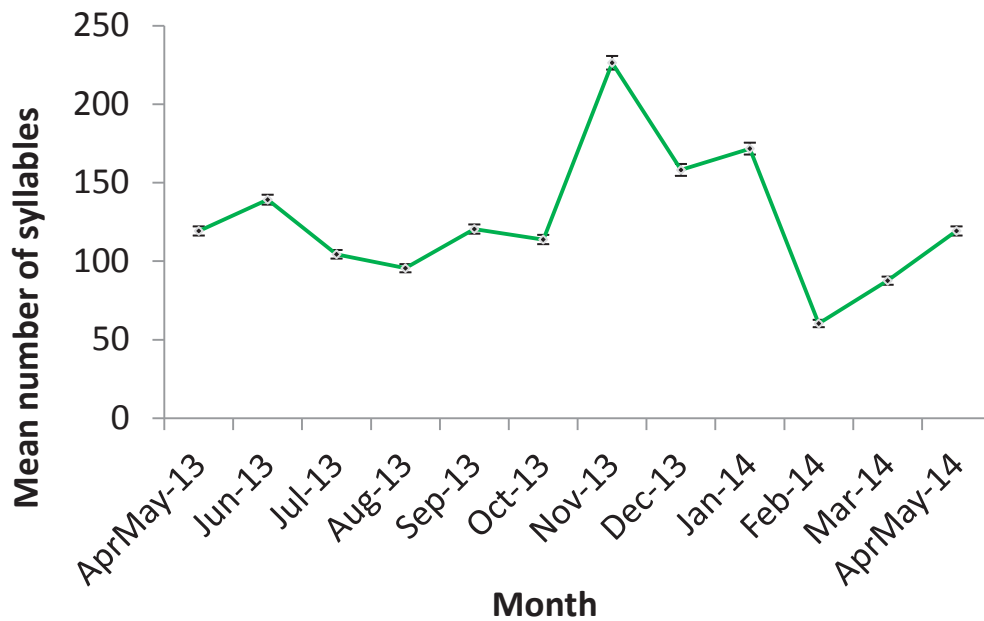


Figure 3.3 Mean number of call syllables per night for each month with standard error bars.

Table 3.2. p-values from pairwise comparisons of the sequential Sidak post hoc test between the 12 months (significant values in bold).

	Apr13	Jun13	Jul13	Aug13	Sep13	Oct13	Nov13	Dec13	Jan14	Feb14	Mar14	Apr14
Apr13		≤0.001	0.002	≤0.001	0.988	0.651	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	1.000
Jun13			≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.002	≤0.001	≤0.001	≤0.001	≤0.001
Jul13				0.159	0.001	0.159	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.002
Aug13					≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.195	≤0.001
Sep13						0.503	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.988
Oct13							≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.651
Nov13								≤0.001	≤0.001	≤0.001	≤0.001	≤0.001
Dec13									0.107	≤0.001	≤0.001	≤0.001
Jan14										≤0.001	≤0.001	≤0.001
Feb14											≤0.001	≤0.001
Mar14												≤0.001
Apr14												

Nightly (Diel) Variation

In morepork calls across a night there were significant differences in number of call syllables recorded per hour of the night (Figure 3.4; Wald Chi-Square: 1447; df: 13, 156; $p \leq 0.001$). Hour 1 (Mean = 67.0 ± 2.5 S.E) and hour 2 (82.0 ± 2.6) were the hours after sunset with the lowest mean number of syllables (Table 3.3 and Appendix 2). There were two peaks of calling activity in hours 5 to 6 (187.6 ± 4.0 and 160.0 ± 3.7 syllables respectively) and hour 14 (216.5 ± 6.0) after sunset which had the highest mean number of syllables. There seemed to be a plateau in mean syllable numbers from hours 7 to 10 and then another flattened grouping of lower means through hours 11 to 13 (Figure 3.4). On further investigation of the sound recordings of the 14th hours, the high count of hour 14 was found to be due to a very close, extended

exchange of *more-pork* calls between at least two birds during April-May 2013. This was an unusually high count of 468 which may have skewed the data point for that hour. If the skewing is removed, the point remained high, but with a less steep increase from hour 13 to 14 (166.2 ± 5.8), so the outlier was left in figure 3.4.

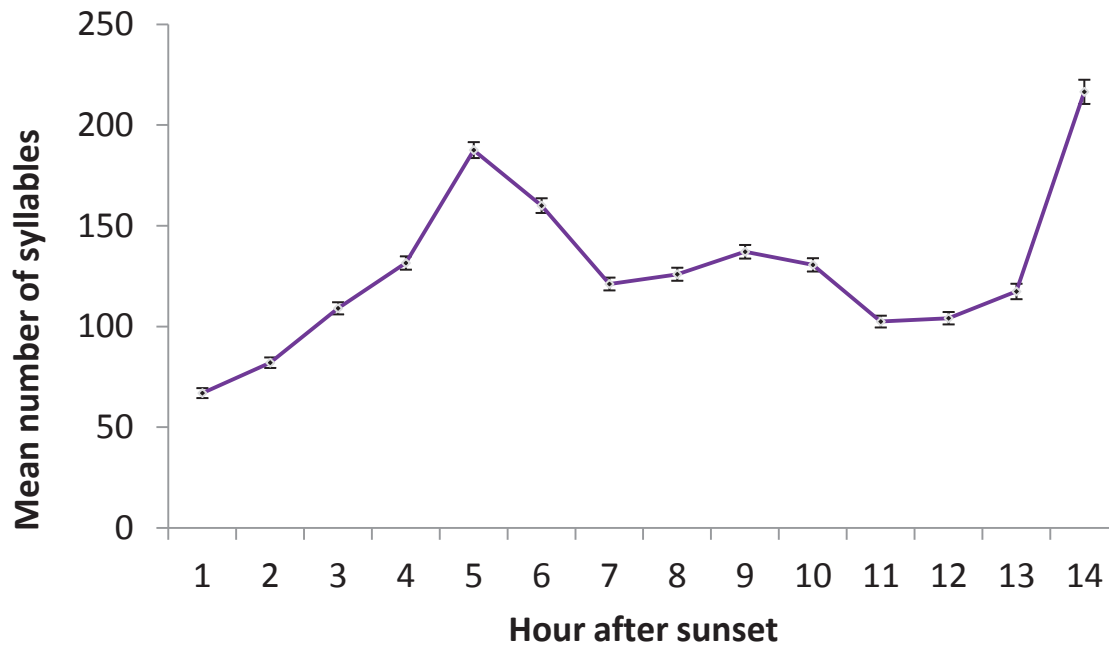


Figure 3.4 Mean number of call syllables in each hour of darkness with standard error bars.

Table 3.3 p-values from pairwise comparisons of the sequential Sidak post hoc test between the 14 hours after sunset (significant values in bold).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1		0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001
2			≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001
3				≤0.001	≤0.001	≤0.001	0.099	0.003	≤0.001	≤0.001	0.711	0.874	0.659	≤0.001
4					≤0.001	≤0.001	0.280	0.874	0.874	0.906	≤0.001	≤0.001	0.096	≤0.001
5						≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.001
6							≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001
7								0.874	0.012	0.396	≤0.001	0.003	0.874	≤0.001
8									0.228	0.874	≤0.001	≤0.001	0.659	≤0.001
9										0.810	≤0.001	≤0.001	0.003	≤0.001
10											≤0.001	≤0.001	0.134	≤0.001
11												0.906	0.037	≤0.001
12													0.110	≤0.001
13														≤0.001
14														

When the 12 months were split into seasons for hour after sunset, the means (Figure 3.5) showed a similar trend to Figure 3.4 with relatively low calling in the early hours of

the night, rising to a peak around five hours into the night, and then decreasing before a peak in the last hour of the night. There were visual differences between the two seasons, including the trend seen in the monthly data that morepork called more in the summer months. Mean number of syllables in hours 11 to 13 showed opposite trends in winter months (Figure 3.5a) compared to summer months (Figure 3.5b). Both data sets showed high amounts of calling in the final hour of the night.

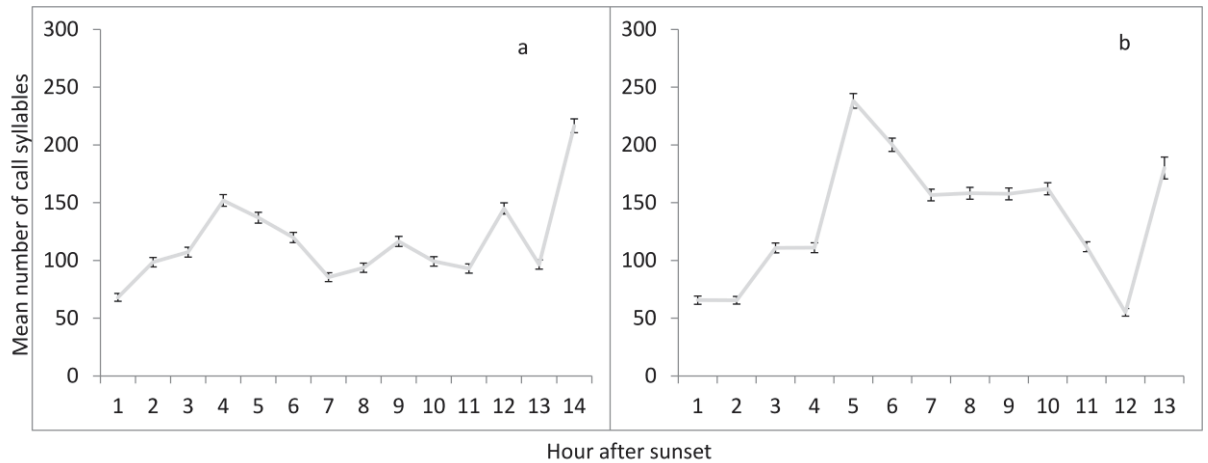


Figure 3.5 Mean number of call syllables in each hour of darkness for each half of the year: a) autumn-winter and b) spring-summer, with standard error bars.

Both month and hour after sunset were found to be good predictors of the number of call syllables heard (Appendix 2; Month, Wald Chi-square 1493, df: 11, 156, $p \leq 0.001$; Hour, Wald Chi-Square: 1448; df: 13, 156; $p \leq 0.001$).

Discussion

While morepork called throughout the year and in each hour of the night, there were significant peaks in calling activity in both temporal periods. Another important finding was that using automated sound recorders proved to be a very efficient, powerful data collection tool that provided a great amount of useful raw data.

Monthly Variation

The mean number of morepork call syllables showed significant differences between months, which were most apparent in November and January with high amounts of calling activity. The most likely explanation for the differences between months - the low calling activity in the winter months and the increase in calling activity in early summer - is the morepork's breeding cycle. The three months of November 2013 to January 2014 all had significantly higher calling than any other months, which coincides with the middle of the breeding season (September to January). Most *copulation squeals* (Chapter Two) were not heard until late September and were heard into November. No nesting behaviour was observed on the island before December 2013, and no chicks were heard or seen before January 2014. My trips to the island, however, did not span entire months, so I may have missed events. The morepork breeding season is accepted to begin in September and has been reported to continue through to May with egg-laying being reported from September to February (Seaton & Hyde, 2013). The Ponui morepork appeared to breed in the latter half of the breeding season 2013/2014. When counting Eurasian Scops Owls' spontaneous calls, Mori et al. (2014) found that calling activity was greater during the breeding season than during the non-breeding season.

Calling activity was low in February 2014. This is still the breeding season and two of my radio-tagged birds still had chicks late into February 2014, one pair probably not fledging until early March, which could have meant that adult birds were more preoccupied with feeding chicks than calling to maintain pair bonds or attract a mate. From March 2014 into April 2014, towards the end of the breeding season and beginning of the non-breeding season (April/May), there was an increase in calling which could be related to juveniles leaving their natal territory and adults re-

establishing non-breeding territory boundaries. An increase in calling for this reason was suggested to occur in Eastern Screech Owls by Ritchison et al. (1988).

The decrease in calling to a plateau during the winter months from June 2013 to September 2013 corresponded with the non-breeding season, but could also be indicative of reduced prey availability during the colder months. Vocalisations can be a physiological indicator of body condition and resource availability as the greater the success at hunting, the longer a bird might be able to spend vocalising. Denny (2009) found on Ponui Island that relative abundance of invertebrates (measured by pitfall and interceptor traps) and small bird species (from five-minute bird counts) both showed a peak in numbers during the summer months, especially November and December, but extending into March, and that these numbers were higher than those of winter months such as August.

The data acquired from long-term sound recording with a view to temporal variation analysis would benefit greatly from further years' data collection because drawing conclusions about monthly or annual variation is difficult from a single 12-month collection period. However, this study's findings do suggest there may be monthly trends in calling, the nature of which suggests this may be linked to the morepork breeding cycle, but also perhaps to prey availability and weather.

It would be interesting to investigate if weather does have an effect on morepork calling. On Mokoia Island, Stephenson (1998) noted how weather appeared not to influence calling frequency and that some nights, regardless of weather, morepork called a lot and on others calling was very infrequent. He did not investigate this further, but field observations in this study would agree and indicate the same occurs on Ponui Island, however, this requires further testing.

Diel Variation

The mean number of syllables per hour after sunset showed peaks and groupings suggestive of variation across the duration of a night. The peaks were significantly different to all other hours and these occurred towards the middle of the night (hours 5 and 6) and the final hour of darkness (hour 14).

The peak in calling at 14 hours after sunset could be influenced by a number of factors. Firstly the sample size for the 14th hour of the night was only six as there are only six months of the year where the night is 14 hours long. This sample size is half that of almost all others with the exceptions being 11 months of 12-hour nights and eight months of 13-hour nights. Although the 14th hour of the night was seen to have higher calling activity than any other month, the standard error was relatively large. It is difficult then to draw inferences about morepork behaviour at dawn due to the differences between months regarding which hour of the night dawn falls – ranging from the 11th hour to the 14th. Therefore there is high confidence in making predictions from the data up to 11 hours of the night but due to sample size inferences made into hours 12 to 14 require caution. Looking at the 11th, 12th and 13th hours, suggests there is reduced calling occurs just before dawn in months with fewer hours of darkness. The six months of 14-hour nights, however, suggest that during the winter months (when nights are longest) there is an increase in calling towards the end of the night.

When the data were split between autumn-winter and spring-summer the trend across a night did not vary much except that there seemed to be more calling in the spring-summer than in the autumn-winter months. The first few hours of the night showed reduced calling in both seasons, with a peak towards the early middle of the night. In autumn-winter this calling rate dropped off, whereas in spring-summer it remained constant. Splitting the data also allowed for the shorter nights of the summer months which did not have 14 hours of darkness. The results presented in Figure 3.3, therefore, should be interpreted with caution because of this seasonal difference in night length resulting in smaller sample sizes for hours 12 to 14 from months with shorter night lengths. Figure 3.3 is useful for giving an idea of how much calling is expected in each hour of the night up to and including hour 11. While multiple years' data would be ideal for making predictions, these results give an idea of calling activity across a night. For months with 14 hours of darkness after sunset, figure 3.4a would be more appropriate in trying to predict the amount of calling in each hour. There were four months of the year (November to February) which had fewer than 13

hours per night, so caution is advised when interpreting these graphs with a view to estimating the amount of calling towards the end of the nights in those months.

The differing trends when the data were split into winter and summer months gives further evidence for there being monthly variation in morepork calling. One trend which remains constant, however, is reduced calling in the early hours of the night. From field observations, on leaving the roost a morepork will call once or twice but subsequently will be relatively quiet. When I tracked individuals after they left their roost, their priority appeared to be hunting and preening, and little calling was heard. Stephenson (1998) studied the time budgets of morepork and found that they spent considerable time calling, but most of the time hunting and that the two activities did not seem to follow a pattern during the night.

It is interesting that the first two hours of darkness had the lowest average calling, yet other owls are often most vocal within three hours of sunset (Clark & Anderson, 1997). Kiwi also have a high call rate during the early hours of the night (Digby et al., 2014). This difference in morepork is useful information for any manager planning a call survey, in order to obtain a representative sample from a time of night where morepork are more likely to be calling. This also has further implications to the planning stages of a monitoring programme whereby call surveys around midnight or later (hours 5 and 6 after sunset) may be more difficult to conduct because it will be more difficult to find willing volunteers. This suggests that other methods of population census for morepork may be appropriate, such as automated recording coupled with automatic sound recognition or manual analysis of the data.

Further Study

Knowledge and data gained from studies into temporal variation in calling can be useful to refine and plan more effective call surveys. While nocturnal call surveys for species like kiwi (*Apteryx* spp.) are most effective in the first couple of hours after sunset, my results suggest that call surveys for morepork would be better conducted closer to the middle of the night as fewer calls were heard towards the beginning of the night. My study aimed to provide baseline data on the temporal calling activity of morepork for use and improvement by further studies. I found that morepork calling

behaviour showed evidence of temporal variation both between months over the duration of a year and between hours after sunset in a night which may need consideration if call surveys are to be used in morepork population census and abundance estimates.



Chapter 4 - Conversations with Ruru

Investigating Morepork response to audio playback



Sometimes there's an owl

And sometimes there isn't

(Yolen, 1992)

Abstract

Playback experiments were conducted in November and December 2013 and March 2014. They involved broadcasting the three main morepork call-types (*more-pork*, *rororo* and *trill*) at three different times of night (dusk, midnight and dawn) to seven marked study birds and four unmarked control birds in different sites. Playback calls were successful in eliciting responses from morepork, but not at a rate that was comparable with responses to natural calls. Session time, call-type and order of playback all had an effect on morepork responses to playback. The *more-pork* and *rororo* calls had significantly greater numbers of responses than the *trill* call. Response call-type also differed to playback call-type, however the small sample size limited analysis to observational conclusions. Season did not appear to influence the number of responses to playback, but the methodology may have limited sensitivity and breeding versus non-breeding seasonal responses require further investigation. Results of these playbacks enabled call functions to be hypothesised for the three main call-types: *more-pork*, *trill* and *rororo*. *More-pork* and *rororo* were hypothesised to be more aggressive calls, whereas the *trill* appeared to be more involved in non-aggressive contact. Call function hypotheses could be useful as a baseline for further study of morepork territoriality; individuality and encoded information in their vocalisations; population census and management; and morepork conservation that can build on this study's findings and improve its methodology.

Introduction

Playback is a popular technique in the study of animal communication and cognition. Deecke (2006) defined playback as “the experimental presentation of recorded sensory stimuli to animals to investigate their behavioural or psychophysiological responses”. While the phrase “experimental playback” can be used to refer to other stimuli, such as visual (e.g. videos), in this study “playback” will be used to refer to acoustic playback which involves the use of pre-recorded sounds broadcast to a target animal (*sensu* Wiley, 2003). The range of animals that have been studied using playback experiments is broad and diverse from song birds (Slater, 2003), to seals (Deutsch et al., 1990; Hayes et al., 2004) to spiders (Uetz & Roberts, 2002). Acoustic playback is particularly effective in the study of species that are cautious, well camouflaged or, in the case of nocturnal animals, whose behaviour is difficult to observe. Vocalisations can be utilised when studying the biology of owls in order to overcome the challenges of their nocturnal, cryptic lifestyles (Galeotti & Pavan, 1991).

The general aim of using sound playback is to elicit a response from the target animal which may be vocal or other types of behaviour. Playbacks can test the responses to conspecific and heterospecific species and playback sounds used can be recordings or synthesised sounds. In scientific study, mostly in the fields of behavioural ecology and bioacoustics, the aims of playback experiments are: 1. to study the response itself, and when one occurs, to infer the meaning or context of the played sound; 2. to investigate what variables influence the likelihood of a response; and 3. to test behavioural theories. Applications of acoustic playback cover a broad range of areas such as studying territorial behaviour and mapping, general communication, predator-prey interactions, personality and motivational states, dominance, function and context of vocalisations, seasonality of certain behaviours and finally population census, including presence/absence of cryptic species and assessment of abundance and density. Experiments using playback allow hypotheses about the meaning and function of calls to be tested both in the field and the laboratory (Douglas & Mennill, 2010). Experiments performed under laboratory conditions differ from those in the field and there are advantages and disadvantages to both. Field tests provide a more natural context, but laboratory experiments allow greater control of variables.

Subjects of acoustic playback experiments (hereon referred to as 'playbacks' for simplicity) are diverse and not limited to avian species. Some mammalian subjects of playbacks include various primates (Fischer et al., 2013), seals (Deutche et al., 1990), and other marine mammals (reviewed by Deecke, 2006). Playback sounds are not limited to vocalisations and can include other sounds such as Vervet monkey (*Cercopithecus aethiops*) grunts (Cheney & Seyfarth, 1982), Bottlenose dolphin (*Tursiops truncatus*) whistles (Sayigh, 1998), and vibratory communication (web-plucking, percussion and stridulation) in Wolf spiders (*Lycosidae: Schizocosa* spp.) (Uetz & Roberts, 2002).

As well as simulating an acoustic competitor, playback can also be used to study the response of a target species to the call of a predator (Reviewed in Hattena et al., 2014). This has applications in the management of pest species which involves broadcasting either a predator's call or the alarm call of the target pest as an audio deterrent in order to disperse gatherings of undesirable birds, both in urban and agricultural situations. In contrast to acoustic deterrents, studies have also investigated the effects of anthropogenic noise on animals and how to lessen their impacts (Deecke, 2006).

Playback calls of target and non-target birds have applications outside direct behavioural study and are used in recreational bird watching to lure birds or confirm their presence or location. This in turn has applications to other types of scientific study when capturing and marking a study population for monitoring. The use of recreational bird-watching playbacks is not always benign however, and carries a risk of their over-use causing habituation and desensitisation in target species, as well as influencing both target and non-target species' behaviour. Consequently, in some places there are restrictions on playback length, target species, and times of year that playback can be used in a recreational context (Harris & Haskell, 2013).

Birds form a large part of the literature as they often rely heavily on acoustic communication and so playback studies of song and calls abound. In the past, the majority of studies that used playback involved song birds, but an increasing number of studies investigate communication of non-oscine birds. There have been a number

of playback-based studies on owls, most commonly involved with territoriality, population census, and vocalisation research, as discussed below.

Behavioural theory tested by playback

The use of playback experiments is very common when studying territoriality, particularly in birds; examples include New Zealand Pukeko (*Porphyrio porphyrio melatonus*) (Clapperton, 1987), North Island Kokako (*Callaeas cinereus wilsoni*) (Molles & Waas, 2006) and Great Tits (*Parus major*) (Amy et al., 2010). In owls specifically, playback has been an important tool for studies of territoriality in Eastern Screech Owls (*Otus asio*) (Ritchison et al., 1988), Tawny Owls (*Strix aluco*) (Redpath, 1994), Little Owls (*Athene noctua*) (Hardouin et al., 2006), and Eurasian Scops Owls (*Otus scops*) (Mori et al., 2014).

Territoriality carries a cost-benefit trade-off. Costs include the time and energy consumption involved in aggressive displays and interactions, as well as the associated increase in stress hormone levels, all of which could lead to reduced short term fitness and an increased predation or injury risk (Alcock, 2009). Benefits range from quality resource ownership to reproductive advantages inherent in such ownership.

Linked to territoriality is the Dear Enemy phenomenon, described by Fisher (1954) cited in Hardouin et al. (2006) as a less aggressive response elicited by neighbours compared to strangers. It was hypothesised by Hardouin et al. (2006) as a way that some territorial animals mitigate some of the costs associated with territoriality by conserving energy. Formerly believed to occur in all territorial situations, Temeles' review (1994) found that the occurrence of the phenomenon is more condition-dependent than initially thought. He found the most influential condition to be the type of territory that is being defended; the Dear Enemy phenomenon occurred most commonly when a defended territory was a multipurpose breeding territory. By inference, Temeles concluded that it is the perceived threat presented by an intruder (neighbour or stranger) which drives the phenomenon. Temeles (1994) reported 47 studies (after excluding studies that found differences between the sexes) that found evidence of the phenomenon, included nineteen species of songbirds, eleven non-songbirds, ten mammals, three reptiles, two amphibians, and two insects. To give an

idea of prevalence and importance of playback calls to the study of territoriality, particularly in birds, over 60% of the 70 studies Temeles reviewed used playback as their method of testing for the phenomenon, and 76% of the 50 studies on birds used playback experiments.

The occurrence of the Dear Enemy phenomenon in birds implies the ability to distinguish and discriminate between neighbours and strangers, and this has been well studied in passerines (reviewed by Temeles, 1994), but less so in territorial non-passerine birds. Some literature covers these birds, including the study by Clapperton (1987) of Pukeko; Bretagnolle (1989) on Petrels; Galeotti & Pavan (1991) on Tawny Owls, and Hardouin et al. (2006) on Little Owls. There have only been a small number of behavioural studies on owls using playback calls to investigate responses, with playback being used more commonly as a population census technique.

While this study does not have the scope required for a territoriality study, territoriality is likely to be a key influence on morepork (*Ninox novaeseelandiae*) vocalisations because this species is a territorial, nocturnal raptor. Territoriality is worth considering in background to this study as the data may be useful in future as a basis to improve research methodology and to study territoriality in morepork.

Despite the morepork being one of New Zealand's well known native, nocturnal birds recognised and named by its disyllabic *more-pork* announcement call, very little is known about the function and context inherent to the morepork's range of vocalisations. Stephenson (1998) wrote a useful description of the different call types of the morepork on Mokoia Island, Rotorua, New Zealand, along with his hypothesised context, but did not test these hypotheses.

Aim

The aim of this chapter is to investigate the responses of the New Zealand morepork to different call-types broadcast in playback experiments over two seasonal periods - the beginning of the breeding season and outside the breeding season, and different times of night - dusk, midnight and dawn. With this information, I hope that the context and function of certain call types can be described in more detail in this owl.

Key goals

To investigate:

1. Whether any broadcast pre-recorded morepork call elicits a response from the wild study birds and, if so, does a certain playback call type elicit more responses than other call types
2. Whether response type varies with playback call type
3. Whether the likelihood of a response varies with season or time of night
4. How responses to playback compare to natural responses to incidental calls of the same type at the same time of night.

Methods

The playback experiments for this study took place on Ponui Island (36°50'S, 175°10'E) in November and December 2013 and March 2014 and involved 11 test subjects (seven radio-tagged study birds and four non-tagged, control birds, two in each season) across 13 sites of varying habitat types (pasture, scrub and forest). Three call types were tested - *more-pork*, *trill*, and *rororo*, as well as a control (white noise) during three randomly assigned two-hour periods of the night - dusk, midnight and dawn. For details of the study site and study species see Chapter One.

Experimental Design and Procedure

To enable individual birds to be identified in the field at night and their sex to be known with certainty, we used mist nets to catch seven morepork in July 2013 and fitted them with individually-numbered leg bands (size-E metal bands, provided by the New Zealand Banding Office) and with radio-transmitters (see Chapter Two for details).

Playback experiments were conducted at the beginning of the breeding season (late November and early December 2013) and again at the end of the breeding season (March 2014). Experiments in each time period ($n = 27$ per season) took place at one of three session times (± 1 hour): dusk (within 30 minutes of sunset), 12 am, or dawn (within 30 minutes of sunrise). Each experiment on any one individual bird was spaced at least 24 hours apart with the aim being a 48 hour interval. If heavy rain or wind occurred within a scheduled session, that experiment was postponed to the next appropriate night.

Due to limited knowledge about the extent of each radio-tagged bird's territory (Chapter Two) and their boundaries, the roost was chosen as the default playback site provided the bird was within range or close by at the time of the trial. It was assumed that conducting playbacks near by the roost would be fairly central within the owl's territory and this was confirmed by tracking these owls for ten days each month over a year. Time constraints meant that home range and territorial mapping was not feasible prior to the playback experiments and so it was inferred that roost location was a site of importance within the morepork's territory. The location of the call and the response it elicits are closely tied with the identity of the caller. Hardouin et al. (2006) found in Little Owls (*Athene noctua*) that a neighbour's call played from their usual position elicited less of a response than a neighbour's call played from an unusual position. They also found that a neighbour's call played from an unusual position elicited about the same response as a stranger's call from either the usual or unusual position.

The calls played to the focal owls in my study were not those of neighbouring birds, so it can be assumed that the playbacks would represent a stranger intruding into the focal owl's territory. There could still be two different levels of response elicited by such an intrusion. It could elicit a greater response as the intruder is within their territory, not just at their boundary, or it could elicit a lesser response than say a neighbour calling within the focal birds' territory. The lesser response would be in recognition of the playback as a transient morepork – having not been heard by the focal morepork before – which may simply be passing through the territory, posing no threat and causing a lesser response than if the bird was known to the focal owl.

Playing calls at the roost also allowed the use of control birds. 'Control' birds were morepork that I had not followed and recorded before and each time were naive of both a field researcher's presence in their immediate surroundings and the use of calls played back through speakers. Two different birds in two separate areas were used each season to ensure this naivety. They acted as experimental controls to the seven study birds which had previously been caught using playbacks (different to those used in the experiment), marked, and followed by the author. Prior to playback, the study birds were located using radio telemetry (Wildlife Telonics TR4 receiver and Yagi

directional antenna), or a control location was chosen by previous experience of vocal morepork at a site distant to that of the marked study birds. When possible, each morepork was located at its roost during the day prior to the evening playback, but if this was not possible the bird was located just prior to the playback session. If the bird was not within the surrounds of their roost and deemed to be 'out of earshot' of playback (defined as a very faint radio-telemetry signal), the bird was located and playback conducted at their location at the time.

Playback was broadcast from two Sony stereo speakers concealed 1.5 to 2 m above the ground on tree trunks, or the fronds of medium-sized tree ferns. Each playback was broadcast at the same volume, approximately equivalent to natural volume as estimated by ear. A 10-m auxiliary cable enabled the operator to sit away from, but still control the stimulus via an MP3 player. Example experimental set up and morepork investigation response are shown in Figure 4.1. A settling period of five minutes silence prior to beginning playback served to mitigate the disturbance noise caused by setting up, although this noise was kept to a minimum.



Figure 4.1 Playback speaker set up and infra-red screen shots of investigating morepork. Left side: subtle Sony speakers set up in trees and ponga and blue mp3 player; right side: infra-red shots of morepork (eye shine is white) investigating speakers and speakers in a tree; far right: wide shot of speakers in a tree fern or ponga.

To minimise noise and its possible impacts on morepork behaviour, the experiments were often conducted by the author alone. The settling period was recorded using a Sennheiser shot-gun microphone (MKH 60 948) coupled to a Marantz Professional solid state sound-recorder (PMD661, DC 5V, 1.4 A) to record unsolicited calls.

Recordings were made with a sampling rate of 44.1 kHz at 24-bit and saved as WAV format audio files.

The rest of the experiment was also sound recorded for later analysis and, where possible, videos of behaviour accompanying the vocalisations were recorded using a Sony Handycam Digital video-camera (DCR-SR45 Hybrid HDD) with an infrared light source (Model IRLamp 6, Wildlife Engineering). Videoing behaviour often proved difficult due to the dense New Zealand bush obscuring the morepork or simply that a third hand was not available whilst audio-recording and operating the radio telemetry gear.

The playback test stimuli consisted of three common morepork call types, *more-pork*, *trill*, and *rororo*, retrieved from manual sound recordings (.WAV sound files) collected beforehand on the island from August to October 2013 (Chapter Two). Stimuli were selected from the recorded calls of my seven study birds. A single call type was tested in each experiment and each bird was tested once for each call type once in the breeding season and once in the non-breeding season. Playback calls were selected for their quality including minimal background and other species' noise, clarity of call, and its loudness. For simplicity, abbreviations have been used to refer to some of the call types with longer names, specifically *more-pork* = mpk; *more-more-pork* = mmpk; and *rororo-more-pork* = rororompk. *Mix* referred to any response where multiple call types were involved.

Playback calls were around 30-60 seconds long and a non-morepork playback – static white noise – was played as a control. I randomised the order of playback type, either call or static. After a playback was broadcast, a waiting period of two minutes for any response was timed by stopwatch and if no response occurred, the next sound was played. It was decided that no more than five playback sounds would be broadcast if no response was elicited to avoid over-stimulation stress, or habituation of the morepork. Therefore up to five sounds were played in each experiment and thus I investigated the effect of playback sequence within a session, and examined whether sounds played in each temporal position could be considered independent from each other.

If a response occurred the experiment was terminated and no further playbacks were broadcast. Field notes were recorded into the microphone along with the call type, estimated distance (by volume of call) and bird I.D. of a response. This was deemed less of a disturbance than turning on a torch and writing notes. A response was defined as a relatively loud or close call which occurred within the two minute post-broadcast wait.

Wiley (2003, p.585) defines committing pseudoreplication in the context of playback experiments as “repeatedly presenting the same stimulus, repeatedly using the same subject, or pooling the results from presentations of similar stimuli”. Therefore to limit the potential impact of pseudoreplication (Kroodsma, 1989), I ensured that recordings used for playback were recorded at different sites of appropriate distance (>200 m) away from the focal owl, however, due to the time constraints of a master’s programme, they were recorded in the same year as the playback experiments themselves.

I ensured that the focal owl was not tested with its own vocalisation by aiming to have a second example of each call type – two versions of a call by each sex. In total I had three versions of each call type (two female versions and one male) where ideally I would have had four as I only had a single male bird in my marked study population. I had multiple versions of each call as the test calls were selected from recordings made of the study owls themselves. None of the study birds shared territory borders as far I could tell, except for two birds - during the early breeding season tests - which may have been a mated pair (found roosting together before the breeding season but not during it) or mother and son pair, but the male moved to a different gully for the second set of experiments.

I alternated between the call versions, randomly using one version per session. This was to avoid testing a focal owl with its own call, but also to attempt to address the negative associations on external validity of the pseudoreplication inherent in using only one version of a call type to represent that whole call type class (Kroodsma et al., 2001). More call versions would have been ideal to minimise the risk of simple pseudoreplication due to being unable to use one good quality example of each call

type per individual. However, I was limited in the number of high quality recordings available.

Playback Analysis

The recordings of the playback experiments (.WAV files) were processed using Raven Pro (Cornell Lab of Ornithology, Ithaca, NY, U.S.A) and data were managed in a Microsoft Excel (Microsoft Office 2007) spreadsheet. The following parameters were extracted from the recordings: unsolicited calls within the five minute settling period; the playback call-type broadcast; time of recording and length of broadcast; evidence of a response; type, time and length of response; number of response call syllables; latency to a suspected response from playback; and bird identity.

Controls

Automated sound recorders were deployed every month on the island to record for entire nights (14 hours) at nine sites for three nights per site (Chapter Three). These recordings were also used in the analyses of the playback experiments. In addition to a control playback call (static), the *natural call occurrence* (number of syllables) was sampled from two-minute periods selected from the all-night sound recordings made at the recording site closest to where the playback experiment was conducted. This was used as a control to compare the number of calls that naturally occurred in the same time period as that used post-playback in the experiments. One two-minute segment was selected for each playback experiment ($n = 54$). The control segments were isolated from the recordings at 22 minutes prior to the time the experiment occurred. This delay between control sample time and experimental time was to allow for the disturbance I may have caused passing through the auto-recorder area, and 20 minutes was deemed an adequate buffer prior to my arrival and disturbance of the environment.

A second control was sampled from the same automatic recording segments as the first control. This second control investigated what the *natural response* was to each of the three call types. In the control segments, if a call of one of the three test call-types occurred then the presence or absence of a response within two minutes of that first call was recorded, as well as the type of response call. These data were then used as

control or expected values and compared to the experimental or observed data. The sample size for the response-type controls gained from this method was quite small, so it was decided to broaden the search scope to ten minutes prior to the previously tested two-minute segments to attempt to increase the sample size to ten *natural response* examples of each of the three test call types. The recording files and the date/location were not changed, nor was the underlying method, to remain consistent with the experimental method and therefore keep the controls comparable to the experiment.

Timing was important in the first control to ensure comparability with the experimental playback data. Timing was of less importance for the second control, because that control investigated the *natural response* that occurred within two minutes of a call heard in a ten minute period. The varied chance of encountering a call in just a two-minute segment of recording and resulting small sample size meant that expanding the search time to ten minutes increased the chance of encountering a natural call. This increased sample size had no effect on the comparability between natural data and playback data as time was not as important to the second control as it was to the first.

Statistical Analysis

Statistical analysis was computed using an online Chi-square analysis calculator retrieved from VassarStats: Website for Statistical Computation (Lowry, 2014). I used Pearson's chi-square without the Yates' correction for continuity because Monte-Carlo simulation research suggests that the Yates' correction is overly conservative even for small sample sizes (Camilli & Hopkins, 1978, 1979; Thompson, 1988). To compensate for the multiple comparisons, I used the Benjamini-Hochberg test (Benjamini & Hochberg, 1995). This procedure is recommended when carrying out many comparisons where the expectation is that a large number of them may be significant and as corrections such as Bonferroni may result in false negatives. I followed Thissen et al. (2002) to conduct the Benjamini-Hochberg procedure using Microsoft Excel.

Results

Morepork responded to playback calls and the effect of time of night and call type on the response was statistically significant, while season had no effect.

Do calls elicit a response?

Playback calls versus Natural calls

Response to a natural call was three times as likely as a response to a playback call (Figure 4.2), suggesting that the playbacks affected the natural calling behaviour of morepork (Chi-square: $\chi^2 = 13.56$, $df = 1$, $p = 0.0002$). Although playbacks appeared to have a response-reducing effect, any responses to playbacks were taken as true responses. This is a conservative approach because although in some instances morepork may be able to identify playbacks as calls which aren't real and therefore not respond, the interpretation is that, on the occasion when a bird responds to playback, the bird is responding to the playback call and has not identified it as fake.

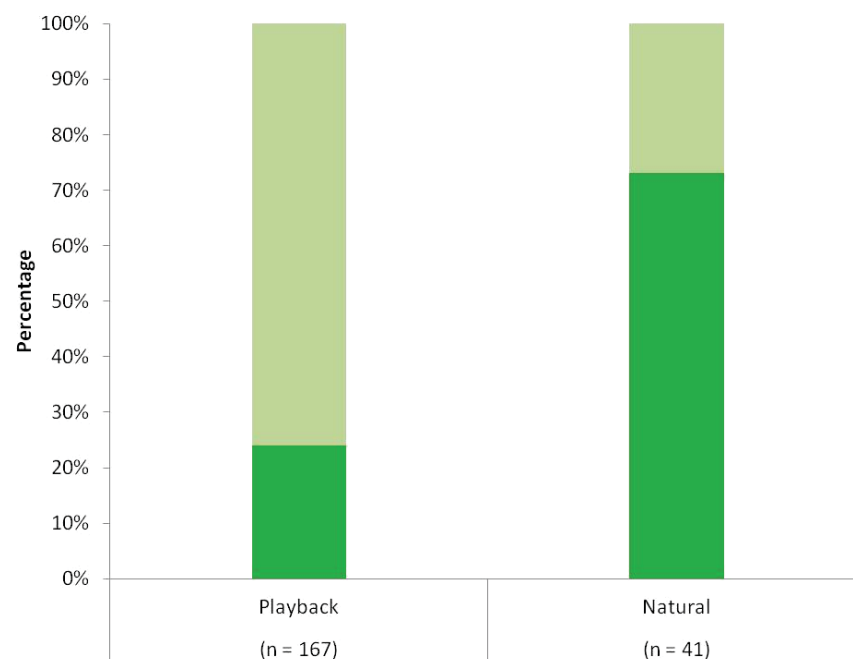


Figure 4.2 Overall stacked percentages of responses (dark green) and non-responses (light green) to playback (n = 167) and control (natural, unsolicited) calls (n = 41).

Effect of season, session time, call type, and order on proportional number of responses.

Effect of season (breeding versus non-breeding)

There was no significant difference between the percentage of calls eliciting responses in each season for natural ($\chi^2 = 1.27$, $df = 1$, $p = 0.26$) or playback ($\chi^2 = 0.03$, $df = 1$, $p = 0.86$) calls (Figure 4.3).

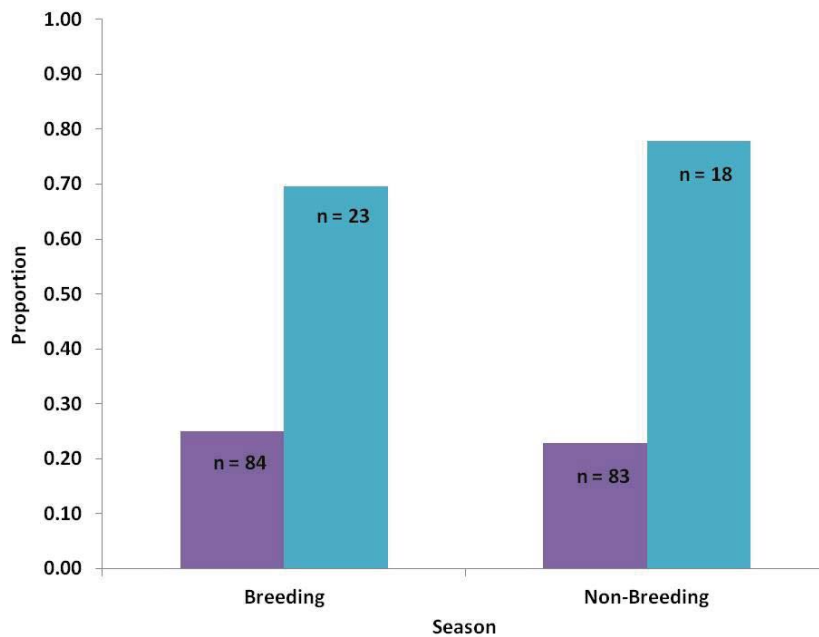


Figure 4.3 Proportions of natural calls (blue) and playback calls (purple) that elicited a response in each season.

Effect of session (time of night) and season

There was a significant difference between the proportion of responses to natural calls between the different session times (Table 4.1., Figure 4.4c). This difference was significant between 12am and dusk and 12am and dawn (Table 4.1), but there was no significant difference between dusk and dawn. There was, however, a significant difference between seasons when natural call responses were compared between dusk and dawn (Table 4.1; Figure 4.4d).

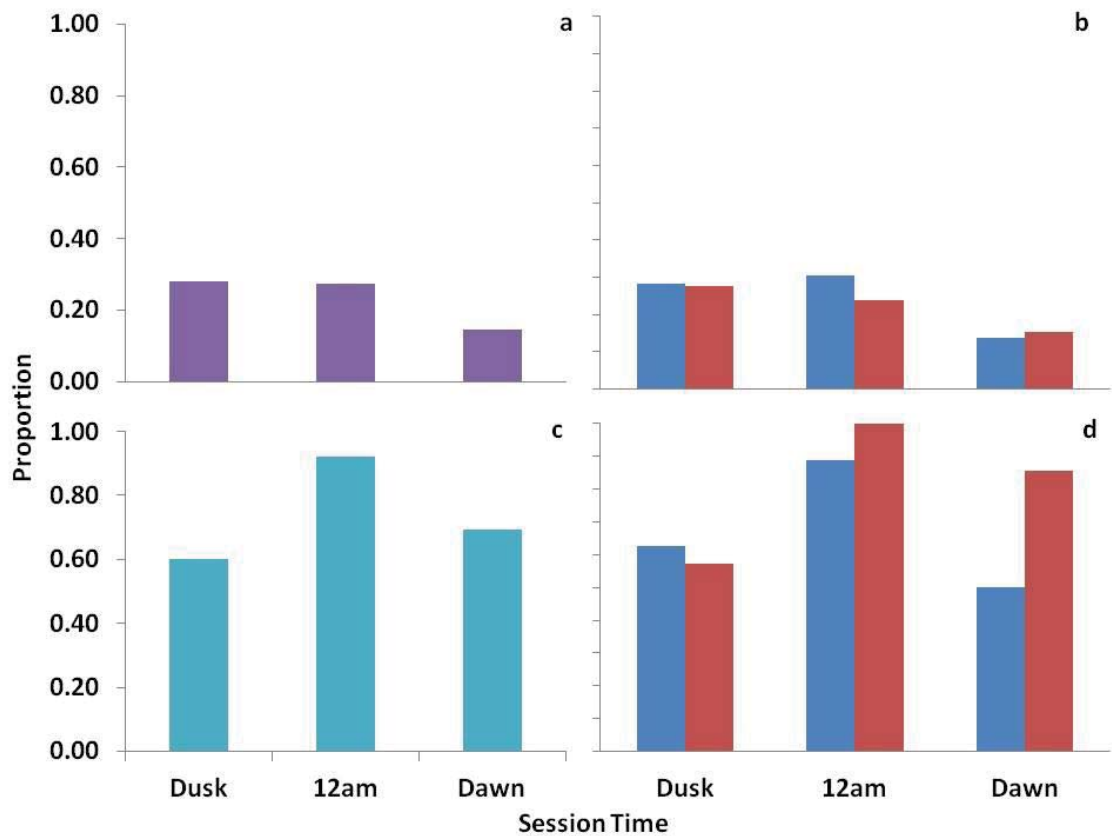


Figure 4.4 Proportion of responses (number of responses in each session out of total playbacks in each session) to a) Playback calls (purple) c) natural calls (light blue) in each session time for both seasons pooled. And proportion of responses (number of responses out of total number of playback and natural calls to b) playback and d) natural calls in each session time per season (blue = breeding; red = non-breeding).

Morepork were more responsive to playback calls at the beginning and in the middle of the night (dusk and midnight) than at dawn (Figure 4.4 a). The difference in proportions was, however, small (within 0.1 of each other) and therefore there was no significant difference in the percentage of responses between session times for the data pooled across seasons (Table 4.1). Likewise, there was no significant difference between seasons or session times for playback calls when the data are split by season (Table 4.1).

Table 4.1 Chi-square test results investigating the effect of call type and session time on the proportional response to playback and natural calls (* indicates significance, 'NS' indicates not significant). Due to the likelihood of error from multiple comparisons, Benjamini-Hochberg (B-H) test (1995) was applied. Index refers to the order of p-values as per B-H test. Significance after B-H correction is achieved when p value is smaller than B-H value. Number of comparisons = 30. Mpk = *more-pork* call.

Trial	Test	Grouping	Comparison	Chi-square	df	p value	Index	B-H value	Significance
Natural	Call type	Response/No response	mpk-trill	6.83	1	0.009	5	0.0217	*
Natural	Call type	Response/No response	mpk-rororo	4.34	1	0.0372	12	0.0158	NS
Natural	Call type	Response/No response	trill-rororo	0.3	1	0.5839	22	0.0075	NS
Playback	Call type	Response/No response	mpk-static	20.37	1	0.0001	1	0.0250	*
Playback	Call type	Response/No response	rororo-static	19.17	1	0.0001	2	0.0242	*
Playback	Call type	Response/No response	trill-static	5.98	1	0.0145	7	0.0200	*
Playback	Call type	Response/No response	mpk-trill	4.97	1	0.0258	9	0.0183	NS
Playback	Call type	Response/No response	trill-rororo	4.34	1	0.0372	11	0.0167	NS
Playback	Call type	Response/No response	mpk-rororo	0.02	1	0.8875	30	0.0008	NS
Natural	Call type	Breeding/Non-breeding	mpk-trill	1.17	1	0.2794	17	0.0117	NS
Natural	Call type	Breeding/Non-breeding	trill-rororo	0.45	1	0.5023	19	0.0100	NS
Natural	Call type	Breeding/Non-breeding	mpk-rororo	0.19	1	0.6629	25	0.0050	NS
Playback	Call type	Breeding/Non-breeding	trill-rororo	2.03	1	0.1542	14	0.0142	NS
Playback	Call type	Breeding/Non-breeding	mpk-trill	1.25	1	0.2636	16	0.0125	NS
Playback	Call type	Breeding/Non-breeding	trill-static	0.26	1	0.6101	23	0.0067	NS
Playback	Call type	Breeding/Non-breeding	rororo-static	0.24	1	0.6242	24	0.0058	NS
Playback	Call type	Breeding/Non-breeding	mpk-rororo	0.13	1	0.7184	26	0.0042	NS
Playback	Call type	Breeding/Non-breeding	mpk-static	0.07	1	0.7913	27	0.0033	NS
Natural	Session	Response/No response	12am-dawn	16.85	1	0.0001	4	0.0225	*
Natural	Session	Response/No response	dusk-12am	28.07	1	0.0001	3	0.0233	*
Natural	Session	Response/No response	dusk-dawn	1.77	1	0.1834	15	0.0133	NS
Playback	Session	Response/No response	dusk-dawn	5.01	1	0.0252	8	0.0192	NS
Playback	Session	Response/No response	12am-dawn	4.34	1	0.0372	10	0.0175	NS
Playback	Session	Response/No response	dusk-12am	0.03	1	0.8625	28	0.0025	NS
Natural	Session	Breeding/Non-breeding	dusk-dawn	6.4	1	0.0114	6	0.0208	*
Natural	Session	Breeding/Non-breeding	12am-dawn	3.44	1	0.0636	13	0.0150	NS
Natural	Session	Breeding/Non-breeding	dusk-12am	0.86	1	0.3537	18	0.0108	NS
Playback	Session	Breeding/Non-breeding	12am-dawn	0.4	1	0.5271	20	0.0092	NS
Playback	Session	Breeding/Non-breeding	dusk-12am	0.34	1	0.5598	21	0.0083	NS
Playback	Session	Breeding/Non-breeding	dusk-dawn	0.02	1	0.8875	29	0.0017	NS

Table 4.2 Chi-square test results investigating the effect of call type on the proportional response to playback and natural calls (* indicates significance, 'NS' indicates not significant). Due to the likelihood of error from multiple comparisons, Benjamini-Hochberg (B-H) test (1995) was applied. Index refers to the order of p-values as per B-H test. Significance after B-H correction is achieved when p value is smaller than B-H value. Number of comparisons = 7. Mpk = *more-pork* call.

Trial	Comparison	Grouping	chi-square	df	p value	Index	B-H value	significance
Natural	trill-trill	Breeding/Non-breeding	24.72	1	0.0001	1	0.0250	*
Natural	rororo-rororo	Breeding/Non-breeding	1.93	1	0.1648	2	0.0214	NS
Playback	rororo-rororo	Breeding/Non-breeding	1.82	1	0.1773	3	0.0179	NS
Playback	trill-trill	Breeding/Non-breeding	1.13	1	0.2878	4	0.0143	NS
Playback	mpk-mpk	Breeding/Non-breeding	0.55	1	0.4583	5	0.0107	NS

Effect of call type

All three playback morepork call-types elicited greater response rates than broadcast static noise (Table 4.1; Figure 4.5), with no significant differences between seasons in response rate to any call type. The relationship inherent in the natural call data did not mirror that of the playback calls. In the playback data, *trill* seemed to elicit the least response (Figure 4.5 a); while within the natural call data *trill* elicited the greatest response (Figure 4.5 c). There were significant differences between the response rates to all three call types in the natural call data (Table 4.1), but none for the playbacks (Table 4.1; Figure 4.5 c), although the difference between *more-pork* and *trill* was close to statistical significance (Table 4.1). There was no significant difference between seasons in the proportional responses for *more-pork* or *rororo* natural calls, but morepork were significantly more likely to respond to a *trill* during the breeding season than outside it (Table 4.2; Figure 4.5 d). During the breeding season, morepork were significantly more likely to respond to a *trill* call than to a *more-pork* call (Table 4.2; Figure 4.5 d: red).

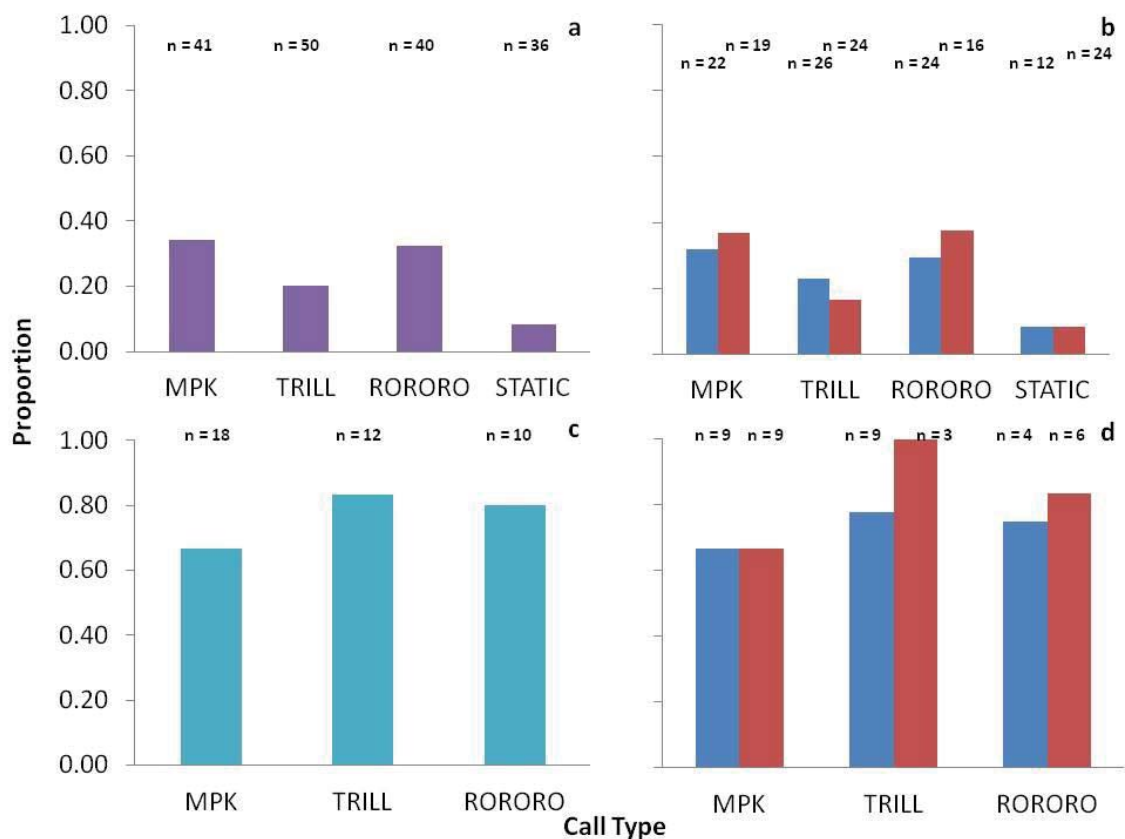


Figure 4.5 Proportion of responses (number of responses to each call type out of total calls) to a) Playback calls (purple); c) natural calls (light blue) for both seasons pooled, and proportion of responses

to b) playback and d) natural calls per call type split between each season (dark blue = breeding; red = non-breeding).

Effect of playback order

No significant difference was found between the proportional response to playback calls between the five playback order positions ($\chi^2 = 5.65$, $df = 4$, $p = 0.2269$). There was, however, a significant difference between seasons ($\chi^2 = 15.13$, $df = 4$, $p = 0.0044$; Figure 4.6 b) where there appears to be differing relationships between the proportional responses recorded in each playback position. In the breeding season there seems to be an increasing trend from order 1 to 5, but the differences between these proportions are small. Also in the non-breeding season there doesn't seem to be a trend, in fact the first playback elicited a greater proportional response where the following four order positions barely varied. From pairwise comparisons of the five playback positions from the seasons pooled data (Figure 4.6 a), there was a significant difference between position one versus four and one versus five, but the other combinations showed no significant difference.

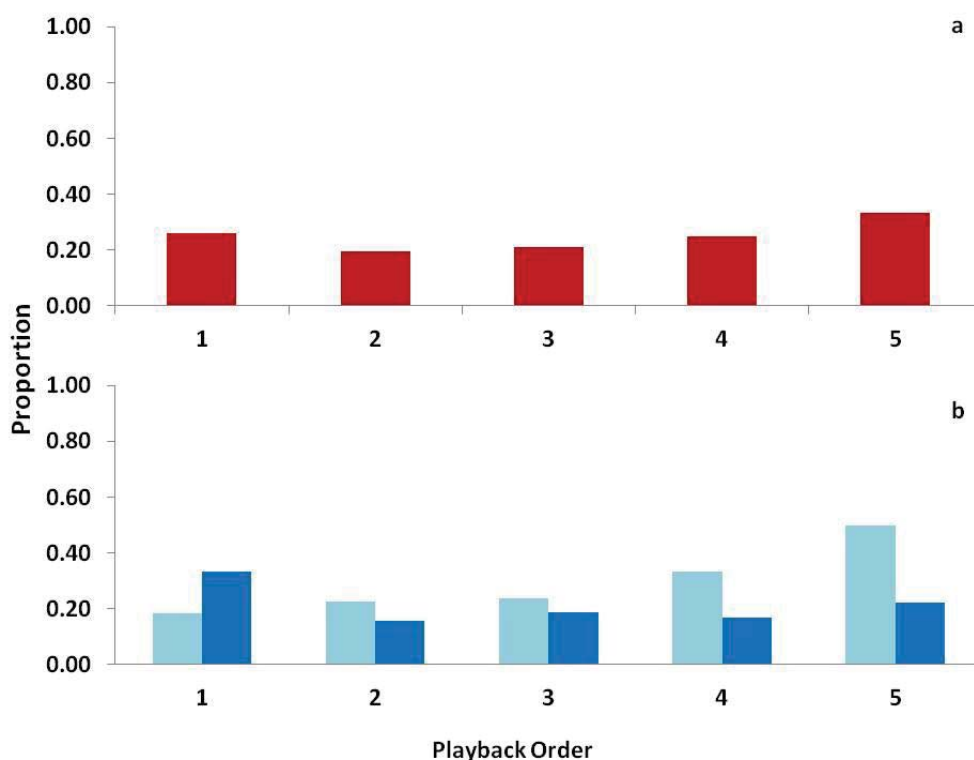


Figure 4.6 Proportion of responses (number of responses that occurred in each order position out of total playbacks) to a) playbacks (red) in each order position for both seasons pooled and b) playbacks (blue) in each order position per season (light blue = breeding; dark blue = non-breeding).

Table 4.3 Chi-square test results investigating the effect of playback call order position on the proportional response to playback and natural calls (* indicates significance, 'NS' indicates not significant). Benjamini-Hochberg (B-H) test (1995) was applied. Index refers to the order of p-values as per B-H test. Significance after B-H correction is achieved when p value is smaller than B-H value. Number of comparisons = 20.

Grouping	Comparison	Chi-square	df	p value	Index	B-H value	Significance
Response/No response	1 vs 2	1.02	1	0.3125	11	0.0125	NS
Response/No response	1 vs 3	0.7	1	0.4028	14	0.0088	NS
Response/No response	1 vs 4	0.03	1	0.8625	19	0.0025	NS
Response/No response	1 vs 5	1.18	1	0.2774	10	0.0138	NS
Response/No response	2 vs 3	0.03	1	0.8625	20	0.0013	NS
Response/No response	2 vs 4	0.72	1	0.3961	13	0.0100	NS
Response/No response	2 vs 5	4.34	1	0.0372	4	0.0213	NS
Response/No response	3 vs 4	0.45	1	0.5023	16	0.0063	NS
Response/No response	3 vs 5	3.65	1	0.0561	5	0.0200	NS
Response/No response	4 vs 5	1.55	1	0.2131	8	0.0163	NS
Breeding/Non-breeding	1 vs 2	4.51	1	0.0337	3	0.0225	NS
Breeding/Non-breeding	1 vs 3	3.53	1	0.0603	6	0.0188	NS
Breeding/Non-breeding	1 vs 4	8.85	1	0.0029	2	0.0238	*
Breeding/Non-breeding	1 vs 5	13.25	1	0.0003	1	0.0250	*
Breeding/Non-breeding	2 vs 3	0.08	1	0.7773	18	0.0038	NS
Breeding/Non-breeding	2 vs 4	0.46	1	0.4976	15	0.0075	NS
Breeding/Non-breeding	2 vs 5	1.23	1	0.2674	9	0.0150	NS
Breeding/Non-breeding	3 vs 4	1.01	1	0.3149	12	0.0113	NS
Breeding/Non-breeding	3 vs 5	2.18	1	0.1398	7	0.0175	NS
Breeding/Non-breeding	4 vs 5	0.16	1	0.6892	17	0.0050	NS

Effect of call type on response type

In the playbacks, the *trill* call did not occur in either of the seasons as a response to a playback *rororo* call, and likewise a *rororo* response did not occur to a playback *trill* (Figure 4.7 a). Conversely, in natural calling, *trill* calls in both seasons appeared to elicit *rororo* responses (Figure 4.7 b). The pattern of response types to playback calls appears similar between seasons, and suggests a consistency in response type likelihoods to a certain call type. For example, morepork respond with *more-pork*, *trill* and *rororo* to a *more-pork* playback, and respond to *rororo* with *more-pork*, *rororo*, *mix* and *more-more-pork* calls. The responses heard to playback do not fully mirror those heard naturally however. Morepork respond with *trill* more often in the playback trials than naturally, and in response to a natural *more-pork* call there is less variation than the range of response calls to a playback *more-pork* call. In the non-breeding season

morepork seemed to respond with similar calls to a *rororo* call in both playback trials and naturally occurring calls, and most commonly it would be a *rororo* response (Figure 4.7 a and 4.7 b).

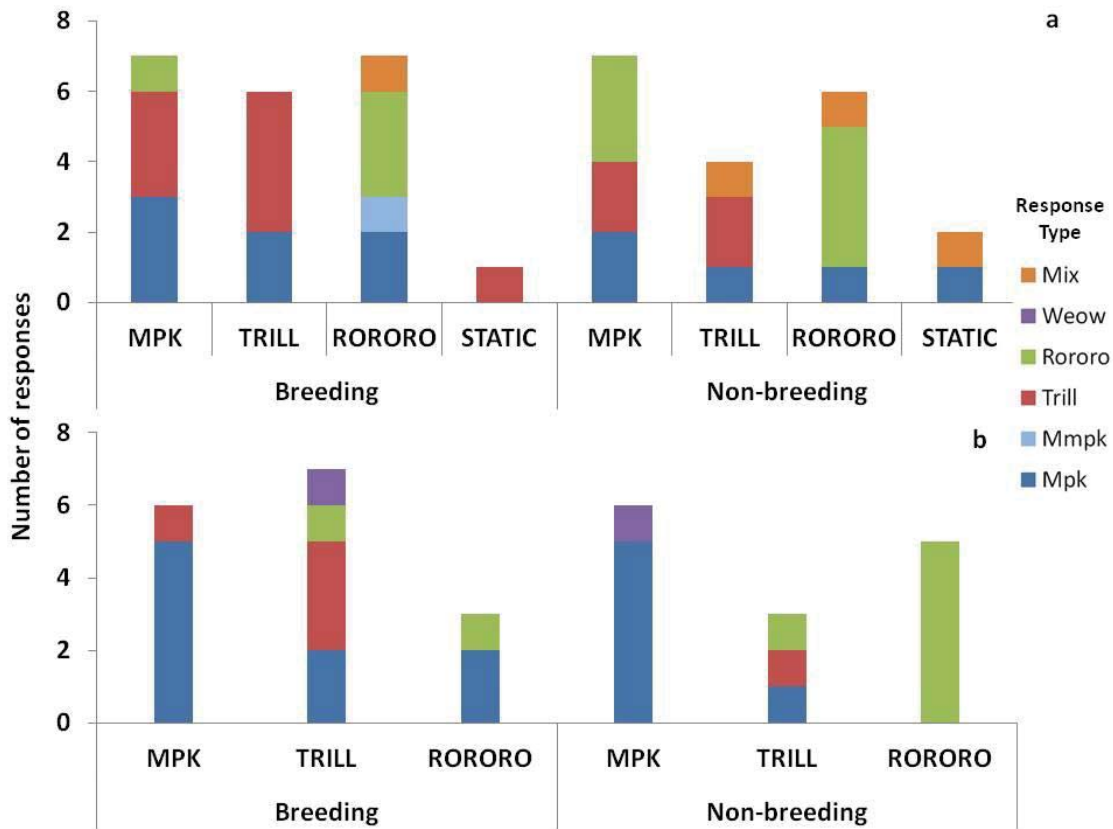


Figure 4.7 Number of responses to each call type split by response type to a) playback calls and b) natural calls per season. Mpk = *more-pork*, Mmpk = *more-more-pork*.

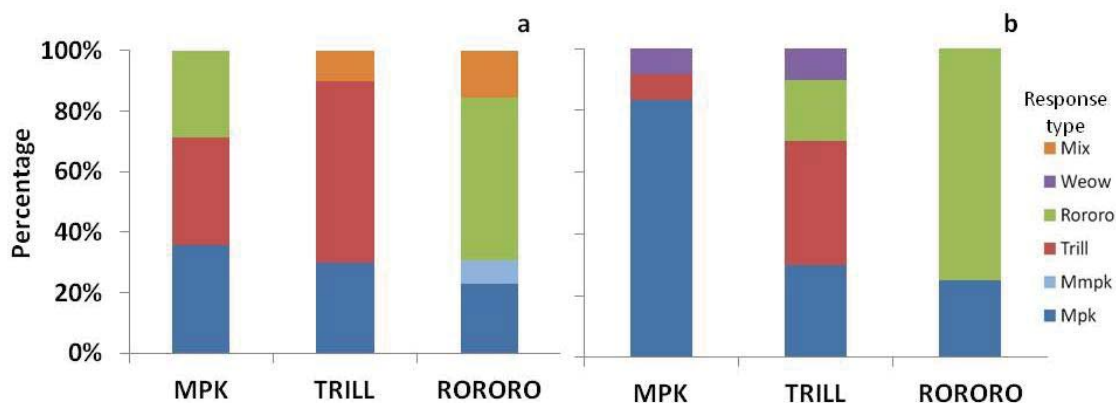


Figure 4.8 Percentage of response types to each call type, pooled seasons to: a) playback calls and b) natural calls. Mpk = *more-pork*, Mmpk = *more-more-pork*.

When the two seasons' data were pooled (Figure 4.8), the apparent trends in response type to call type is clearer. *Trill* was the most common response in both data sets to the *trill* call and this was also true of the *rororo* call in response to *rororo*. No *trill* calls occurred in response to *rororo* calls in either the playback or the natural call data, but *rororo* was not a common response to *trill* calls either. When compared to the playback data, a *more-pork* response seemed to be more common in response to a *more-pork* call in the natural calls (Figure 4.8 b), whereas in the playback data the responses were almost an even split of *more-pork*, *trill* and *rororo* calls (Figure 4.8 a). What is apparent is that *more-pork*, *trill* and *rororo* were by far the most common responses to both natural and playback calls, with the other calls types (*more-more-pork*, *weow* and *mix*) barely featuring as responses, and accounting for just 10% of all responses when both data sets are combined, 12.5% of all responses in the playback data, and 6.7% in the natural incidence call data. The sample size limitations meant that further statistical analysis was not deemed appropriate and was not pursued, and while it was initially planned to further investigate the effect of season, time of night (session) and call type, the data would not lend itself well to drawing robust conclusions from a more detailed analysis.

The observed trend towards specific response types being uttered in response to each of the three calls tested means that, in combination with field observations and previous descriptions (Stephenson, 1998), function can be hypothesised (Table 4.3).

Table 4.4 Hypothesised meaning of the main morepork calls (Hypotheses formed from results of Playback experiments and field observations of Chapter Two).

Other Studies			This Study		
Call	Hypothesised Function	Reference	Hypothesised Response	Observed Response	
				Playback	Natural
More-pork (Mpk)	Announcement/ Territorial call	Stephenson (1998)	Mpk Mmpk	Mpk Trill Rororo	Mpk Trill Weow
Trill	Contact/ Location call	'Purr' (Stephenson, 1998)	Trill	Trill Mpk Mix	Mpk Trill Rororo Weow
Rororo	Aggressive, close contact call	'More' (Stephenson, 1998)	Rororo Rororompk Mmpk	Mpk Mmpk Rororo Mix	Mpk Rororo
Weow	Series location / Alarm call	Pew (Stephenson, 1998) Peow (Stephenson, 1998)	-	-	-
More-more-pork (Mmpk)	Emphasised more-pork call similar announcement/territorial	Classed as part of rororo ('more') call (Stephenson, 1998)	Mpk Rororo(mpk) Mmpk	-	-

Discussion

Morepork in this study responded differently to playbacks and natural calls, and the response rate to playback calls was greater than to broadcast static. Proportional responses to both playback and natural calls varied depending on the time of night but did not vary between breeding and non-breeding seasons. Call type also seemed to affect the proportional responses to playback calls. However, a relatively low sample size meant that testing the temporal, diel and call-type variation within all the response data statistically was challenging, and even more so when splitting the data into playback call type to analyse its effect. Some trends did begin to emerge, suggesting that with a larger sample size these differences may become significant and conclusions more robust.

Responses to playback compared to natural calls.

The playback calls seemed to either not elicit responses, or to suppress the natural proportional response by two thirds, meaning a response to a natural call was three times more likely than a response to a playback call. Despite this overall lower proportional response to playbacks compared to natural calls, the fact that there were responses to playbacks allows the inference that any response heard to the playback calls can be deemed a true response. This uses the assumption that if it was not a response then it too would have been suppressed by playbacks and not occurred.

Vocal territoriality is a game of trade-offs, and there are arguments for playbacks both eliciting and not eliciting responses. Using territoriality theory, both engaging and not engaging in a vocal territorial defence carry costs to the animal, but these are weighed against the benefits of each strategy. Engaging in territorial disputes entails energy and time investment, especially if aggression escalates, which could otherwise be spent foraging or establishing pair bonds (Alcock, 2009). On the other hand, costs of not engaging in vocal territoriality may mean territorial intrusion and loss of both territory ground and potentially of mates.

The lower proportion of responses to playbacks raises questions about the recognition and perception of the playbacks used in this study by morepork. Did morepork recognise a conspecific competitor in the calls played through the speaker or were

they perceived as fake? Evidence that the playbacks were perceived as acoustic competitors rather than just a novel noise can be found in the types of responses heard to the calls. One might expect that if the playbacks were perceived as a strange noise then the responses heard would largely be of alarm, but the hypothesised alarm call, 'weow', (Chapter Two) was not often heard. It is difficult to know for certain how the playbacks are perceived by owls and what value judgements are involved in an owl's decision to respond to playback calls. Given that responses do not appear to be alarm and confusion, but rather bouts of territorial and contact calls as if responding to a conspecific, it can be assumed that playbacks are a useful method of studying morepork communication. This raises the further question of the impact of call familiarity. When comparing responses to natural and playback calls, there is the possibility that in the natural incidence calls there is a higher degree of familiarity between the birds involved, including communication between pairs, territory boundaries and local birds. This would be unlike a playback call which is an unfamiliar, played-back call of a bird whose territory is not near the playback site and is therefore a foreign call. This could have a bearing on the different rates of calls heard in response to natural and playback calls.

As later discussed, there may be information about morepork inherent in their calls (as yet unstudied) which influences the number of responses heard in the field. This information may include status, age, sex, and dominance, which may have led to a reduction in proportional responses by intimidation of the focal owl by the playback call, if value judgements were made by the focal owl in the decision of whether to respond or not.

Many studies have successfully elicited responses to playback and enabled the study of various aspects communication systems. This method is particularly prevalent to the study of both passerines and owls (Ritchison et al., 1988; Galeotti & Pavan, 1991; Appleby et al., 1999; Herting & Belthoff, 2001; Hardouin et al., 2006; Odom & Mennill, 2010; Mori et al., 2014). Morepork responded here to playback calls in a way consistent with Stephenson's (1998) field observations of morepork.

Olsen et al. (2002b), however, suggested that due to the artificial nature of playbacks, the behaviour of the bird may not mirror a natural response. This is worth bearing in mind and could account for the observed difference between responses to playbacks and to natural calls.

My findings here suggest that playback calls elicit a third fewer responses than natural calls in morepork, but whether this applies nationally cannot be determined from a single year's trial at a single island site, and further testing would be worthwhile. If further study confirms this lower proportional response then this would have implications for population census and monitoring of morepork that use playbacks to stimulate vocalisation.

Comparison between playback calls and static

The greater response of morepork to playback calls than to broadcast static suggests that morepork are not just responding to a novel disturbance in their environment, and that the responses heard were true responses and not just random calls.

Olsen et al. (2002b) elicited "duel" responses in mated pairs of Southern boobook (*Ninox boobook*) by playing an unfamiliar boobook call close to their nest. The magnitude of the response varied seasonally, with males finding playback calls particularly threatening just prior to egg-laying. The authors suggest that the response to playbacks is one of alarm and confusion to a perceived threat of a stranger, but this duelling behaviour, where both birds of a pair give un-synchronised calls in response to an intruder, was not seen throughout the rest of the 37 month study when playback was not used.

Effects on responses of call type, session time, season, and order of presentation.

Effect of call type

The fewer responses that playback *trill* calls elicited compared to playback *more-pork* and *rororo* calls is interesting because this is opposite to the responses seen to natural calls. The natural *trill* call elicited higher responses, which were significantly different in the non-breeding season, although not in the breeding or seasons-pooled data. A

proposed reason behind this is the familiarity of the calls. Natural calls and responses heard in the automatic recordings are likely to be between familiar neighbours or mated pairs of morepork and thus familiar to the focal morepork, whereas playback calls are more likely to be perceived as a stranger. This would suggest that a difference could be expected in the proportional response, because each call type has a different hypothesised function that likely varies depending on the identity of the caller. When looking at responses elicited by calls of neighbours and strangers in Little Owls (*Athene noctua*), Hardouin et al. (2006) found that calls of strangers elicited a greater response than neighbour calls. Similarly, in an earlier study Galeotti & Pavan (1991) elicited responses from Tawny Owls (*Strix aluco*) which varied in intensity of response. These owls called in response to neighbour's calls but in response to stranger's calls they combined calling, aggressive displays, and approached the speakers' location. The same graded, increasing response from group member, to neighbour, to most aggressive in response to a stranger's call, was found in pukeko (*Porphyrio p. melanotus*) (Clapperton, 1987) and has been well demonstrated in passerines (Reviewed by Temeles, 1994).

This phenomenon of a lesser response to a familiar 'enemy' is known as the Dear Enemy phenomenon and could explain the difference between proportional responses between natural and playback call types in this study. Likewise, when Hardouin et al. (2006) tested the effect of location of playback, they found that a call of a neighbour in an unusual position relative to the focal owl's territorial boundary elicited a greater response than a neighbour call from a usual position. They also found that stranger calls from either usual or unusual position elicited a higher response than a neighbour from a usual position and about equal to that of a neighbour in an unusual position. This could also explain the difference between playback and natural calls, as the playback calls in this study were conducted at roost sites which were presumed, from radio telemetry data, to be fairly central to the focal owl's territory, and potentially not a site where the territory holder often heard unfamiliar morepork calling.

These theories have the common underlying assumption of vocal individuality. For an owl or other bird to discriminate between its neighbour and a stranger, particularly for nocturnal animals which are active in darkness, they must be able to identify

individuals, so there must be sufficient individual variation among the species' calls to enable this (Galeotti & Pavan, 1991). Individual variation in morepork call characteristics was found both in the spectral (fundamental frequency) and temporal (syllable duration and inter-syllable duration) (Chapter Two) components of calls, but I did not test whether the variation is sufficient to enable individual recognition. This would make for interesting future study.

Differences in the pitch of morepork calls may be due to sexual dimorphism (Stephenson, 1998), but no evidence of sexual variation in call frequencies was found here (Chapter Two). The single male in the study population showed considerable overlap in frequency with the females' calls suggesting that any sexual dimorphism in morepork calls is unlikely to relate to the parameters studied here.

Trill is hypothesised to be a contact call (See Chapter Two and Stephenson, 1998), whereas the two calls, *more-pork* and *rororo*, are more likely to be territorial and aggressive calls. The lower proportional response to *trill* seen in the playbacks suggests that a foreign bird looking to establish contact using a *trill* may not be recognised or responded to by the resident morepork, whereas a foreign *more-pork* or *rororo* call are met with a response more often because they represent an intruder or threat to the resident.

While multiple versions of each call type that varied by sex and identity were used, analysis of the effect of these two factors could not be conducted. With such apparently little sexual dimorphism (Chapter Two) in morepork calls, I hypothesise that it is perhaps the identity of the caller that is more important than their sex. Both intruding males and females pose threats to a resident bird, although those threats may vary depending on the sex of the resident bird and the time of year. Males threaten males with territorial and mate loss, whereas intruding males threaten females with inferior mate quality or resource competition. Conversely, an intruding male may offer superior mate quality and compete with the resident male. Likewise, intruding females threaten resident females as resource competitors. There are also potential benefits of an intruder, whereby an intruding male may represent a better quality mate to the resident female and intruding females offer males extra-pair

copulations. In morepork, whose territories are relatively small, residents are surrounded by known birds, so intruders of either sex represent potential costs, but also benefits, to both male and female residents. I hypothesise that age, status, and dominance are more important than sex in the encoded information of morepork calls.

Response Type

An analysis of response types that natural and playback calls elicited would have been interesting from the point of attempting to establish the meaning inherent in morepork calls via contextual inferences. This was not possible, though, due to sample size limitations. Of the 70 responses heard across both seasons in the natural call and playback call data, over a quarter (25.7%) were single incidences of a response type. The maximum number of a single response type across all pooled data was just five calls and there was little perceivable difference between response types and playback types. Nevertheless, there were non-significant trends. For instance, *more-pork* (mpk) (43%), *trill* (27%), and *rororo* (30%) were the most common response types to both natural and playback calls which accounted for 90% of the response types. There also appeared to be trends forming in the type of call that certain call types would elicit. For example, *rororo* was mostly heard in response to a *rororo* call in both the playback and natural incidence call data, and also heard in response to *more-pork* calls, but infrequently heard in response to the *trill* call. *More-pork* and *trill* responses were less easily distinguished in their tendency to occur in response to a particular call; however, these calls were mainly heard in response to the same test call type (*more-pork* and *trill*).

These findings concur with the hypothesised meanings in both Chapter Two and the results (Table 1), and discussion on call types above. The *rororo* call is associated with more aggressive or excited interactions, and such a call could be assumed to elicit a similar call type. *Trill* on the other hand appears to be more involved with communication of location, and establishing and maintaining contact. The *more-pork* call appears to be multi-functional in that in short bouts it seems to be used to announce presence, location, and to make contact, whereas in prolonged bouts it seems to be a territorial announcement call. This could account for the mix of *more-pork* and *trill* responses elicited by the *more-pork* and *trill* calls. What is interesting,

and furthers the idea of functional separation between *rororo* and *trill*, is the absence of any *trill* calls in all responses to the *rororo* call, whereas there is overlap between *rororo* and *more-pork* responses.

Effect of session (time of night) on proportional responses

Within the natural call data, session times were found to have differing proportional responses, with calling rates around midnight being significantly higher than at either dusk or dawn in both the seasons-pooled data and season-specific data. A commonly held belief presented in the limited literature on the calling behaviour of the morepork suggests that they are more active and vocal at the beginning of the night. While they may be more active, the data presented here indicates peak calling and vocal responsiveness towards the middle of the night, consistent with the data presented in Chapter Three.

In the playback data there were no significant differences in the proportional numbers of responses in each session type, although there was a greater response at dusk and midnight than at dawn. The smaller sample size of playback calls compared to natural calls may explain the variation found. The test results also suggest that with a larger sample size this difference may be significant. This is similar to the higher number of proportional responses heard in the midnight session of natural calls.

The difference in responses at dusk and midnight compared to dawn could be due to the different activities that morepork are likely to be engaged in at such times. At dusk they have just left the roost and may look to make contact, advertise themselves and begin hunting. After feeding and towards midnight they may focus more on calling, whereas towards dawn they will be more focussed on returning to their roost. This does not concur with Olsen et al. (2002a) who cited Debus (1997) who found that Southern boobook in New South Wales were most vocal in the first half of the night. However, Redpath (1994), when experimenting with imitation calls of Tawny Owls, found no difference between responses and temporal factors such as time of night, or time since sunset.

Again, other factors, for example the meaning inherent within calls, could have a bearing on the proportional response of birds at different times of night due to there being different meanings behind certain calls at certain times.

Effect of season on proportional responses

The lack of significant seasonal difference within either the playback or natural calling data in total proportional responses suggests that morepork are equally responsive to the calls of other morepork across the breeding and non-breeding seasons. From these data, conclusions can be made about the likelihood of responses to other birds' calls, but not conclusions as to the monthly calling rates of morepork. In a concurrent study, morepork calling was found to differ between months, loosely conforming to the breeding cycle (Chapter Three).

In other studies, the varying hypotheses tested show a split between playback studies conducted solely in the breeding season and studies conducted both in and outside the breeding season. Of those which compare breeding and non-breeding seasons directly, Mori et al. (2014) found Eurasian Scops Owl (*Otus scops*) response numbers to playbacks to be significantly greater in the breeding season. Ritchison et al. (1988) found there to be seasonal variation in Eastern Screech Owl responses to playback and that this was linked to breeding, pair bonds and juvenile contact. In Redpath's imitation call study (1994) no seasonal variation in Tawny Owl responses was seen. It was suggested that although the owls advertise less in mid-winter, they will still readily defend territories to the same extent, thus no seasonal variation is seen in responses. This may be true also of morepork.

The methodology may have been a limiting factor in trying to test for a difference in seasonality of proportional responses to playback. March may not have been sufficiently outside the breeding season for a seasonal difference to be apparent. Ritchison et al. (1988) discussed that at the end of the breeding season there will still be a fair amount of contact between juveniles and parents, and one of this study's birds still had dependent, fledged chicks in March, 2014. The reason behind conducting the second series of playbacks in March was the time constraints of a short research project. However, March would seem to be the very earliest boundary of the non-

breeding season, where really July would have been a more appropriate test of non-breeding season had there been time.

It is also difficult to test for a seasonal difference when only one year of data is available, and ideally another two or three years' data are needed to clarify seasonal patterns.

Effect of playback order on responses to playback

The number of playbacks used per session was a trade-off between a potentially greater sample size (with more chances of a playback eliciting a response) and possible habituation to the playbacks, human presence, and associated non-natural noises.

The method of playback used in this study was a non-interactive or fixed-stimulus (Douglas & Mennill, 2010) playback whereby a stimulus was played followed by a quiet period followed by a stimulus until an owl responded, or until five stimuli had been played. Another method is interactive playback, where a greater knowledge of the communication system of a target species facilitates dynamic manipulations of the broadcast during the experiment, depending on the subject's behaviour. Douglas and Mennill (2010) comment that interactive playback often leads to more intense responses because it presents a more relevant and meaningful stimuli than a stand-alone playback. For future playbacks with morepork this method is worth trialling, and during this study's second re-capture mission to remove transmitters from the study birds, a more interactive playback method was used to lure owls into the netting site. This was very effective in getting both responses and successful captures, which suggests it would be a successful playback experimental improvement.

Limitations

Responses, vocal or behavioural, may not have been caused by playbacks themselves as other variables which may have influenced the subjects were present during the tests, despite efforts to minimise their effects. These included other birds not visible to the observer, observer presence, and motivational state of the focal owl.

Only three versions of each call were used due to restricted availability of quality recordings early in the study. While more examples of each call would have reduced the risk of pseudoreplication, at the same time with very limited knowledge of the

context and variation within each call and its inherent function, more examples would run the risk of testing different calls each with a different meaning. Marler & Slabbekoorn (2004) describe how context, age, sex and social status can all affect the rate, volume, and frequency of calls, which may in turn impact their function and meaning. Without the certainty of the context of each call, recorded early on in the study, three examples of each were deemed sufficient.

Field work does not offer the precision of a laboratory testing environment, so it is a trade-off between controlling all the variables and being in a natural environment. Observer presence may have been an influential factor as being too well hidden meant that observations and the ability to record sound would be impeded. Similarly, in an attempt to limit researcher disturbance at a site, I often worked alone. This juggling act of operating playback, sound recording, timing, video, and telemetry equipment meant that occasionally observations may have been missed. However, having a second researcher on hand would not necessarily have helped due to not wanting to cause disturbance by talking. Speaking into the sound recorder was necessary for field notes due to working in often total darkness. This may have caused a disturbance though, as an owl's hearing is much better than a human's. Verbal note taking was deemed less of a disturbance than constantly turning on a light to write. Despite sitting still during the test, my arrival would have disturbed environment as would setting up. We assumed that five minutes was adequate settling time, however, this may not have been the case. Very little is known about startle response behaviour in morepork, however, Imboden (1975) noted that close following using telemetry seemed to disturb their natural behaviour. All of the above factors may have influenced the morepork's likelihood of responding to playback.

A limitation could be the wait time itself, which may have been too short despite being constant across playback and natural call sampling. Often a perceived response occurred after the two minute wait time and was not recorded despite being close and loud (Pers. obs., 2013). This gives rise to questions of where the bird was at the time of playback, would they fly in and how long it would take them to approach, listen for another intruder call, and respond, or would they simply respond immediately. The assumption was made that a response would be made soon after playback and be

relatively loud and close. The fact that the playback may have been perceived as a stranger however, may have necessitated a longer wait than assuming an immediate although reduced response that would be expected to an intruding neighbour. Although using imitations instead of playbacks, Redpath (1994) found that if a wait less than ten minutes had been used, then around 35% of responses in the study would have not been recorded. Likewise, Galeotti and Pavan (1991) found that as many as 50% of their perceived responses did not occur within ten minutes. Both these studies involved Tawny Owls (*Strix aluco*). A longer wait period might be an improvement to the method I used.

The length of the playbacks themselves may also have been a limiting factor, and a longer bout length of the playback calls may have been more appropriate. Most playback calls were less than 30 seconds long, where natural calling bouts of the three call types, especially *more-pork* and *rororo* calls, often last more than a few minutes. The playbacks may have been too short to properly imitate an intruder and gain a representative response; however, the experiment was completed with the calls that were available. Recording trips began in August and playback experiments in November giving only a short period in which to collect recordings of the study birds. Many of the lengthy bouts recorded in the four week-long trips prior to the playback experiments were either lower quality, punctuated by interference (weather, other people, operator movement towards the calling bird, and other species' noise), or were bouts including multiple morepork, which may have had a differing influence on the type of response elicited to a bout from a single morepork. For these reasons, the playbacks selected for the experiment were shorter than ideal, but were high quality recordings of single calling morepork with had minimal interference.

Applications of playbacks

Capture

For this research project, morepork were captured using mist nets. A crucial component in capture methodology was the use of playback calls, with certain call types proving more effective at luring and capturing morepork than others. The contrast in success rate between the initial capture effort to transmitterise the birds

and the effort to re-capture and remove the transmitters was interesting. The initial effort caught eight birds over ten nights where the subsequent effort caught thirteen birds in the same time frame. The most effective call for drawing birds to the netting site was *rororo*, and to a lesser extent the *more-pork* call. The problem with using *more-pork* was that, when used by itself without *rororo*, it was more likely to initiate long bouts of *more-pork* calls from the birds with little movement towards the speakers or around the net. Interestingly however, Stephenson (1998) reports success in capturing morepork in mist nets using this call, so perhaps it is dependent on the motivational state of the bird. *Weow* and *trill* seemed to have little effect as a lure. Once the owls had been drawn in, if the playback had an interaction between two birds (such as a feeding or copulation squeal) this seemed to provoke movement towards the speakers with more frequent passing flights over the net. Frequently switching call types did not achieve many captures and may have confused the birds, but using just one or two of the effective call types aroused curiosity and more importantly movement towards the speakers and net.

The playbacks used for capture were longer than those used for the playback experiments and were often lesser quality and contained more interference noise. As the vocal response was not being studied and the idea was to invoke interest and investigation by morepork of the netting area, broadcast call quality for capture was less important, which enabled the use of longer poorer quality recordings. This may account for the greater behavioural (flight) response to the capture playbacks than the experiment, but vocal response was not quantified whilst capturing birds. This suggests that playback length is more important than my playback study allowed for and a study comparing calls of different lengths and the responses they elicit would be worthwhile.

Acoustic population management

Not only did careful use of certain playback calls draw birds in that were not in the immediate vicinity of the net at the beginning of a capture, but it also had the effect of keeping the owls within the net area for some time, almost anchoring them. Playback song has been used to test the theory of acoustic anchoring to a site in translocated kokako (Molles et al., 2008) and was successful in combination with other factors such as a relatively large number of translocated individuals released in a short space of time and the use of captive individuals. Playback sounds have also been used effectively as an acoustic deterrent. A native predatory bird, morepork have a dietary strategy of exploiting the most abundant prey species. This often leads to a conflict between conservation release of endangered yet morepork-prey species and negative impacts of morepork predation. Conversely to acoustic anchoring, as morepork are such a vocal bird defending territories with calls perhaps future study could investigate the potential of using playback aggressive calls as an acoustic deterrent to deal with the problem of morepork exploitation of the release of predator-naïve captive-bred endangered birds. If further investigation into morepork response and perception includes a territoriality aspect to the study and finds that morepork recognise playback calls as an acoustic competitor, then an acoustic territory boundary could be rigged with an array of speakers around release sites to deter morepork from attacking a recently released endangered species.

Further Study

Playbacks were effective in eliciting responses, but the rate of response was lower than that for natural calls. Response did not seem to be affected by season, but session time, order of playback and call type all had an effect. The study gave an informative view of morepork calling behaviour from a more interactive perspective than passive recordings and observations alone. The study was useful for testing hypotheses on functions of call types. This study's data present a base line for further study into territoriality, individuality and encoded information in vocalisations, population census and management, and conservation of morepork by building on this study's findings and improving its methodology.



Chapter 5 - General Discussion



*When you go owling,
You have to be brave
(Yolen, 1992)*

Overview

Vocalisations are an effective mode of communication that overcomes the visual limitations of darkness for nocturnal species. The morepork is one of New Zealand's most easily recognised birds, known by its disyllabic call which also gives the bird its common names. Calls are important to the morepork's lifestyle, so much so that these birds are more often heard than seen, with different types of call associated with different behaviour. In this study I identified eleven call types: *more-pork*, *trill*, *rororo*, *more-more-pork*, *low trill*, *weow*, *copulation squeal*, *single hoot*, *distress squeak*, *chicketting* and *juvenile begging trill*. There have been few studies on the vocalisations of Hawk-owls (*Ninox* spp.) and only four studies attempted to describe full repertoires. All of the other studies have focussed on just one or two main call types (Table 5.1).

Table 5.1 Table of current knowledge of *Ninox* species vocalisations from scientific literature

Species Name	Common Name	Repertoire Identified	Author(s)	Spectrograms Presented
<i>Ninox novaeseelandiae</i>	NZ Morepork	Eleven calls	Current study	All calls
<i>Ninox novaeseelandiae</i>	NZ Morepork	Seven calls	Stephenson, 1998	One of <i>more-pork</i>
		Ten calls	Higgins, 1999	Some sourced from Southern boobook
<i>Ninox boobook</i>	Southern Boobook	Ten calls	Olsen et al., 2002a Higgins, 1999	None Six
<i>Ninox natalis</i>	Christmas Island Hawk-owl	Six calls	Hill & Lill, 1998	All except <i>squeal</i>
<i>Ninox burhani</i>	Togian boobook	Two calls	King, 2008	Both an alarm call and 'song' plus comparison spectrograms of five other Sulawesi <i>Ninox</i> spp.
<i>Ninox rudolfi</i>	Sumba boobook	Four calls	Olsen et al., 2009	Only for the two territorial call types
<i>Ninox sumbaensis</i>	Little Sumba Hawk-owl	Two calls	Olsen et al., 2009	Both calls
<i>Ninox connivens</i>	Barking Owl	Four calls	Olsen, 2011	None
<i>Ninox strenua</i>	Powerful Owl	Three calls	Olsen, 2011	None
<i>Ninox philippensis complex</i>	7 Philippine Hawk-owl subspecies		Rasmussen et al., 2012	A Mix of 'long songs' and duets of each subspecies

The importance of reporting spectrograms cannot be emphasised enough as this is the only way to compare calls between individuals, regions, and species. Phonetic and other descriptive words do not provide a sufficiently firm base to enable comparisons of calls or repertoires.

Characterisation

This project characterised morepork calls by matching qualitative descriptions with quantitative measurements taken from recordings of individual birds. Knowledge of call repertoires and vocal behaviour can provide insight into the ecology of cryptic or nocturnal animals. As vocal analysis technology advances, calls are increasingly being used to establish species and sub-species boundaries, for example the Philippine Hawk-owl complex investigation conducted by Rasmussen et al. (2012). Likewise, Olsen et al. (2010) compared an owl's call to a DNA fingerprint. They analysed the calls of two *Ninox* owls giving evidence that one of the owls, the Timor Southern boobook (*N. n. fusca*), was a separate species, and Olsen et al. (2002c) distinguished the Little Sumba Hawk-owl (*N. sumbaensis*) as a separate species by its call characteristics. I hope that the data from this study can form a baseline from which to progress knowledge and the study of morepork, both directly and comparatively with other species, in particular the Australian Southern boobook.

Repertoire

I identified eleven different calls made by the morepork (named above), and described their sound, hypothesised their context, and observed associated behaviours (Chapter Two). My more detailed analysis of three most common morepork calls, *more-pork*, *trill*, and *rororo*, using measured spectral (fundamental frequency) and temporal (syllable and inter-syllable durations) characteristics, showed significant variation between the different call types, and also variation between individuals for the same call type, for almost all the measured parameters.

Individual Variation

This study highlights individual variation in morepork calls in both spectral and temporal call characteristics. It was not possible here to test the potential for individual identification by call analysis, or to test whether morepork themselves

recognise the calls of specific individuals, but the finding of individual variation indicates that these may be fruitful lines for enquiry. With individual variation there is scope for more than just announcement of presence; for example, certain calls may deliver information about identity, sex, status, age, dominance, and motivational states.

A difficulty found in morepork call census is that these birds can move quickly from one position to another, thereby confounding the use of bearings and time to indicate separate calling individuals. The possibility of counting a bird more than once and at more than one site was noted by Morgan and Styche (2012) and observed in call surveys conducted in 2013 on Ponui Island (Brighten, unpub. data, 2013). If automatic recordings and software to test individual recognition were to be used alongside call surveys, there could be more certainty about whether one bird has just moved to call in another position or whether this separate call is another bird. This knowledge of individual identity could add accuracy to population estimates of cryptic species, as has been suggested by Otter (1996), and Hill and Lill (1998). This proposed census method would require certainty that an individual bird's calls are consistent over time. My study's findings provide fledgling evidence of this, but confirmation in different sites over a longer study period using a larger sample size may prove beneficial.

Sexual Dimorphism in Calls

Another important finding was the lack of apparent sexual dimorphism in the parameters measured from the three main morepork calls. Despite a heavy sex bias towards females (6:1), the values of the measured parameters of the single wild study male often fell within the ranges of the study females. The individual variation within this study population's calls when there is such a female bias suggests that call differences may be more important in individual identification than sex identification. In territorial disputes, intruders of different sexes pose different threats, but still threats of territorial incursion nonetheless. With such small territories as seen in the island morepork, it is perhaps more important to know the identity of the intruder over its sex when resources are in such demand. The apparent lack of sexual dimorphism in the call parameters measured suggests that morepork identify the sex of an individual in other ways. I propose this could be related to the way a bird of one

sex delivers certain calls, the frequency with which a certain call is uttered, or other measurable characteristics within their calls which were not considered in my study.

This lack of sexual dimorphism was also apparent when body size index and call frequency were compared. A large body size is often associated with a lower frequency call, but my study birds did not show a strong correlation between larger body size and lower call frequency. Neither did I find evidence supporting the suggestions in the literature that morepork and Southern boobook show sexual dimorphism in body size, nor evidence that variation in call frequency is related to sex. Further study into sexual dimorphism with a larger sample size would be interesting.

Temporal Variation

Investigating how vocal behaviour varies over time is not only useful to building an understanding of the communication behaviour of a vocal species, but it can also assist inferences about hunting, habitat bioacoustics, vocalisation functions, and seasonal behaviour such as reproductive season and territoriality. A sound knowledge base of the acoustic ecology and behaviour of a nocturnal, cryptic species has applications in both population monitoring and conservation, whereby more effective and efficient methods of monitoring can be designed using that knowledge base. For example, if there is temporal variation in calling behaviour, this might have an effect on detectability if call surveys are used to investigate abundance and density. This project aimed to investigate whether morepork calling showed temporal variation both across a night (per hour) and across a year (per month).

Temporal variation during a year could be a source of bias in estimates of numbers and would need to be considered. The better the knowledge, the more effective the strategies stand to be.

The use of automated sound recorders combined with sound recognition software was successful in obtaining useful data on the longer term aspects of morepork calling. The software, while initially a challenge to optimise, was very effective in speeding up the analysis of a huge data set compared to manual sound analysis. Through this study I discovered that many sound recognition software packages are less than user friendly to an ecologist who does not have access to advice from a computer and sound

engineer. This study highlighted a gap in the market for sound recognition software that is more accessible to ecologists.

For example, the raw output data from SoundID was a challenge to process. Output files were separate .txt files for each hour-long recording, meaning that with 12 months of 14 hour-long files for each of 5 sites, SoundID produced 840 .txt output files detailing incidence of call-type. To extract the numeric data required for analysis from each of these output files would have required the same method of manually copying and pasting the contents of each text file into an excel spreadsheet. Due to time constraints I decided not to pursue the analysis to call-type level. These data, however, are available and would make an interesting line of investigation in the future where more time is available. Studying the seasonality of call-types would offer useful insight into the function of calls, for example, whether certain call types are used more at certain times of the year or the night than others.

Monthly variation in morepork calling seemed to follow the breeding cycle of morepork, showing an increase in calling in the summer breeding months when compared to the non-breeding winter months. This increase could also be related to prey availability as a study into the morepork diet on Ponui Island (Denny, 2009) found prey numbers increased in summer also. Morepork showed significantly higher amounts of calling five or six and fourteen hours after sunset when compared to other times of the night.

Information about the temporal variation of morepork calling may be useful to both wildlife managers and behavioural ecologists who may be looking for the optimum time to conduct population census or to sample morepork calls. Call patterns might also be shaped by environmental factors such as weather, moonlight, temperature, and social factors such as population density, breeding and age status. The influence of these factors should be investigated to gain a clearer picture of factors that affect the temporal variation identified here. It would also be useful to investigate whether temporal patterns in calling are consistent around New Zealand. This would help greatly in designing population monitoring strategies.

Bioacoustic Methodology

Call Surveys versus Automated Sound Recorders

Bioacoustics analysis provides an effective way of monitoring cryptic populations. When the methods of automated sound recorders and sound recognition software are compared to the more traditional bioacoustic method of call surveys, both have specific advantages and disadvantages. Until recently, manual techniques such as call surveys and visual observations have been favoured for biodiversity monitoring, species specific surveying and conservation, leaving the use of technology-based bioacoustics largely restricted to academia (Steer, 2010).

Call surveys involving human observers are often weather dependent, not only for comfort but also due to the noise interference caused by wind and rain. Weather and wind are taken into account and surveys are often not carried out when it is raining or windy. These conditions vary at different times of year. Calling behaviour may be influenced in an unknown way by the same factors that influence when surveys are conducted. Interestingly, although automated sound recorders are typically able to withstand rain and wind storms, they suffer similar weather-related problems to people when it comes to detecting calls, with even moderate rain and wind masking quieter calls, and heavy rain or wind potentially obscuring all other sounds. Digby et al. (2013) suggest that automated sound recorders are most negatively affected by wind. Unlike human observers who cannot overcome the challenge of hearing other sounds through wind or rain, software engineers are increasingly able to remove certain interference noise from spectrograms to make sounds easier to distinguish (Priyadarshani, Pers. Comm., 2014). Whether this can be applied effectively to very long recordings affected by wind and rain is the subject of on-going research. Interestingly, when it comes to determining annual variation in calling of a species, both field surveys and ASRs produced similar results. (Digby et al., 2013).

Variations in methodologies prompted Clark and Anderson (1997) to discuss the need for standardisation in the way nightly calling in owls is reported, but the difficulty in making cross-study comparisons remains, with a wide variety of methods still being used. The manual process of quantifying calls by visual analysis of whole-night

spectrograms used here was very time consuming, and while it was initially planned as the method in which the whole data set would be extracted from the recordings, automated software was chosen as a more time-efficient method instead. This is a trade-off between greater estimate accuracy from a careful human analyst versus greater time-efficiency from the software, but with a lower accuracy.

Using automated bioacoustic identification techniques offers a potentially more time-efficient method of surveying populations and has been used in a diverse range of animal species (Chesmore, 2004). Chesmore (2004) used a method (IBIS, Intelligent Bioacoustic signal Identification System) for sound recognition of four British orthopterans, and they could successfully distinguish between species under natural conditions in a noisy field environment.

Steer (2010) highlighted some drawbacks of using automated sound recorders such as the battery power necessary for 24-hour recordings. Recent advances in energy solutions, solar charging for example, have largely remedied this. Also, the degradation issue suffered by the equipment in Steer's (2010) study should no longer be a problem because, as suggested at the time, more weather-proof equipment is now readily available, such as the song meter (SM2, SM2+) used to collect data for this chapter. A combination of using automated sound recorders and acoustic analysis was concluded to be an effective non-invasive detection and monitoring method for elusive and nocturnal species (Rognan et al., 2012), and long-term studies stand to benefit most from the reduced field-effort by the researcher afforded by the use of automated sound recorders (Bardeli et al., 2010).

The advantage of using automated sound recorders is highlighted by some of the challenges in using manual sound recorders described in Chapter Two. Automated sound recorders alleviate the potential bias caused by observer presence that may alter owl behaviour – a problem shared with call surveys. Imboden (1975) noted that morepork changed their behaviour if followed too closely, and with manual sound recording the operator must get fairly close to the subject, so it was possible that a disproportionate number of alarm calls were observed despite taking care to move quietly.

Comparison of the efficacy of the software method versus the call survey method requires consideration of time, funding, man-power, and computer literacy. Both methods are unfortunately time-expensive. It currently takes a long time and considerable computer engineering knowledge to optimise software such as SoundID to recognise specific call types in order to obtain acceptable identification accuracy. Likewise with call surveys; to get comparable results, multiple surveys using trained individuals are required. As studies may take place over a number of years, it is in the time scale of the project where the software method begins to win out. While it takes considerable time to optimise the software to specific bird calls in an area, once that is done it should not be necessary again because the software remains optimised to those bird calls. The raw recordings then only require a few cuts (to ensure appropriate file lengths) or programming the automated sound recorder to record a certain file length. The software used in this study had its own file cutter, which when pointed at a hard drive of many large recording files and cut them all into time-specified chunks. Access to multiple computers or a couple of high-RAM, fast processor capable machines was then required for analysis. The advantage of automated sound recorders is that man-hours are removed from data collection, allowing work to be done in other areas. In the long-term, the software option has the potential for being more time efficient when large data sets are required.

In terms of accuracy, however, the software's 40% identification rate of the total calls occurring in a night (cross-check by careful visual spectrogram inspection) means that the software cannot yet rival the human ear and attention to detail of manual sound analysis. Within this 40% though, the software can be optimised to a very accurate true-positive rate of over 90%. This consistency means that while it may lack accuracy in total call estimates, it is very useful for plotting overall time-series trends.

There have not been many studies published directly comparing automated sound recording and analysis to established manual call surveying, although Digby et al. (2013) made this comparison in his study of another of New Zealand's cryptic, nocturnal species, the Little Spotted kiwi. Digby et al. (2013) confirmed the precision and low time cost, but similarly to this study, found that it was less sensitive than manual sound analysis with visual spectrogram analysis finding 80% of the total calls.

Digby et al. (2013) highlighted that sensitivity is related to the strength of a sound or how loud it is. Both techniques have benefits and drawbacks, so perhaps a combination of initial call surveys followed up by a permanent record of the sound recorded by automated sound recorder would be most effective.

SoundID, while saving considerable time over having to manually search 14-hour recordings, did require extensive time to isolate and cut a large number of reference call examples and then to optimise the software, which required advice and assistance from a software engineer and sound expert (Brighten & Priyadarshani, unpub. data, 2014). There is certainly room for the development of more non-engineer ecologist-friendly software with greater accuracy.

Call Function

Not only repertoire, but an understanding of the behaviour and function behind each call type of a species provides valuable knowledge to further studies of their behavioural ecology. Most commonly this is studied with behavioural experiments involving analysis of an individual's response to playbacks of pre-recorded calls broadcast to them in the field or laboratory. This project investigated the responses of New Zealand morepork to different call types broadcast in playback experiments with the aim to describe the context and function of certain call types.

Playbacks were effective in this study in eliciting responses from morepork, but the proportion of responses to playback was lower than to natural calls. Playback experiments allow greater control over the study, and although field playbacks do not enable the extent of control possible in the laboratory, it is at least a natural environment where the focal owl can behave as naturally as possible. In this study, response did not seem to be affected by season, although this may have been limited by the methodology. Session time, order of playback and playback call-type all had an effect on proportional responses.

In the control data of this investigation, temporal variation across the duration of a night was found and was concordant with the suggestion in chapter three of morepork calling varying according to time after sunset. This trend was supported by the playback data but, perhaps due to a limited sample size, the differences were not

significant. In contrast to the findings of Chapter Three, however, no difference found between 'season', perhaps due to March being classified as non-breeding when July may have been a more appropriate month to use, had there been time.

The study gave an interesting view of morepork calling behaviour from a more interactive perspective than passive recordings and observations alone. The study was useful for testing hypotheses on functions of call-types. The data will hopefully be useful in future as a base line for further study into territoriality, individuality and encoded information in vocalisations, population census and management, and conservation of morepork, building on this study's findings and improving methodology.

My findings that there were a lower number of responses to playback calls when compared to natural calls of the same type have implications to field monitoring of morepork. A common method of population survey of owls involves using playbacks to elicit responses. While playbacks do elicit a response, this may not be a reliable method in estimating morepork population sizes because I found that morepork do not reply in the numbers expected from natural observation data. This technique should be used with caution in morepork population surveys.

Encoded information

A factor beyond the scope of this experiment worth mentioning here is the information inherent in a call. Most owls are active in darkness which means that they must overcome the challenge of communicating in low light where the efficacy of visual displays is limited. As previously discussed, vocalisations are a very effective method of nocturnal communication and are a critical part of the ecology of almost all members of the Strigidae family. A particularly interesting area of research is that investigating vocal individuality and the information encoded within vocalisations.

Calls have the potential to contain information about the status, age and sex of the caller. This encoded information could influence the responses that a certain caller exhibits. Appleby et al. (1999) found the sex of caller in Tawny Owls significantly affected the likelihood of a response in females, but not in males. Interestingly, Appleby et al. (1999) cited studies that found a significantly greater response if the

playback or intruder is of the same sex as the respondent. Their experiment likewise found that female Tawny Owls were more likely to respond to female calls, but this was not true of male Tawny Owls in response to male playback calls, where they found no significant difference in response to either playback sex. This study found no evidence of sexual dimorphism in calling from the spectral and temporal call parameters analysed (Chapter Two), but further research is necessary into whether morepork can discriminate the sex of a calling bird and whether they respond differently to calls of different sex as this was not investigated by this study.

The reduced response to playbacks in my study could be due to the methodology. Only relatively short recordings were available and this may not have been a long enough stimulus to engage a bird. Played back calls were often shorter due to interference or another bird calling later in the recording. It was not possible to find equally short calls in the automatic natural recordings, so the bouts responded to by wild birds in the natural controls were likely longer call bouts than the playback calls used. While every effort was taken to play only high quality recordings, there was still a certain degree of background-noise in the played back call due to the speakers. Regarding the order of playback, as it was a fixed-stimulus experiment, there was not often a follow-up playback call after the initial play back to enforce a simulated acoustic competitor's presence, and likewise it begs the question of how natural a relatively short bout of a call played at two-minute intervals was. There is a distinct possibility that the owls recognised that the speakers were not an immediate threat worth responding to.

Territoriality

Territoriality was not tested in this study, focussing on investigating the function of certain morepork call types, which generated hypothesised functions from field observations and then tested if playback delivered similar responses to those heard in the field. While this study did not have the scope required for a territoriality study, because morepork are territorial, this is likely a key influence on their vocalisations and is a gap in morepork behaviour knowledge worth investigating further. In this way this study's data may be useful in future as a basis to study territoriality in morepork by building on its findings and improving methodology.

Implications

The morepork is often compared to the Australian Southern boobook, until recently classified as the same species, and inferences into behaviour of morepork often rely on studies of boobook. There is debate surrounding whether the morepork and boobook should be classed as separate species and this now prompts the question of whether it is still appropriate to draw inferences about morepork from the boobook. An avenue of further investigation would be a direct comparative study into the difference between the calls of the morepork and boobook. A study would also be useful that includes comparisons with calls from other *Ninox* species, for example the Christmas Island Hawk-owl to the morepork in the way that Rasmussen et al. (2012) compared the Philippine Hawk-owl complex, and Olsen et al. (2002c) compared the Southern boobook and two Indonesian species, distinguishing the Little Sumba Hawk-owl (*N. sumbaensis*) as a separate species. Through this study, I have described the various calls of the morepork and many, if not all, appeared to resemble vocalisation descriptions of the boobook and Christmas Island Hawk-owl (spectrograms in Chapter One). Comparative statistical analysis would offer fascinating insight into how these species differ.

Another implication of vocalisation studies is to build on the technique of using vocalisations as a population census method. Predators like morepork, and owls in general, can be good biomonitors, or indicators of habitat health and ecosystem status (Stephenson et al., 1998). Owls have been found to be very sensitive to environmental contaminants and have been reportedly underused as sentinel species to monitor environmental contamination (Sheffield, 1997). With New Zealand's continued and increased use of poison as the main control method for introduced mammalian pest species, a close watch needs to be kept on non-target native species populations which may be at risk of secondary poisoning.

Capture Methodology

Eight morepork were successfully captured over ten nights early in the study using methods and advice from previous published studies and researchers' experience. The

methods are described in detail in chapter two and what follows is further discussion which may be of use to future studies involving capture efforts.

In this study, only captures at night were attempted, but it is difficult to define an optimum capture time of night due to each site having many variables which may have affected capture success. These include the amount of light; the density of the vegetation at a site; the speed at which darkness falls at a site; the openness of the site; the proximity of other nets; and the potential to unknowingly be on a territory edge or centre giving varying results with playback. All these factors may have affected capture success at a site to varying degrees. Early evening did appear more successful than later on, but a study into this was not attempted and the small sample size is by no means conclusive. This observation does, however, concur with previous studies such as Denny (2009) who reported early evening and early morning to be optimum capture times.

Mist-nets were deployed in areas where morepork had previously been sighted or heard, but also in areas where morepork were calling at the time, so while some capture sites were pre-defined, others were created on a more reactionary basis, resulting in a degree of flexibility in site choice methodology. See Chapter Two methods and figure 2.2 for more detail. Using multiple netting locations in a night was deemed impractical and not time efficient due to the time needed to power down nets, move between locations, and set the nets up again and wait for the environment to settle after the disturbance. Generally it was clear after about an hour whether the morepork were interested in the playback calls or items at the nets, but once a bird was interested, the time taken for it to approach the net varied greatly.

Use of playback calls was a highly successful strategy in attracting and capturing morepork. It involved the use of multiple, mostly high-quality locally-made recordings of the different morepork call-types broadcast through high-quality portable Sony speakers hidden beneath the nets. The protocol of using playback calls as a lure began with little knowledge of the optimum calls to play, however, it was agreed that calls played should vary and that none should be too heavily used. Over-use of playback calls had the potential to induce confusion, habituation and reduce the probability of a

capture if the environment became saturated with playback calls. Toward the end of the capture effort, a pattern became apparent and it was noted that certain calls elicited different responses. Over-use of the *more-pork* call often instigated a long bout of response calling where the target birds remained in nearby trees, not flying around, whereas *trills*, a recording of two birds at once, and the *copulation squeal* resulted in increased movement to investigate the source of the foreign calls. It was these reconnaissance flights that resulted in most captures.

As discussed in Chapter Four, the lengths of the playbacks for mist-netting were often longer than those used in the experiments. In future, I think that longer playback calls may be more effective than the shorter versions I used in my experiments. This is because shorter calls may simply not have been long enough to be sufficient stimulus for a morepork to respond. In future it would be beneficial to focus on recording longer, high-quality, interference-free calls specifically for use in playback, but in my study there was not time. This may address the apparent disparity in effectiveness of eliciting responses, whether vocal or investigatory flight behaviour, between the playback experiments and mist-netting missions. There is also, however, the possibility that the thresholds to elicit an investigatory flight versus a vocal response are different and that call types used to capture birds were not all tested by the playback experiments.

Having only two trips prior to July 2013 to collect lure calls for capture playback meant that the range of calls available for the initial capture effort was limited. In a second capture mission to attempt to remove the transmitters from the study birds, the whole study's worth of recordings could be chosen from. Also, after a year of studying morepork calls, I was better placed to make inferences into which calls might be more successful than others. In addition to morepork calls, calls of prey species were trialled with mixed success. While purely observational, the calls of a myna bird (*Acridotheres tristis*) in distress (recorded in August 2013 when Macchiato caught one in the trees), and the noise of tree weta (*Hemideina thoracica*) certainly provoked investigatory flights around the nets.

In addition to the calls, various items to invoke interest in the net area were trialled with varying success. These included an 'Original Mockingbird™ Audubon bird caller to mimic a distressed small-bird call; egg-carton cut outs of moths and bugs; two plush morepork (one small; the other, Murphy, large), or Saddleback placed in a net pocket or perched nearby; and a plush bat on fishing twine strung over a nearby branch and manipulated from a distance.

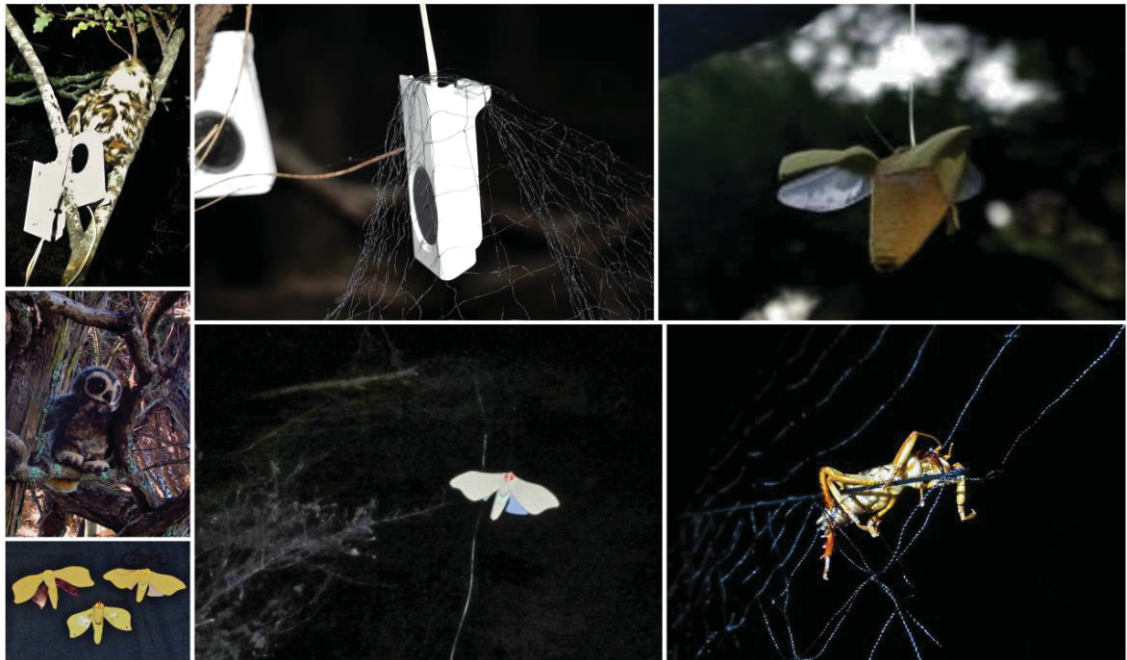


Figure 5.1 Lures used during morepork capture missions: Plush morepork and speakers in a tree (Top left); Speakers net after a gust of wind (top centre); Shaun's egg carton decoy beetle in flight (top right); Murphy the large plush morepork (Left mid); Three egg carton moth decoys (bottom left); Deployed decoy moth (bottom centre); Dead and dry Tree Weta from an entomology collection (bottom right).

The plush moreporks certainly drew attention, one even being attacked, however, it is unclear how useful the saddleback and bat were. It was intended that a taxidermy decoy morepork be placed near to the net to enforce the presence of a stranger in their territory along with unfamiliar playback calls. Unfortunately, this decoy suffered predation or defaulted in an early netting practice at dusk and remains missing in action. Perhaps an ode to the potential effectiveness of a taxidermy decoy if it is not securely fastened to its perch to ensure continued use! In the re-capture efforts dead insects sourced from Massey University's surplus entomological collection, such as tree weta and large moths, were trialled hung in the mist nets. It was difficult to define how effective they were.

To reduce the stress on the morepork during handling, I recommend the use of a falconer's hood. Other studies have used cotton bags placed over the head of the bird. However, the benefit of a hood is that it is securely fitted over the bird's head, so the bird can be moved and manipulated without the inconvenience of the bag slipping off. The hood is secured by two pairs of braces, one pair loosens the hood, and the other tightens. These are designed to be stiff and sit away from the bird and enable the handler to tighten and loosen the hood with one hand whilst holding the bird (Figure 5.2). While I could not source a bespoke morepork hood, one made for the Australasian Harrier (*Circus approximans*) worked well.



Figure 5.2 Use of a falconer's hood on morepork: Hood showing braces (top left); Morepork being hooded (top right); Use of hood to keep morepork calm whilst measurements are taken (bottom left); Morepork with hood and hood tighten/loosen with one hand technique (bottom centre and right).

For identification in at night, the combined use of radio-transmitters and reflective tape on leg bands was very effective and this has also been reported by Stephenson et al. (1998) in morepork. The reflective tape adds visual confirmation of identity if there is any doubt about telemetry signal.

Recommendations for Further Study

Further investigation into whether individual morepork can be identified by their calls by use of methods such as discriminant function analysis (Hill & Lill, 1998) will be useful to confirm whether individual morepork could be identified in the field. Field observations from this study suggest this may be difficult however there were three birds that I could identify by ear from their calls. Other studies have reported identification by call as a challenge in the field, but if sound recognition software is able to use spectral or temporal characteristics of calls to identify individuals, then this could have useful implications to monitoring populations using automated sound recording and recognition techniques.

As well as individual variation, geographic variation would be interesting to study further. Hill and Lill (1998) found no evidence of geographic variation or dialect in *Ninox natalis* and may offer insight into whether calls vary geographically. While the Ponui Island morepork and Wingspan captive morepork did not seem to vary a great deal in the parameters measured, this would be an interesting line of study to conduct with a larger sample size. This information would add to the investigation of whether morepork and boobook should be separate species. Along the same lines, an investigation into direct comparisons between recordings and analysis of morepork and boobook calls would be worth pursuing to add evidence to the debate on whether they are separate species.

Further study should aim to investigate the behaviour associated with calling in morepork by improving on the methodology of this study. Regarding sexual dimorphism, morepork may identify sex using behaviour instead of call characteristics, for example, how often sexes use each call. Also, a study into their territoriality would be useful as this study did not investigate whether the Ponui Island birds favour certain calling posts from which to give territorial calls, as has been identified in other studies. A follow-on study could involve using playbacks to further study the perception of different examples of the same call to investigate whether morepork respond differently to different versions of the same call-type.

Although behaviour cannot be observed in the context of the automatic recordings, they could provide useful information about the function of different calls types in a temporal sense by quantifying the amount they are used and if variation exists in when they occur across a night and year. The nature of the output from the software and time limitation meant that this was not possible in this thesis. Likewise, for this thesis, environmental influences on calling such as weather and lunar cycle were not analysed, however, call type, weather, and lunar data are available and would be an interesting follow-up research report. The resulting data and inferences would hopefully build on my findings from this study and be useful to the design of monitoring programs and add further knowledge of nocturnal avian communication to the growing amount of literature on the subject.

Currently a common native bird species that is a very vocal, the morepork could be used to develop or improve call survey techniques and the up-and-coming sound recognition software. It could be used to optimise methods intended for monitoring rarer vocal species for which there are fewer opportunities to test methods. There is room for improvement in sound recognition software, and this could also be addressed in future in order to provide a much-needed ecologist-friendly software package.



Literature Cited

- Adobe Audition CC. (Version 2014.2). [Computer Software]. San Jose, CA: Adobe Systems Inc.
- Aikman, H. (1999). Attempts to establish Shore Plover (*Thinornis novaeseelandiae*) on Motuora Island, Hauraki Gulf. *Notornis*, 46, 195-205.
- Alcock, J. (2009). *Animal Behavior: an evolutionary approach, (Ninth Ed.)*. MA, USA: Sinauer Associates.
- Amy, M., Sprau, P., de Goede, P., & Naguib, M. (2010). Effects of personality on territorial defence in communication networks: a playback experiment with radio-tagged great tits. *Proceedings of the Royal Society B*, 277, 3685-3692.
- Anderson, S. H. (1992). Shearwaters and saddlebacks as prey at a morepork ground nest. *Notornis*, 39, 69-70.
- Asia Pacific Defence Reporter (APDR). (2012). *NINOX: all-seeing hunter of the night*. Retrieved from:
<http://www.asiapacificdefencereporter.com/articles/268/Ninox-all-seeing-hunter-of-the-night>
- Appleby, B. M., & Redpath, S. M. (1997). Indicators of male quality in the hoots of tawny owls (*Strix aluco*). *Journal of Raptor Research*, 31(1), 65-70.
- Appleby, B. M., Yamaguchi, N., Johnson, P. J., & MacDonald, D. W. (1999). Sex-specific territorial responses in Tawny owls *Strix aluco*. *Ibis*, 141, 91-99.
- Baker, M. C. (2001). Bird song research: the past 100 years. *Bird Behavior*, 14, 3-50.
- Baptista, L. F., & Gaunt, L. L. (1997). Chapter 9: Bioacoustics as a tool in conservation studies. In R. Buchholz & J. R. Clemmons (Eds.), *Behavioural approaches to conservation in the wild*. (pp. 212-242). Cambridge, UK: Cambridge University Press.
- Bardeli, R., Wolff, D., Kurth, F., Koch, M., Tauchert, K.-H., & Frommolt, K.-H. (2010). Detecting bird sounds in a complex acoustic environment and application to bioacoustic monitoring. *Pattern Recognition Letters*, 31, 1524-1534.
- Bellingham, P. J. (1979). The birds of Ponui (Chamberlin's) island, Hauraki Gulf, August 1978. *Tane*, 25, 17-21.

- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57, 289-300.
- Bioacoustics Research Program. (2011). Raven Pro: Interactive Sound Analysis Software (Version 1.4) [Computer Software]. Ithaca, NY: The Cornell Lab of Ornithology. Available from <http://www.birds.cornell.edu/raven>
- BirdLife International. (2009). *Ninox novaeseelandiae*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Retrieved from www.iucnredlist.org
- BirdLife International. (2014a) *The BirdLife checklist of the birds of the world: Version 7*. Retrieved from: http://www.birdlife.org/datazone/userfiles/file/Species/Taxonomy/BirdLife_Checklist_Version_70.zip
- BirdLife International. (2014b). *IUCN Red List for birds*. Retrieved from <http://www.birdlife.org>
- Borkin, K. M., & Ludlow, E. (2009). Notes on New Zealand mammals 9: long-tailed bat (*Chalinolobus tuberculatus*) chased by morepork (*Ninox novaeseelandiae*), *New Zealand Journal of Zoology*, 36(1), 11-12.
- Boucher, N. J., Jinnai, M. & Aston, D. (2003). SoundID: for sound recognition and monitoring. Retrieved from <http://www.soundid.net>
- Brandes, S. T. (2008). Automated sound recording and analysis techniques for bird surveys and conservation. *Bird Conservation International*, 18, S163-S173
- Bretagnolle, V. (1989). Calls of Wilson's Storm Petrel: functions, individual and sexual recognitions, and geographic variation. *Behaviour*, 111(1), 98-112.
- Brittan-Powell, E. F., Lohr, B., Hahn, D. C., & Dooling, R. J. (2005). Auditory brainstem responses in the Eastern Screech Owl: an estimate of auditory thresholds. *Journal of the Acoustical Society of America*, 118(1), 314-321.
- Brown, E. A. (1979). Vegetation and flora of Ponui Island, Hauraki Gulf, New Zealand. *Tane*, 25, 5-16.
- Brown, K., & Mudge, D. (1999). Feeding sign of moreporks (*ninox novaeseelandiae*) on birds. *Notornis*, 46, 346-353.
- Camilli, G., & Hopkins, K. D. (1978). Applicability of chi-square to 2 x 2 contingency tables with small expected call frequencies. *Psychological Bulletin*, 85(1), 163.
- Camilli, G., & Hopkins, K. D. (1979). Testing for association in 2 x 2 contingency tables with very small sample sizes. *Psychological Bulletin*, 86(5), 1011.

- Campbell, N. A., & Reece, J. B. (2008). *Biology* (Eighth ed.). San Francisco, CA, USA: Pearson Education Inc.
- Castro, I. C., Brejaart, R., & Owen, K. (2000). *Status of weka (Gallirallus australis greyi) on Mokoia Island*. Department of Conservation: *Conservation Advisory Science Notes* 314.
- Catchpole, C. K., & Slater, P. J. B. (2008). *Bird song: biological themes and variations* (2nd ed.). Cambridge, England. Cambridge University Press.
- Catchpole, C. K. (1979). *Vocal communication in birds*. London, England. Edward Arnold Publishers Ltd.
- Charif, R. A., Strickman, L. M., & Waack, A. M. (2010). Raven Pro 1.4 User's Manual. The Cornell Lab of Ornithology, Ithaca, NY.
- Cheney, D. L., & Seyfarth, R. M. (1982). How Vervet Monkeys perceive their grunts: field playback experiments. *Animal Behaviour*, 30, 739-751.
- Chesmore, D. (2004). Automated bioacoustic identification of species. *Annals of the Brazilian Academy of Sciences*, 76(2), 435-440.
- Christidis, L. & Boles, W. (2008). *Systematics and taxonomy of Australian birds*. Melbourne, Australia. CIRSO Publishing.
- Clapperton, B. K. (1987). Individual recognition by voice in the pukeko, *Porphyrio porphyrio melanotus* (Aves: Rallidae), *New Zealand Journal of Zoology*, 14(1), 11-18.
- Clark, K. A., & Anderson, S. H. (1997). Temporal, climatic and lunar factors affecting owl vocalisations of Western Wyoming. *Journal of Raptor Research*, 31(4), 358-363.
- Clark, J. M. (1992). Food of the morepork in taranaki. *Notornis*, 39, 94.
- Corfield, J. (2005). *Description, duetting, seasonal variations, and individual identification of the vocalisations of the Brown Kiwi (Apteryx mantelli)*. (M.App.Sc. Thesis), Auckland University of Technology, Auckland, New Zealand.
- Corfield, J., Gillman, L., & Parsons, S. (2008). Vocalisations of the North Island Brown Kiwi (*Apteryx mantelli*). *The Auk*, 125(2), 326–335.
- Crawford, S. C. (1934). The habits and characteristics of nocturnal animals. *The Quarterly Review of Biology*, 9(2), 201-214.
- Cunningham, J. M. (1948). Food of a Morepork. *New Zealand Bird Notes*, 3, 22-24.

- Dalla Costa, E., Minero, M., Lebelt, D., Stucke, D., Canali, E., Leach, M. C., (2014). Development of the horse grimace scale (HGS) as a pain assessment tool in horses undergoing routine castration. *PLoS ONE*. 9(3), 1-10.
- Darwin, C. (1872). The expression of the emotions in man and animals. London, England. Murray.
- Debus, S. J. S. (1996). Mating behaviour of the Southern Boobook. *Australian Bird Watcher*, 16, 300-301.
- Debus, S. (1997). Vocal behaviour of the Southern Boobook (*Ninox novaeseelandiae*) and other nocturnal birds. In G. Czechura & S. Debus (Eds.) *Australian Raptor Studies II*. Birds Australia Monograph 3: 71-85. Melbourne: Birds Australia.
- Deecke, V. B. (2006). Studying marine mammal cognition in the wild: a review of four decades of playback experiments. *Aquatic Mammals*, 32(4), 461-482.
- del Hoyo, J., Elliott, A., & Sargatal, J. (Eds.) (1999). *Handbook of the Birds of the World, Volume 5, Barn-owls to hummingbirds*. Lynx Edicions, Barcelona.
- del Hoyo, J., Collar, N. J., Christie, D. A., Elliott, A., Fishpool, L. D. C. (2014). *Handbook of Birds of the World and BirdLife International Illustrated Checklist of the Birds of the World*. Lynx Edicions BirdLife International.
- Denny, K. M. (2009). *The diet of moreporks (Ninox novaeseelandiae) in relation to prey availability, their roost site characteristics and breeding success on Ponui Island, Hauraki Gulf, New Zealand*. (M.Sc.Thesis) Massey University, Albany, New Zealand.
- Department of Conservation (DoC) (n.d.) Morepork/ruru: Threats. Retrieved from: <http://www.doc.govt.nz/nature/native-animals/birds/birds-a-z/morepork-ruru/>
- Department of Conservation (DoC). (2012a). Critically endangered New Zealand Shore Plover released on Motutapu Island. Retrieved from: <http://www.doc.govt.nz/news/media-releases/2012/critically-endangered-nz-shore-plover-released-on-motutapu-island/>
- Department of Defence, Australian Government. (2000). *New defence projects approved* Retrieved from: <http://www.defence.gov.au/minister/1tpl.cfm?CurrentId=167>
- Deutch, C. J., Haley, M. P., & Le Boeuf, B. J. (1990). Reproductive effort of male Northern elephant seals: estimates from mass-loss. *Canadian Journal of Zoology*, 68(12), 2580-2593.

- Digby, A., Towesy, M., Bell, B. D., & Teal, P. D. (2013). A practical comparison of manual and autonomous methods for acoustic monitoring. *Methods in Ecology and Evolution*, 4, 675-683.
- Digby, A., Towesy, M., Bell, B. D., & Teal, P. D. (2014). Temporal and environmental influences on the vocal behaviour of a nocturnal bird. *Journal of Avian Biology*, 45, 591-599.
- Douglas, S. B., & Mennill, D. J. (2010). A review of acoustic playback techniques for studying avian vocal duets. *Journal of Field Ornithology*. 81(2), 115-129.
- Duan, S., Zhang, J., Roe, P., Wimmer, J., Dong, X., Trusking, A., & Towsey, M. (2013). Timed probabilistic automaton: a bridge between Raven and Song Scope for automatic species recognition. Proceedings of the 25th Innovative Applications of Artificial Intelligence Conference.
- Everett, M. (1977). A natural history of owls. The Hamlyn Publishing Group Ltd. London, England.
- Fischer, J., Noser, R., & Hammerschmidt, K. (2013). Bioacoustic field research: a primer to acoustic analyses and playback experiments with primates. *American Journal of Primatology*, 75(7), 643-663.
- Fisher, J. B. (1954). Evolution and bird sociality. In J. Huxely, A. C. Hardy, & E. B. Ford. (Eds.) *Evolution as a Process*. pp 71-83. London, England. Allen & Unwin.
- Fleay, D. (1968). *Nightwatchmen of bush and plain. Australian owls and owl-like birds*. Brisbane, Australia. Jacaranda Press.
- Foote, J. R., Palazzi, E., & Mennill, D. J. (2013). Songs of the Eastern Phoebe, a subcine songbird, are individually distinctive but do not vary geographically. *Bioacoustics*, 22(2), 137-151.
- Fox, N. C., & Lock, J W. (1978). Organochlorine residues in New Zealand birds of prey. *New Zealand Journal of Ecology*. 1, 118-125.
- Fraser, E. A., & Hauber, M. E. (2008). Higher call rates of morepork, *Ninox novaeseelandiae*, at sites inside an area with ongoing brodifacoum poisoning compared with matched non-managed sites. *New Zealand Journal of Ecology*, 35(1), 1-7.
- Freeberg, T. M., & Lucas, J. (2010). Communication; an overview. In: M. D. Breed, & J. Moore, (Eds.), *Encyclopedia of Animal Behavior, Volume 1*, (pp. 337-339) Oxford: Academic Press.

- Galeotti, P., & Pavan, G. (1991). Individual recognition of male Tawny owls (*Strix aluco*) using spectrograms of their territorial calls. *Ethology, Ecology & Evolution*, 3(2), 113-126.
- Garcia, M., Charrier, I., Rendall, D., Iwaniuk, A. N. (2012). Temporal and spectral analyses reveal individual variation in a non-vocal acoustic display: the drumming display of the ruffed grouse (*Bonasa umbellus*, L.). *Ethology*, 118, 292-301.
- Geyer, T., Sarradj, E., & Fritzsche, C. (2014). Measuring owl flight noise. In *INTER-NOISE Congress and Conference Proceedings*, 249(8), (pp. 183-189). Institute of Noise Control Engineering.
- Greene, T. C., Dilks, P. J., Westbrooke, I. M., & Pryde, M, A. (2013). Monitoring of selected forest bird species through aerial application of 1080 baits, Waitutu, New Zealand. *New Zealand Journal of Ecology*. 37(1), 41-50.
- Hardouin, L. A., Reby, D., Bavoux, C., Burneleau., & Bretagnolle, V. (2007). Communication of male quality in owl hoots. *The American Naturalist*, 169(4), 552-562.
- Hardouin, L. A., Tabel, P., & Bretagnolle, V. (2006). Neighbour-stranger discrimination in the little owl, *Athene noctua*. *Animal Behaviour*, 72, 105-112.
- Harris, J. B. C., & Haskell, D.G. (2013). Simulated birdwatchers' playback affects behaviour of two tropical birds. *PLoS ONE*, 8(10), 1-8.
- Hattena, A. M., Munoz, M., & Blumstein, D. T. (2014). Prey responses to predator's sounds: A review and empirical study. *Ethology*, 1(20), 427-452.
- Haw, J. M., & Clout, M. N. (1999). Diet of morepork (*Ninox novaeseelandiae*) throughout New Zealand by analysis of stomach contents. *Notornis*, 46, 333-345.
- Haw, J. M., Clout, M. N., & Powlesland, R. G. (2001). Diet of moreporks (*Ninox novaeseelandiae*) in Pureora forest determined from prey remains in regurgitated pellets. *New Zealand Journal of Ecology*, 25(1), 61-67.
- Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., & Le Boeuf, B. J. (2004). Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Animal Behaviour*, 67(6), 1133-1139.
- Heather, B. D., & Robertson, H. A. (2005). Morepork (Ruru) *Ninox novaeseelandiae*. In *The field guide to the birds of New Zealand*. (pp 142-143, 365-366) Auckland, Penguin Books.

- Herting, B. L., & Belthoff, J. R. (2001). Bounce and double trill songs of male and female Western Screech-owls: characterisation and usefulness for classification of sex. *The Auk*, 118(4), 1095-1011.
- Higgins, P. J. (Ed.) (1999) *Handbook of Australian, New Zealand and Antarctic birds, volume four: Parrots to Dollarbirds*. Melbourne, Australia. Oxford University Press.
- Hill, R. F. A., & Lill, A. (1998). Vocalisations of the Christmas Island Hawk-owl *Ninox natalis*: individual variation in advertisement calls. *Emu*, 98(3), 221-226.
- Hojem, C. (2006). *The real New Zealand national anthem: calling structure and calling rate of North Island Brown Kiwi (Apteryx mantelli) on Ponui Island and comparisons with Rarewarewa Reserve*. (M.Sc. Thesis), University of Auckland, Auckland, New Zealand.
- IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.
- Imboden, C. (1975). A brief radio-telemetry study on moreporks. *Notornis* 22(3), 221-230
- Imboden, C. 1985. Morepork *Ninox novaeseelandiae novaeseelandiae*. In: C. J. R. Robertson (Ed.), *Reader's Digest complete book of New Zealand birds*. (pp. 257). Sydney, Australia. Reader's Digest.
- Karl, B. J. & Clout, N. (1987). An improved radio transmitter harness with a weak link to prevent snagging. *Journal of Field Ornithology*, 58, 73-77
- King, B. (2002) Species limits in the Brown Boobook *Ninox scutulata* complex. *Bulletin of the British Ornithologists Club*, 122, 250–256.
- King, B. (2008). Vocalisations of the Togian Boobook *Ninox burhani*. *Forktail*, 24, 122-123.
- King, B., & Icaragnal, N. (2008). Territorial behaviour of Northern Boobook *Ninox japonica*, on Calayan Island, northern Philippines. *Forktail*, 24, 124-125.
- Konig, C., Weick, F. & Becking, J. H. (1999). *Owls, A guide to owls of the world*. Pica Press, Sussex, UK.
- Konishi, M. (1973). How the owl tracks its prey: experiments with trained barn owls reveal how their acute sense of hearing enables them to catch prey in the dark. *American Scientist*, 61(4), 414-424.
- Kroodsmas, D. E. (1989). Suggested experimental designs for song playbacks. *Animal Behaviour*, 37, 600-609.

- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S., & Liu, W. (2001). Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour*, 67, 1029-1033.
- Langford, D. J., Bailey, A. L., Chanda, M. L., Clarke, S. E., Drummond, T. E., Echols, S., Glick, S., Ingrao, J., Klassen-Rose, T., La Croix-Fralish, M. L., Matsumiya, L., Sorge, R. E., Sotocinal, S. G., Tabaka, J. M., Wong, D., van de Maagdenberg, A. M. J. M., Ferrari, M. D., Craig, K. D. & Mogil, J. S. (2010). Coding of facial expressions of pain in the laboratory mouse. *Nature Methods*, 7(6), 447-449.
- Leach, M. (1992). *The complete owl*. London, England. Chatto & Windus Ltd.
- Lowry, R. (2014). Chi-square calculator matrix. VassarStats: Website for Statistical Computation. Retrieved August 2014 from www.vassarstats.net
- Marler, P. (1961). The logical analysis of animal communication. *Journal of Theoretical Biology*, 1, 295-317.
- Marler, P. & Slabbekoorn, H. (Eds.) (2004). *Nature's Music. The science of bird song*. London, UK. Elsevier Academic Press.
- Martinez, J. A., & Zuberogoitia, I. (2003). Factors affecting the vocal behaviour of Eagle owls *Bubo bubo*: effects of season, density and territory quality. *Ardeola*, 50(2), 255-258.
- McCann, C. (1959). Early breeding of the morepork in 1958. *Notornis*, 8(4), 120-121.
- McDonald, P. G., Olsen, P. D., & Cockburn, A. (2005). Selection on body size in a raptor with pronounced reversed sexual size dimorphism: are bigger females better? *Behavioural Ecology*, 16(1), 48-56.
- Mees, G. F. (1964). A revision of the Australian owls. *Zoologische Verhandelingen*, 65, 1-62.
- Melville, D. S. (2011). New Zealand national bird banding scheme: bird bander's manual. Department of Conservation. Wellington, New Zealand.
- Mikkola, H. (1983). *Owls of Europe*. Staffordshire, England. T & A D Poyser Ltd.
- Molles, L. E., & Waas, J. R. (2006). Are two heads better than one? Responses of the duetting kokako to one-and two-speaker playback. *Animal behaviour*, 72(1), 131-138.

- Molles, L. E., Calcott, A., Peters, D., Delamare, G., Hudson, J., Innes, J., Flux, I., & Waas, J. (2008). "Acoustic anchoring" and the successful translocation of North Island kokako (*Callaeas cinerea wilsoni*) to a New Zealand mainland management site within continuous forest. *Notornis*, 55(2), 57-68.
- Møller, A. P. (1988). Spatial and temporal distribution of song in the Yellowhammer *Emberiza citronella*. *Ethology*, 78, 321-331.
- Morgan, D. K. J., & Styche, A. (2012). Results of a community-based acoustic survey of ruru (moreporks) in Hamilton city. *Notornis*, 59, 123-129.
- Mori, E., Menchetti, M., & Ferretti, F. (2014). Seasonal and environmental influences on the calling behaviour of Eurasian Scops Owls. *Bird Study*, 61(2), 277-281.
- Morrell, T. E., Yahner, R. H., & Harkness, W. L. (1991). Factors affecting the detection of Great Horned owls by using broadcast vocalisations. *Wildlife Society Bulletin*, 19(4), 481-488.
- Morton, E. S. (1975). Ecological sources of selection on avian sounds. *The American Naturalist*, 109(965), 17-34.
- Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, 111(981), 855-869.
- Murphy, E. C., Clapperton, B. K., Bradfield, P. M. F. & Speed, H. J. (1998). Brodifacoum residues in target and non-target animals following large-scale poison operations in New Zealand podocarp-hardwood forests. *New Zealand Journal of Zoology*. 25(4), 307-314.
- Neuhaus, W., Bretting, H., & Schweizer, B. (1973). Morphologische und funktionelle Untersuchungen über den 'laut-loosen' Flug der Eulen (*Strix aluco*) im Vergleich zum Flug der Enten (*Anas platyrhynchos*). *Biologisches Zentralblatt*, 92, 495-512.
- Norberg, R. A. (1977). Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy. *Philosophical Transactions of the Royal Society of London. Series B Biological Sciences*. 280(973): 375-408.
- Odom, K. J., & Mennill, D. J. (2010). A quantitative description of the vocalizations and vocal activity of the barred owl. *The Condor*, 112(3), 549-560.
- O'Donnell, C. F. J. (1980). Morepork calling frequency in Nelson. *Notornis*, 27, 397-399.
- O'Donnell, C. F. J., Williams, E. M., & Cheyne, J. (2013). Close approaches and acoustic triangulation: techniques for mapping the distribution of booming Australasian bittern (*Botaurus poiciloptilus*) on small wetlands. *Notornis*, 60, 279-284.

- Olsen, P. (1997). Egg weight loss during incubation, and growth and development of captive- bred Southern Boobooks *Ninox novaeseelandiae*. In Czechura, G. & Debus, S. (eds.) *Australian Raptor Studies II*. Monograph 3: 92-97. Melbourne: Bird Australia.
- Olsen, J. (2011). *Australian high country owls*. Victoria, Australia. CSIRO Publishing Ltd.
- Olsen, J., & Debus, S. (2005). A comment on some errors in the literature regarding Australian owls. *Corella*, 29, 97-98.
- Olsen, J., & Trost, S. (1997). Territorial and nesting behaviour in Southern Boobook (*Ninox novaeseelandiae*). In Duncan, J. R., Johnson, D. H. & Nicholls, T. H. (Eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium*. General Technical Report NC-190: (pp. 308-313), St Paul, MN, USDA Forest Service.
- Olsen, J., & Trost, S. (2007). Duelling and nest failures in Southern Boobooks *Ninox novaeseelandiae*. *Australian Field Ornithology*, 24, 13-25.
- Olsen, J., Trost, S., & Hayes, G. (2002a). Vocalisations used by Southern Boobooks (*Ninox novaeseelandiae*) in the Australian Capital Territory. In I. Newton, R. Kavanagh, J. Olsen, & I. Taylor (Eds.). *Ecology and conservation of owls*. (pp. 305-319). CSIRO Publishing.
- Olsen, J., Marcot, B. G., & Trost, S. (2002b) Do Southern Boobooks *Ninox novaeseelandiae* duet? In I. Newton, R. Kavanagh, J. Olsen, & I. Taylor (Eds.). *Ecology and conservation of owls*. (pp. 320-328). CSIRO Publishing.
- Olsen, J., Wink, M., Sauer-Gurth, H., & Trost, S. (2002c). A new *Ninox* owl from Sumba, Indonesia. *Emu*, 102, 223-231.
- Olsen, J., Trost, S., & Meyers, S. D. (2009). Owls on the island of Sumba, Indonesia. *Australian Field Ornithology*, 26, 2-14.
- Olsen, J., Debus, S., & Trost, S. (2010). Is the Timor Southern Boobook a separate species? *Boobook*, 28(1): 10.
- Olsen, J., Downs, J. A., Tucker, T., & Trost, S. (2011). Home-range size and territorial calling of Southern Boobooks (*Ninox novaeseelandiae*) in adjacent territories. *Journal of Raptor Research*, 45(2), 136-142.
- Otter, K. (1996). Individual variation in the advertising call of male northern saw-whet owls. *Journal of Field Ornithology*, 67(3), 398-405.
- Parrish, G. R., & Gill, B. J. (2003). Natural history of the lizards of the three kings islands, New Zealand. *New Zealand Journal of Zoology*, 30(3), 205-220.

- Pavey, C. R. (2008). Evolution of prey holding behaviour and large male body size in *Ninox* owls (Strigidae). *Biological Journal of the Linnean Society*, 95, 284-292.
- Penteriani, V. (2002). Variation in the function of Eagle Owl vocal behaviour: territorial defence and intra-pair communication? *Ethology, Ecology & Evolution*, 14(3), 275-281.
- Penteriani, V., Delgado, M. d M., Camponi, L., Lourenco, R. (2010). Moonlight makes owls more chatty. *PLoS ONE*, 5(1), e8696.
- Penteriani, V., Kuparinen, A., Delgado, M. d M., Lourenco, R., & Campioni, L. (2011). Individual status, foraging effort, and need for conspicuousness shape behavioural responses of a predator to moon phases. *Animal Behaviour*, 82, 413-420.
- Powlesland, R. G., Merton, D. V., & Cockrem, J. F. (2006). A parrot apart: the natural history of the kakapo (*Strigops habroptilus*), and the context of its conservation management. *Notornis*, 53(1), 3-26.
- Rasmussen, P. C., Allen, D. N. S., Collar, N. J., De Meulemeester, B., Hutchinson, R. O. Jakosalem, P. G. C., Kennedy, R. S., Lambert, F. R., & Paguntalan, L. M. (2012). Vocal divergence and new species in the Philippine hawk owl *Ninox philippensis* complex. *Forktail*, 28, 1-20.
- Redpath, S. M. (1994). Censusing Tawny Owls *Strix aluco* by the use of imitation calls. *Bird Study*, 41(3), 192-198.
- Ritchison, G., Cavanagh, P. M., Belthoff, J. R., & Sparks, E. J. (1988). The singing behavior of Eastern Screech-owls: seasonal timing and response to playback of conspecific song. *The Condor*, 90(3), 648-652.
- Robertson, H., Dowding, J., Elliot, G., Hitchmough, R., Miskelly, C., O'Donnell, C., Powlesland, R., Sagar, P., Scofield, P., & Taylor, G. (2013). Conservation status of New Zealand birds. Department of Conservation: New Zealand Threat Classification Series 4.
- Robisson, P. (1990). The importance of the temporal pattern of syllables and the syllable structure of display calls for individual recognition in the genus *Aptenodytes*. *Behavioural Processes*, 22, 157-163
- Rognan, C. B., Szewczak, J. M., & Morrison, M. L. (2012). Autonomous recording of great gray owls in the Sierra Nevada. *Northwestern Naturalist*, 93, 138-144.
- Saint Girons, M. C., Newman, D.G., & McFadden, I. (1986). Food of the morepork (*Ninox novaeseelandiae*) on Lady Alice Island (Hen & Chicken group). *Notornis*, 33(3), 189-190.

- Saunders, A. A. (1915). Some suggestions for better methods of recording and studying bird songs. *Auk*, 32, 173-183.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solows, A. R., Scott, M. D., Irvine, A. B. (1998). Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour*, 57, 41-50.
- Schwimmer, E. (1963). Guardian animals of the Maori. *The journal of Polynesian society*. 72(4), 397-410
- Seaton, R. & Hyde, N. (2013). Morepork. In Miskelly, C. M. (Ed.) New Zealand birds online. Retrieved from: www.nzbirdsonline.org.nz
- Sheffield, S. R. (1997). Owls as biomonitors of environmental contamination. United States department of Agriculture Forest Service General Technical report NC, 383-398.
- Silvy, N. J., Lopez, R. R., & Peterson, M. J. (2005). Wildlife marking techniques. *Techniques for wildlife investigation and management. 6th edition. The Wildlife Society, Bethesda, Maryland*, 339-376.
- Sirtrack: Wildlife Tracking Solutions. (2013). Ultimate lite single stage harness transmitters. Retrieved from: http://www.sirtrack.com/images/pdfs/Lite_Harness_Transmitters.pdf
- Slater, P. J. B. (2003). Fifty years of bird song research: a case study in animal behaviour. *Animal Behaviour*, 65, 633-639.
- Smith, G. C., & Jones, D. N. (1997). Vocalisations of the marbled frogmouth I: descriptions and an analysis of sex differences. *Emu*, 97, 290-295.
- Somervuo, P., Harma, A., & Fagerlund, S. (2006). Parametric representations of bird sound for automatic species recognition. *IEEE Transactions on Audio, Speech, and Language Processing*, 14(6), 2252-2263.
- Sosa-Lopez, J. R., & Mennill, D. J. (2014). The vocal behaviour of the Brown Throated Wren (*Troglodytes brunneicollis*): song structure, repertoires, sharing, syntax and diel variation. *Journal of Ornithology*, 155, 435-446.
- Sotocinal, S. G., Sorge, R. E., Zaloum, A., Tuttle, A. H., Martin, L. J., Wieskopf, J. S., Mapplebeck, J. C. S., Wei, P., Zhan, S., Zhang, S., McDougall, J. J., King, O. D., & Mogil, J. S. (2011). The rat grimace scale: a partially automated method for quantifying pain in the laboratory rat via facial expressions. *Molecular Pain*. 7, 55.
- Steer, J. (2010). Bioacoustic monitoring of New Zealand birds. *Notornis*, 27, 75-80.

- Stephenson, B. M. (1998). *The ecology and breeding biology of morepork (Ninox novaeseelandiae) and their risk from secondary poisoning in New Zealand. (M.Sc. Thesis)*, Massey University, Palmerston North, New Zealand.
- Stephenson, B. M., Minot, E. O., & Olsen, P. (1998). Capturing, marking and radio-tracking a small owl, the Southern Boobook *Ninox novaeseelandiae* in Australasia. *Corella*, 22(4), 104-107.
- Stephenson, B. M., Minot, E. O., & Armstrong, D. P. (1999). Fate of Moreporks (*Ninox novaeseelandiae*) during a pest control operation on Mokoia island, Lake Rotorua, North Island, New Zealand. *New Zealand Journal of Ecology*, 23(2), 233-240.
- Stephenson, B. M., & Minot, E. O. (2006). Breeding biology of Morepork (*Ninox novaeseelandiae*) on Mokoia Island, Lake Rotorua, New Zealand. *Notornis*, 53, 308-315.
- Temeles, E. J. (1994). The role of neighbours in territorial systems: when are they 'dear enemies'? *Animal Behaviour*, 47, 339-350.
- Terry, A. M. R., Peake, T.M., & McGregor, P.K. (2005). The role of vocal identity in conservation. *Frontiers in Zoology*, 2(1), 10.
- Thissen, D., Steinberg, L., & Kuang, D. (2002). Quick and easy implementation of the Benjamini-Hochberg procedure for controlling the false positive rate in multiple comparisons. *Journal of Educational and Behavioural Statistics*, 27(1), 77-83.
- Thompson, B. (1988). Misuse of chi-square contingency-table test statistics. *Educational & Psychological Research*, 8(1), 39-49.
- Thorpe, W. H. (1961). *Bird-Song: the biology of vocal communication and expression in birds*. London, England. Cambridge University Press.
- Timbergen, N. (1939). The behaviour of the snow bunting in spring. *Transactions of the Linnaean Society of New York*, 5, 1-95.
- Uetz, G. W., & Roberts, J. A. (2002). Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain, behaviour and Evolution*, 59, 222-230.
- Varland, D. E., Smallwood, J. A., Young, L.S., & Kochert, M. N., (2007). Chapter 13: Marking techniques. In D. M. Bird & K. L. Bildstein (Eds.) *Raptor research and management techniques*. (pp. 221-222) Hancock House Publishers Ltd. WA, USA.
- von Frisch, K. (1956) *The dancing bees*. New York, USA. Harcourt Brace Jovanovich.

- Wiley, R. H., & Richards, D. G. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. In D. E. Kroodsma, & E. H. Miller, (Eds.). *Acoustic communication in birds. Volume 1.* (pp. 131-181), Academic Press, New York.
- Wiley, R. H. (2003). Is there an ideal behavioural experiment? *Animal Behaviour*, 66, 585-588.
- Wingspan Birds of Prey Centre. (2013). Maori & birds of prey: Raptor weather forecasts. Retrieved from:
http://www.wingspan.co.nz/maori_and_raptor_weather_forecasts.html.
- Wink, M., Heidrich, P., Sauer-Gurth, H., Elsayed Abdel-Aziz., & Gonzalez, J. (2008). Molecular phylogeny and systematics of owls (Stigiformes). In C. König, & F. Weick, (Eds.) *Owls of the World*. (pp. 42-63) Christopher Helm, London.
- Yolen, J. (1992). *Owl Moon*. Illustrated by John Schloenherr. England: Liber Press.
- Zherebtsova, O. V. (2006). Morphofunctional interpretation of the quills stridulating in tenrecs (Lipotyphla, Tenrecidae). *Russian Journal of Theriology*, 5(1), 1-11.



Appendix 1 – Chapter Two – Kruskal-Wallis Pairwise Tests

Table A1.01: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Frequency (F1) of More syllables (significant p-values in bold). Italicised p-values are no longer significant after applying a Benjamini-Hochberg test.

Morepork FF1	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	1.000	1.000	0.000	0.003	1.000	1.000
Fdub			0.028	1.000	1.000	0.000	0.054	1.000	1.000
Macchiato				0.006	0.001	0.000	0.000	0.048	0.064
Calypso					1.000		0.192	1.000	1.000
Espresso						0.004	0.925	1.000	1.000
Perico							1.000	0.000	1.000
Ristretto								0.032	1.000
Whisper									1.000
Frodo									

Table A1.02: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Frequency (F2) of Pork syllables (significant p-values in bold).

Morepork FF2	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	0.614	1.000	1.000	0.000	1.000	1.000	1.000
Fdub			0.000	1.000	1.000	0.000	1.000	1.000	1.000
Macchiato				0.024	0.053	0.000	0.000	0.000	0.111
Calypso					1.000	0.000	1.000	1.000	1.000
Espresso						0.000	1.000	1.000	1.000
Perico							0.001	0.003	1.000
Ristretto								1.000	1.000
Whisper									1.000
Frodo									

Table A1.03: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Duration (D1) of More syllables (significant p-values in bold).

Morepork FD1	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	0.044	1.000	1.000	1.000	0.000	0.251
Fdub			1.000	0.000	1.000	1.000	0.053	0.000	0.015
Macchiato				0.011	1.000	1.000	1.000	0.000	0.219
Calypso					0.001	0.000	1.000	1.000	1.000
Espresso						1.000	0.600	0.000	0.075
Perico							0.036	0.000	0.012
Ristretto								0.035	1.000
Whisper									1.000
Frodo									

Table A1.04: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Duration (D2) of Pork syllables (significant p-values in bold).

Morepork FD2	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	0.328	1.000	1.000	1.000	1.000	0.425
Fdub			1.000	0.000	1.000	1.000	1.000	0.032	0.009
Macchiato				0.173	1.000	0.280	1.000	1.000	0.416
Calypso					0.000	0.000	0.061	1.000	1.000
Espresso						1.000	1.000	0.014	0.005
Perico							0.692	0.002	0.002
Ristretto								1.000	0.242
Whisper									1.000
Frodo									

Table A1.05: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Total Duration (TD) of both more-pork syllables combined (significant p-values in bold).

Morepork TD	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	0.000	1.000	1.000	0.510	0.006	0.193
Fdub			0.627	0.000	1.000	1.000	0.000	0.000	0.001
Macchiato				0.000	1.000	1.000	0.252	0.001	0.160
Calypso					0.000	0.000	0.437	1.000	1.000
Espresso						1.000	0.121	0.000	0.104
Perico							0.021	0.000	0.038
Ristretto								1.000	1.000
Whisper									1.000
Frodo									

Table A1.06: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Inter-syllable Duration between more and pork syllables (significant p-values in bold).

Morepork IS	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	0.007	0.181	0.010	0.044	1.000	1.000
Fdub			1.000	0.000	0.003	0.000	0.000	1.000	1.000
Macchiato				0.001	0.059	0.001	0.009	1.000	1.000
Calypso					1.000	1.000	1.000	0.000	0.005
Espresso						1.000	1.000	0.001	0.056
Perico							1.000	0.000	0.007
Ristretto								0.000	0.020
Whisper									1.000
Frodo									

Table A1.07: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Frequency of Ro syllables (significant p-values in bold).

Rororo FF	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		0.009	0.001	1.000	0.001	0.715	1.000	0.000	0.000
Fdub			1.000	0.000	1.000	1.000	0.093	0.000	1.000
Macchiato				0.000	1.000	1.000	0.012	0.001	1.000
Calypso					0.000	0.016	1.000	0.000	0.000
Espresso						1.000	0.010	0.001	1.000
Perico							1.000	0.000	0.191
Ristretto								0.000	0.000
Whisper									0.023
Frodo									

Table A1.08: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Duration of Ro syllables (significant p-values in bold).

Rororo FD	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	1.000	1.000	1.000	0.081	1.000	0.000
Fdub			1.000	0.663	1.000	1.000	0.011	1.000	0.000
Macchiato				1.000	1.000	1.000	0.037	1.000	0.000
Calypso					0.060	0.543	1.000	1.000	0.314
Espresso						1.000	0.000	0.162	0.000
Perico							0.008	1.000	0.000
Ristretto								1.000	1.000
Whisper									0.123
Frodo									

Table A1.09: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Inter-Syllable Duration of Ro syllables (significant p-values in bold).

Rororo IS	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	1.000	1.000	0.631	1.000	0.000	0.000
Fdub			1.000	0.002	0.036	1.000	1.000	0.003	0.004
Macchiato				0.040	0.425	1.000	1.000	0.000	0.000
Calypso					1.000	0.000	0.651	0.000	0.000
Espresso						0.004	1.000	0.000	0.000
Perico							0.883	0.030	0.030
Ristretto								0.000	0.000
Whisper									1.000
Frodo									

Table A1.10: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Frequency of Trill syllables (significant p-values in bold).

Trill FF	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	0.033	0.144	0.000	0.073	1.000	1.000
Fdub			1.000	0.000	0.001	0.000	0.000	0.010	1.000
Macchiato				0.029	0.129	0.000	0.065	0.996	1.000
Calypso					1.000	1.000	1.000	1.000	0.000
Espresso						0.546	1.000	1.000	0.001
Perico							0.950	0.061	0.000
Ristretto								1.000	0.001
Whisper									0.022
Frodo									

Table A1.11: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Duration of Trill syllables (significant p-values in bold).

Trill FD	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		0.000	1.000	1.000	1.000	0.004	1.000	1.000	1.000
Fdub			0.064	0.000	0.029	1.000	0.001	0.000	0.003
Macchiato				1.000	1.000	1.000	1.000	0.001	1.000
Calypso					1.000	0.072	1.000	0.234	1.000
Espresso						1.000	1.000	0.004	1.000
Perico							0.159	0.000	0.472
Ristretto								0.109	1.000
Whisper									0.031
Frodo									

Table A1.12: Pairwise comparison results of an independent samples Kruskal-Wallis test showing the differences between individual birds regarding the response variable Fundamental Duration of Trill syllables (significant p-values in bold).

Trill FF	Kahlua	Fdub	Macchiato	Calypso	Espresso	Perico	Ristretto	Whisper	Frodo
Kahlua		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Fdub			0.148	1.000	1.000	1.000	1.000	1.000	1.000
Macchiato				1.000	1.000	0.006	0.375	1.000	0.108
Calypso					1.000	0.166	1.000	1.000	1.000
Espresso						1.000	1.000	1.000	1.000
Perico							1.000	1.000	1.000
Ristretto								1.000	1.000
Whisper									1.000
Frodo									

Table A1.13: Table of number of significant differences from Kruskal-Wallis pairwise tests per bird per parameter Fundamental Frequency (FF1 for *more* and FF2 for *pork* and FF for *ro* and *trill*), Fundamental Duration (FD1 for *more*, FD2 for *pork* and FD for *ro* and *trill*), Inter-Syllable Duration (IS), and Total Duration (TD for *more-pork* call). Maximum possible differences: per bird = 8 (single cell); max per pairwise test = 36 (column); max per all parameters = 96 (row).

Table	More-pork						Ro			Trill		
	FF1	FF2	FD1	FD2	IS	TD	FF	FD	IS	FF	FD	IS
	A1.0	A1.0	A1.03	A1.0	A1.0	A1.0	A1.0	A1.0	A109	A1.1	A1.1	A1.1
Kahlua	1	2		4	5	6	7	8		0	1	2
Fdub	2	1	1	0	2	2	5	1	2	1	2	0
Macchiato	1	2	3	2	4	4	3	2	3	5	5	0
Calypso	4	4	2	0	2	3	4	1	2	1	1	1
Espresso	2	1	4	3	5	5	5	0	4	2	1	0
Perico	2	1	2	3	2	2	4	2	3	2	1	0
Ristretto	6	7	3	3	2	5	1	2	2	4	2	1
Whisper	2	2	0	0	1	3	4	3	2	2	1	0
Frodo	1	2	5	2	5	4	7	0	6	1	4	0
	0	0	2	3	1	2	3	5	6	4	1	0

Appendix 2 – Chapter Three – Generalised Linear Model SPSS Output

```
* Generalized Linear Models.
GENLIN Syllables BY Month# HourAfterSunset (ORDER=ASCENDING)
  /MODEL Month# HourAfterSunset Month#*HourAfterSunset INTERCEPT=YES
  DISTRIBUTION=POISSON LINK=LOG
  /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100
  MAXSTEPHALVING=5 PCONVERGE=1E-006 (ABSOLUTE) SINGULAR=1E-012
  ANALYSISTYPE=3 (WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL
  /EMMEANS TABLES=Month# SCALE=ORIGINAL COMPARE=Month#
  CONTRAST=PAIRWISE PADJUST=SEQSIDAK
  /EMMEANS TABLES=HourAfterSunset SCALE=ORIGINAL
  COMPARE=HourAfterSunset CONTRAST=PAIRWISE PADJUST=SEQSIDAK
  /MISSING CLASSMISSING=EXCLUDE
  /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.
```

Generalized Linear Models BOTH SEQUENTIAL SIDAK ADJUSTMENT

Notes		
Output Created		15-MAR-2015 17:08:08
Comments		
Input	Data	F:\Morepork MSc\Morepork Recordings\Chapter 3 - Temporal\CURRENT\SUMS DATA.sav
	Active Dataset	DataSet2
	Filter	<none>
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data	157
	File	
Missing Value	Definition of Missing	User-defined missing values for factor, subject and within-subject variables are treated as missing.
Handling	Cases Used	Statistics are based on cases with valid data for all variables in the model.
Weight Handling		not applicable

Syntax	GENLIN Syllables BY Month# HourAfterSunset (ORDER=ASCENDING) /MODEL Month# HourAfterSunset Month#*HourAfterSunset INTERCEPT=YES DISTRIBUTION=POISSON LINK=LOG /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100 MAXSTEPHALVING=5 PCONVERGE=1E- 006(ABSOLUTE) SINGULAR=1E-012 ANALYSISTYPE=3(WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL /EMMEANS TABLES=Month# SCALE=ORIGINAL COMPARE=Month# CONTRAST=PAIRWISE PADJUST=SEQSIDAK /EMMEANS TABLES=HourAfterSunset SCALE=ORIGINAL COMPARE=HourAfterSunset CONTRAST=PAIRWISE PADJUST=SEQSIDAK /MISSING CLASSMISSING=EXCLUDE /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.	
Resources	Processor	00:00:01.69
	Time	
	Elapsed Time	00:00:01.71

Model Information

Dependent Variable	Syllables
Probability Distribution	Poisson
Link Function	Log

Case Processing Summary

	N	Percent
Included	156	99.4%
Excluded	1	0.6%
Total	157	100.0%

Categorical Variable Information

			N	Percent
Factor	Month#	1	14	9.0%
		2	14	9.0%
		3	14	9.0%

HourAfterSunset	4	14	9.0%
	5	14	9.0%
	6	13	8.3%
	7	12	7.7%
	8	11	7.1%
	9	12	7.7%
	10	11	7.1%
	11	13	8.3%
	12	14	9.0%
	Total	156	100.0%
	1	11	7.1%
	2	12	7.7%
	3	12	7.7%
	4	12	7.7%
	5	12	7.7%
	6	12	7.7%
	7	12	7.7%
	8	12	7.7%
	9	12	7.7%
	10	12	7.7%
	11	12	7.7%
	12	11	7.1%
	13	8	5.1%
	14	6	3.8%
	Total	156	100.0%

Continuous Variable Information

	N	Minimum	Maximum	Mean	Std. Deviation
Dependent Variable: Syllables	156	1	510	125.42	99.046

Goodness of Fit^a

	Value	df	Value/df
Deviance	.000	0	.
Scaled Deviance	.000	0	.
Pearson Chi-Square	.000	0	.
Scaled Pearson Chi-Square	.000	0	.

Log Likelihood ^b	-488.942		
Akaike's Information Criterion (AIC)	1289.884		
Finite Sample Corrected AIC (AICC)	.		
Bayesian Information Criterion (BIC)	1765.662		
Consistent AIC (CAIC)	1921.662		

Dependent Variable: Syllables

Model: (Intercept), Month#, HourAfterSunset, Month# * HourAfterSunset^a

a. Information criteria are in smaller-is-better form.

b. The full log likelihood function is displayed and used in computing information criteria.

Omnibus Test^a

Likelihood Ratio Chi-Square	df	Sig.
11698.004	155	.000

Dependent Variable: Syllables

Model: (Intercept), Month#, HourAfterSunset,

Month# * HourAfterSunset^a

a. Compares the fitted model against the intercept-only model.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	110107.747	1	.000
Month#	1492.874	11	.000
HourAfterSunset	1455.230	13	.000
Month# * HourAfterSunset	6454.134	131	.000

Dependent Variable: Syllables

Model: (Intercept), Month#, HourAfterSunset, Month# * HourAfterSunset

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi- Square	df	Sig.
(Intercept)	4.949	.0842	4.784	5.114	3453.122	1	.000
[Month#=1]	1.200	.0961	1.011	1.388	155.955	1	.000
[Month#=2]	.738	.1024	.538	.939	51.990	1	.000
[Month#=3]	-.314	.1296	-.568	-.060	5.870	1	.015
[Month#=4]	-.221	.1263	-.469	.026	3.074	1	.080
[Month#=5]	.239	.1126	.018	.459	4.491	1	.034
[Month#=6]	.501	.1932	.123	.880	6.735	1	.009
[Month#=7]	-						
	1.099	.2309	-1.551	-.646	22.630	1	.000
[Month#=8]	-.073	.0926	-.254	.109	.619	1	.432
[Month#=9]	-.654	.1974	-1.041	-.267	10.972	1	.001
[Month#=10]	-						
	1.833	.3109	-2.442	-1.223	34.742	1	.000
[Month#=11]	1.905	.1635	1.585	2.226	135.869	1	.000
[Month#=12]	0 ^a
[HourAfterSunset=1]	-						
	1.483	.1958	-1.867	-1.099	57.361	1	.000
[HourAfterSunset=2]	-.759	.1491	-1.051	-.467	25.906	1	.000
[HourAfterSunset=3]	-						
	2.310	.2802	-2.859	-1.760	67.940	1	.000
[HourAfterSunset=4]	.620	.1044	.415	.824	35.190	1	.000
[HourAfterSunset=5]	.255	.1122	.035	.475	5.176	1	.023
[HourAfterSunset=6]	-.089	.1218	-.328	.150	.533	1	.465
[HourAfterSunset=7]	-						
	1.904	.2339	-2.363	-1.446	66.277	1	.000
[HourAfterSunset=8]	-.483	.1363	-.750	-.216	12.544	1	.000
[HourAfterSunset=9]	.379	.1093	.165	.593	12.031	1	.001
[HourAfterSunset=10]	.181	.1141	-.042	.405	2.522	1	.112
[HourAfterSunset=11]	.540	.1059	.333	.748	25.996	1	.000
[HourAfterSunset=12]	-.631	.1429	-.911	-.351	19.510	1	.000
[HourAfterSunset=13]	-						
	1.188	.1742	-1.529	-.846	46.471	1	.000
[HourAfterSunset=14]	0 ^a
[Month#=1] *							
[HourAfterSunset=1]	-.904	.2525	-1.399	-.409	12.829	1	.000
[Month#=1] *	-						
		.2063	-1.786	-.978	44.876	1	.000
[HourAfterSunset=2]	1.382						

[Month#=1] *	1.646	.2912	1.075	2.217	31.948	1	.000
[HourAfterSunset=3]							
[Month#=1] *	-	.1378	-1.914	-1.374	142.279	1	.000
[HourAfterSunset=4]	1.644						
[Month#=1] *	-	.1675	-2.415	-1.758	155.126	1	.000
[HourAfterSunset=5]	2.086						
[Month#=1] *	-	.1628	-1.725	-1.086	74.538	1	.000
[HourAfterSunset=6]	1.406						
[Month#=1] *	-.748	.2952	-1.326	-.169	6.415	1	.011
[HourAfterSunset=7]							
[Month#=1] *	-	.1774	-1.481	-.785	40.784	1	.000
[HourAfterSunset=8]	1.133						
[Month#=1] *	-	.1587	-2.339	-1.717	163.206	1	.000
[HourAfterSunset=9]	2.028						
[Month#=1] *	-	.2384	-3.619	-2.684	174.825	1	.000
[HourAfterSunset=10]	3.152						
[Month#=1] *	-	.1466	-2.164	-1.589	163.839	1	.000
[HourAfterSunset=11]	1.876						
[Month#=1] *	-.892	.1799	-1.245	-.540	24.596	1	.000
[HourAfterSunset=12]							
[Month#=1] *	-	.2300	-1.520	-.618	21.609	1	.000
[HourAfterSunset=13]	1.069						
[Month#=1] *	0 ^a
[HourAfterSunset=14]							
[Month#=2] *	-.061	.2400	-.531	.410	.064	1	.800
[HourAfterSunset=1]							
[Month#=2] *	-.817	.2050	-1.219	-.415	15.882	1	.000
[HourAfterSunset=2]							
[Month#=2] *	1.177	.3040	.581	1.773	14.977	1	.000
[HourAfterSunset=3]							
[Month#=2] *	-	.1418	-1.437	-.881	66.795	1	.000
[HourAfterSunset=4]	1.159						
[Month#=2] *	-	.1597	-1.601	-.975	65.082	1	.000
[HourAfterSunset=5]	1.288						
[Month#=2] *	-.186	.1507	-.482	.109	1.530	1	.216
[HourAfterSunset=6]							
[Month#=2] *	1.651	.2499	1.161	2.141	43.634	1	.000
[HourAfterSunset=7]							
[Month#=2] *	-	.2458	-2.428	-1.464	62.660	1	.000
[HourAfterSunset=8]	1.946						
[Month#=2] *	-	.2946	-4.004	-2.850	135.361	1	.000
[HourAfterSunset=9]	3.427						

[Month#=2] *	-	.2964	-3.810	-2.648	118.719	1	.000
[HourAfterSunset=10]	3.229						
[Month#=2] *	-	.1802	-2.555	-1.849	149.298	1	.000
[HourAfterSunset=11]	2.202						
[Month#=2] *	.926	.1623	.608	1.244	32.533	1	.000
[HourAfterSunset=12]							
[Month#=2] *	.789	.1969	.403	1.175	16.043	1	.000
[HourAfterSunset=13]							
[Month#=2] *	0 ^a
[HourAfterSunset=14]							
[Month#=3] *	.314	.2816	-.238	.866	1.244	1	.265
[HourAfterSunset=1]							
[Month#=3] *	.167	.2225	-.269	.603	.566	1	.452
[HourAfterSunset=2]							
[Month#=3] *	2.319	.3128	1.706	2.932	54.979	1	.000
[HourAfterSunset=3]							
[Month#=3] *	-.680	.1759	-1.024	-.335	14.934	1	.000
[HourAfterSunset=4]							
[Month#=3] *	-.046	.1737	-.386	.295	.069	1	.792
[HourAfterSunset=5]							
[Month#=3] *	-.228	.1946	-.610	.153	1.376	1	.241
[HourAfterSunset=6]							
[Month#=3] *	.853	.3036	.258	1.448	7.892	1	.005
[HourAfterSunset=7]							
[Month#=3] *	1.052	.1838	.692	1.412	32.761	1	.000
[HourAfterSunset=8]							
[Month#=3] *	-	.2041	-1.502	-.702	29.144	1	.000
[HourAfterSunset=9]	1.102						
[Month#=3] *	.857	.1617	.540	1.174	28.111	1	.000
[HourAfterSunset=10]							
[Month#=3] *	-	.1939	-1.461	-.701	31.054	1	.000
[HourAfterSunset=11]	1.081						
[Month#=3] *	.314	.2085	-.095	.723	2.269	1	.132
[HourAfterSunset=12]							
[Month#=3] *	1.700	.2142	1.281	2.120	63.027	1	.000
[HourAfterSunset=13]							
[Month#=3] *	0 ^a
[HourAfterSunset=14]							
[Month#=4] *	2.136	.2276	1.689	2.582	88.041	1	.000
[HourAfterSunset=1]							
[Month#=4] *	1.474	.1882	1.105	1.843	61.348	1	.000
[HourAfterSunset=2]							

[Month#=4] *	2.025	.3149	1.408	2.642	41.363	1	.000
[HourAfterSunset=3]							
[Month#=4] *	-.398	.1639	-.719	-.077	5.906	1	.015
[HourAfterSunset=4]							
[Month#=4] *	.397	.1614	.081	.714	6.060	1	.014
[HourAfterSunset=5]							
[Month#=4] *	-.419	.1960	-.803	-.035	4.570	1	.033
[HourAfterSunset=6]							
[Month#=4] *	-.521	.4044	-1.313	.272	1.657	1	.198
[HourAfterSunset=7]							
[Month#=4] *	-	.2881	-1.919	-.790	22.096	1	.000
[HourAfterSunset=8]	1.354						
[Month#=4] *	-	.2140	-1.837	-.998	43.883	1	.000
[HourAfterSunset=9]	1.418						
[Month#=4] *	-	.3243	-3.059	-1.788	55.840	1	.000
[HourAfterSunset=10]	2.424						
[Month#=4] *	-	.2390	-2.440	-1.503	68.073	1	.000
[HourAfterSunset=11]	1.972						
[Month#=4] *	.622	.1955	.239	1.005	10.139	1	.001
[HourAfterSunset=12]							
[Month#=4] *	.289	.2469	-.195	.773	1.369	1	.242
[HourAfterSunset=13]							
[Month#=4] *	0 ^a
[HourAfterSunset=14]							
[Month#=5] *	-.660	.3026	-1.253	-.067	4.756	1	.029
[HourAfterSunset=1]							
[Month#=5] *	.368	.1900	-.005	.740	3.742	1	.053
[HourAfterSunset=2]							
[Month#=5] *	1.767	.3061	1.167	2.367	33.303	1	.000
[HourAfterSunset=3]							
[Month#=5] *	-	.1743	-1.872	-1.189	77.073	1	.000
[HourAfterSunset=4]	1.530						
[Month#=5] *	-.689	.1637	-1.010	-.368	17.720	1	.000
[HourAfterSunset=5]							
[Month#=5] *	-.328	.1700	-.661	.005	3.716	1	.054
[HourAfterSunset=6]							
[Month#=5] *	1.932	.2564	1.429	2.434	56.772	1	.000
[HourAfterSunset=7]							
[Month#=5] *	.345	.1749	.003	.688	3.899	1	.048
[HourAfterSunset=8]							
[Month#=5] *	.134	.1445	-.149	.417	.859	1	.354
[HourAfterSunset=9]							

[Month#=5] *	- .926	.1742	-1.267	- .584	28.235	1	.000
[HourAfterSunset=10]							
[Month#=5] *	-	.1919	-2.192	-1.439	89.544	1	.000
[HourAfterSunset=11]	1.816						
[Month#=5] *	.144	.1874	-.223	.512	.594	1	.441
[HourAfterSunset=12]							
[Month#=5] *	.263	.2236	-.175	.701	1.381	1	.240
[HourAfterSunset=13]							
[Month#=5] *	0 ^a
[HourAfterSunset=14]							
[Month#=6] *	.658	.2800	.109	1.207	5.519	1	.019
[HourAfterSunset=1]							
[Month#=6] *	-.214	.2527	-.709	.281	.716	1	.398
[HourAfterSunset=2]							
[Month#=6] *	.791	.3583	.089	1.494	4.877	1	.027
[HourAfterSunset=3]							
[Month#=6] *	-	.2249	-1.847	-.966	39.096	1	.000
[HourAfterSunset=4]	1.406						
[Month#=6] *	-	.2477	-2.202	-1.231	48.023	1	.000
[HourAfterSunset=5]	1.717						
[Month#=6] *	-.243	.2260	-.686	.200	1.159	1	.282
[HourAfterSunset=6]							
[Month#=6] *	1.838	.2992	1.252	2.425	37.746	1	.000
[HourAfterSunset=7]							
[Month#=6] *	-.362	.2426	-.838	.113	2.230	1	.135
[HourAfterSunset=8]							
[Month#=6] *	-	.2372	-2.032	-1.102	43.612	1	.000
[HourAfterSunset=9]	1.567						
[Month#=6] *	-.607	.2232	-1.045	-.170	7.405	1	.007
[HourAfterSunset=10]							
[Month#=6] *	-	.2267	-1.820	-.931	36.817	1	.000
[HourAfterSunset=11]	1.375						
[Month#=6] *	.469	.2361	.007	.932	3.952	1	.047
[HourAfterSunset=12]							
[Month#=6] *	0 ^a
[HourAfterSunset=13]							
[Month#=7] *	2.663	.3019	2.072	3.255	77.846	1	.000
[HourAfterSunset=1]							
[Month#=7] *	1.978	.2734	1.442	2.514	52.317	1	.000
[HourAfterSunset=2]							
[Month#=7] *	4.343	.3571	3.643	5.043	147.871	1	.000
[HourAfterSunset=3]							

[Month#=7] *	1.015	.2476	.530	1.500	16.809	1	.000
[HourAfterSunset=4]							
[Month#=7] *	1.508	.2500	1.018	1.998	36.385	1	.000
[HourAfterSunset=5]							
[Month#=7] *	1.600	.2565	1.097	2.103	38.922	1	.000
[HourAfterSunset=6]							
[Month#=7] *	3.912	.3222	3.281	4.544	147.423	1	.000
[HourAfterSunset=7]							
[Month#=7] *	1.956	.2640	1.438	2.473	54.871	1	.000
[HourAfterSunset=8]							
[Month#=7] *	1.217	.2500	.727	1.707	23.717	1	.000
[HourAfterSunset=9]							
[Month#=7] *	1.398	.2523	.904	1.892	30.715	1	.000
[HourAfterSunset=10]							
[Month#=7] *	1.234	.2471	.749	1.718	24.920	1	.000
[HourAfterSunset=11]							
[Month#=7] *	0 ^a
[HourAfterSunset=12]							
[Month#=8] *	-.908	.3509	-1.596	-.220	6.694	1	.010
[HourAfterSunset=1]							
[Month#=8] *	.160	.1940	-.220	.540	.679	1	.410
[HourAfterSunset=2]							
[Month#=8] *	2.088	.2992	1.501	2.674	48.684	1	.000
[HourAfterSunset=3]							
[Month#=8] *	-	.1615	-1.522	-.888	55.654	1	.000
[HourAfterSunset=4]	1.205						
[Month#=8] *	.475	.1332	.214	.736	12.693	1	.000
[HourAfterSunset=5]							
[Month#=8] *	.496	.1463	.209	.783	11.504	1	.001
[HourAfterSunset=6]							
[Month#=8] *	1.582	.2583	1.076	2.088	37.519	1	.000
[HourAfterSunset=7]							
[Month#=8] *	1.179	.1545	.876	1.482	58.234	1	.000
[HourAfterSunset=8]							
[Month#=8] *	-.090	.1384	-.361	.181	.425	1	.514
[HourAfterSunset=9]							
[Month#=8] *	.464	.1360	.198	.731	11.662	1	.001
[HourAfterSunset=10]							
[Month#=8] *	0 ^a
[HourAfterSunset=11]							
[Month#=9] *	1.177	.2979	.593	1.761	15.615	1	.000
[HourAfterSunset=1]							

[Month#=9] *	.507	.2677	-.017	1.032	3.591	1	.058
[HourAfterSunset=2]							
[Month#=9] *	2.786	.3448	2.110	3.461	65.271	1	.000
[HourAfterSunset=3]							
[Month#=9] *	.394	.2185	-.034	.822	3.249	1	.071
[HourAfterSunset=4]							
[Month#=9] *	1.276	.2178	.849	1.703	34.332	1	.000
[HourAfterSunset=5]							
[Month#=9] *	2.029	.2207	1.596	2.461	84.518	1	.000
[HourAfterSunset=6]							
[Month#=9] *	2.952	.3023	2.359	3.544	95.348	1	.000
[HourAfterSunset=7]							
[Month#=9] *	1.312	.2375	.846	1.778	30.508	1	.000
[HourAfterSunset=8]							
[Month#=9] *	.614	.2211	.181	1.048	7.721	1	.005
[HourAfterSunset=9]							
[Month#=9] *	.269	.2315	-.185	.723	1.350	1	.245
[HourAfterSunset=10]							
[Month#=9] *	-.903	.2504	-1.394	-.412	13.007	1	.000
[HourAfterSunset=11]							
[Month#=9] *	0 ^a
[HourAfterSunset=12]							
[Month#=10] *	-.748	.5584	-1.842	.347	1.793	1	.181
[HourAfterSunset=2]							
[Month#=10] *	2.489	.4529	1.602	3.377	30.209	1	.000
[HourAfterSunset=3]							
[Month#=10] *	-.270	.3630	-.981	.441	.554	1	.457
[HourAfterSunset=4]							
[Month#=10] *	1.408	.3325	.756	2.059	17.923	1	.000
[HourAfterSunset=5]							
[Month#=10] *	1.473	.3399	.806	2.139	18.770	1	.000
[HourAfterSunset=6]							
[Month#=10] *	2.314	.4168	1.498	3.131	30.838	1	.000
[HourAfterSunset=7]							
[Month#=10] *	1.833	.3459	1.155	2.511	28.067	1	.000
[HourAfterSunset=8]							
[Month#=10] *	1.741	.3269	1.101	2.382	28.375	1	.000
[HourAfterSunset=9]							
[Month#=10] *	.797	.3453	.120	1.474	5.327	1	.021
[HourAfterSunset=10]							
[Month#=10] *	-	.4603	-2.361	-.557	10.047	1	.002
[HourAfterSunset=11]	1.459						

[Month#=10] *	0 ^a
[HourAfterSunset=12]							
[Month#=11] *	-	.4481	-4.303	-2.547	58.414	1	.000
[HourAfterSunset=1]	3.425						
[Month#=11] *	-	.3538	-4.303	-2.916	104.088	1	.000
[HourAfterSunset=2]	3.610						
[Month#=11] *	-	.5460	-4.005	-1.865	28.890	1	.000
[HourAfterSunset=3]	2.935						
[Month#=11] *	-	.3374	-5.650	-4.327	218.562	1	.000
[HourAfterSunset=4]	4.989						
[Month#=11] *	-	.1868	-1.559	-.827	40.776	1	.000
[HourAfterSunset=5]	1.193						
[Month#=11] *	-	.2759	-4.128	-3.046	168.996	1	.000
[HourAfterSunset=6]	3.587						
[Month#=11] *	-	.3221	-2.055	-.792	19.529	1	.000
[HourAfterSunset=7]	1.423						
[Month#=11] *	-	.2148	-1.956	-1.114	51.050	1	.000
[HourAfterSunset=8]	1.535						
[Month#=11] *	-	.2092	-3.236	-2.416	182.528	1	.000
[HourAfterSunset=9]	2.826						
[Month#=11] *	-	.1965	-2.302	-1.532	95.165	1	.000
[HourAfterSunset=10]	1.917						
[Month#=11] *	-	.3948	-6.088	-4.541	181.242	1	.000
[HourAfterSunset=11]	5.315						
[Month#=11] *	-	1.0198	-8.222	-4.224	37.231	1	.000
[HourAfterSunset=12]	6.223						
[Month#=11] *	0 ^a
[HourAfterSunset=13]							
[Month#=12] *	0 ^a
[HourAfterSunset=1]							
[Month#=12] *	0 ^a
[HourAfterSunset=2]							
[Month#=12] *	0 ^a
[HourAfterSunset=3]							
[Month#=12] *	0 ^a
[HourAfterSunset=4]							
[Month#=12] *	0 ^a
[HourAfterSunset=5]							
[Month#=12] *	0 ^a
[HourAfterSunset=6]							
[Month#=12] *	0 ^a
[HourAfterSunset=7]							

[Month#=12] *	0 ^a
[HourAfterSunset=8]							
[Month#=12] *	0 ^a
[HourAfterSunset=9]							
[Month#=12] *	0 ^a
[HourAfterSunset=10]							
[Month#=12] *	0 ^a
[HourAfterSunset=11]							
[Month#=12] *	0 ^a
[HourAfterSunset=12]							
[Month#=12] *	0 ^a
[HourAfterSunset=13]							
[Month#=12] *	0 ^a
[HourAfterSunset=14]							
(Scale)	1 ^b						

Dependent Variable: Syllables

Model: (Intercept), Month#, HourAfterSunset, Month# * HourAfterSunset

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Estimated Marginal Means 1: Month#

Estimates				
Month#	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
1	87.06	2.841	81.67	92.82
2	89.84	3.378	83.46	96.71
3	86.59	2.711	81.44	92.07
4	61.87	2.751	56.71	67.50
5	102.05	3.025	96.29	108.15
6	102.96	2.953	97.34	108.92
7	196.07	4.851	186.79	205.81
8	121.77	4.396	113.45	130.70
9	128.45	3.771	121.27	136.06
10	36.78	2.469	32.25	41.95
11	27.86	2.825	22.84	33.98
12	86.31	3.098	80.45	92.60

Pairwise Comparisons

(I) Month#	(J) Month#	Mean Difference (I-J)	Std. Error	df	Sequential Sidak Sig.	95% Wald Confidence Interval for Difference ^a	
						Lower	Upper
1	2	-2.78	4.414	1	.983	-14.27	8.71
	3	.48	3.927	1	.999	-8.93	9.88
	4	25.20 ^b	3.955	1	.000	13.05	37.34
	5	-14.98 ^b	4.150	1	.004	-26.95	-3.02
	6	-15.90 ^b	4.098	1	.002	-28.10	-3.70
	7	-109.01 ^b	5.622	1	.000	-127.90	-90.11
	8	-34.70 ^b	5.234	1	.000	-51.02	-18.39
	9	-41.38 ^b	4.722	1	.000	-57.23	-25.53
	10	50.28 ^b	3.764	1	.000	37.66	62.90
	11	59.21 ^b	4.007	1	.000	45.79	72.62
	12	.76	4.204	1	.999	-9.59	11.11
2	1	2.78	4.414	1	.983	-8.71	14.27
	3	3.25	4.332	1	.983	-8.35	14.85
	4	27.97 ^b	4.357	1	.000	14.49	41.46
	5	-12.20	4.534	1	.069	-24.90	.49
	6	-13.12 ^b	4.487	1	.037	-25.82	-.42
	7	-106.23 ^b	5.911	1	.000	-125.99	-86.46
	8	-31.93 ^b	5.544	1	.000	-48.81	-15.05
	9	-38.60 ^b	5.063	1	.000	-54.53	-22.67
	10	53.06 ^b	4.184	1	.000	39.09	67.03
	11	61.99 ^b	4.404	1	.000	47.30	76.67
	12	3.53	4.584	1	.983	-8.76	15.83
3	1	-.48	3.927	1	.999	-9.88	8.93
	2	-3.25	4.332	1	.983	-14.85	8.35
	4	24.72 ^b	3.863	1	.000	12.81	36.63
	5	-15.46 ^b	4.062	1	.002	-27.43	-3.48
	6	-16.37 ^b	4.009	1	.001	-28.40	-4.35
	7	-109.48 ^b	5.557	1	.000	-127.99	-90.98
	8	-35.18 ^b	5.165	1	.000	-51.38	-18.98
	9	-41.86 ^b	4.645	1	.000	-57.30	-26.41
	10	49.81 ^b	3.667	1	.000	37.63	61.98
	11	58.73 ^b	3.916	1	.000	45.75	71.71
	12	.28	4.117	1	.999	-9.25	9.81
4	1	-25.20 ^b	3.955	1	.000	-37.34	-13.05
	2	-27.97 ^b	4.357	1	.000	-41.46	-14.49

	3	-24.72 ^b	3.863	1	.000	-36.63	-12.81
	5	-40.18 ^b	4.089	1	.000	-53.71	-26.64
	6	-41.09 ^b	4.036	1	.000	-54.43	-27.76
	7	-134.20 ^b	5.577	1	.000	-152.61	-115.80
	8	-59.90 ^b	5.186	1	.000	-76.98	-42.82
	9	-66.58 ^b	4.668	1	.000	-81.93	-51.23
	10	25.09 ^b	3.696	1	.000	13.53	36.64
	11	34.01 ^b	3.943	1	.000	21.06	46.96
	12	-24.44 ^b	4.144	1	.000	-37.11	-11.77
5	1	14.98 ^b	4.150	1	.004	3.02	26.95
	2	12.20	4.534	1	.069	-.49	24.90
	3	15.46 ^b	4.062	1	.002	3.48	27.43
	4	40.18 ^b	4.089	1	.000	26.64	53.71
	6	-.92	4.227	1	.999	-11.45	9.61
	7	-94.03 ^b	5.717	1	.000	-112.76	-75.29
	8	-19.72 ^b	5.336	1	.003	-35.34	-4.10
	9	-26.40 ^b	4.834	1	.000	-41.05	-11.75
	10	65.27 ^b	3.904	1	.000	52.49	78.04
	11	74.19 ^b	4.139	1	.000	60.67	87.71
	12	15.74 ^b	4.330	1	.004	3.15	28.32
6	1	15.90 ^b	4.098	1	.002	3.70	28.10
	2	13.12 ^b	4.487	1	.037	.42	25.82
	3	16.37 ^b	4.009	1	.001	4.35	28.40
	4	41.09 ^b	4.036	1	.000	27.76	54.43
	5	.92	4.227	1	.999	-9.61	11.45
	7	-93.11 ^b	5.679	1	.000	-111.62	-74.60
	8	-18.81 ^b	5.296	1	.005	-33.94	-3.67
	9	-25.48 ^b	4.790	1	.000	-39.93	-11.04
	10	66.18 ^b	3.849	1	.000	53.66	78.70
	11	75.11 ^b	4.087	1	.000	61.83	88.38
	12	16.65 ^b	4.280	1	.002	3.88	29.43
7	1	109.01 ^b	5.622	1	.000	90.11	127.90
	2	106.23 ^b	5.911	1	.000	86.46	125.99
	3	109.48 ^b	5.557	1	.000	90.98	127.99
	4	134.20 ^b	5.577	1	.000	115.80	152.61
	5	94.03 ^b	5.717	1	.000	75.29	112.76
	6	93.11 ^b	5.679	1	.000	74.60	111.62
	8	74.30 ^b	6.546	1	.000	53.09	95.52
	9	67.62 ^b	6.145	1	.000	47.75	87.50
	10	159.29 ^b	5.443	1	.000	141.72	176.86
	11	168.21 ^b	5.614	1	.000	150.14	186.29

	12	109.76 ^b	5.756	1	.000	91.27	128.26
8	1	34.70 ^b	5.234	1	.000	18.39	51.02
	2	31.93 ^b	5.544	1	.000	15.05	48.81
	3	35.18 ^b	5.165	1	.000	18.98	51.38
	4	59.90 ^b	5.186	1	.000	42.82	76.98
	5	19.72 ^b	5.336	1	.003	4.10	35.34
	6	18.81 ^b	5.296	1	.005	3.67	33.94
	7	-74.30 ^b	6.546	1	.000	-95.52	-53.09
	9	-6.68	5.792	1	.899	-22.47	9.12
	10	84.99 ^b	5.042	1	.000	68.83	101.15
	11	93.91 ^b	5.225	1	.000	77.20	110.62
	12	35.46 ^b	5.378	1	.000	18.76	52.16
9	1	41.38 ^b	4.722	1	.000	25.53	57.23
	2	38.60 ^b	5.063	1	.000	22.67	54.53
	3	41.86 ^b	4.645	1	.000	26.41	57.30
	4	66.58 ^b	4.668	1	.000	51.23	81.93
	5	26.40 ^b	4.834	1	.000	11.75	41.05
	6	25.48 ^b	4.790	1	.000	11.04	39.93
	7	-67.62 ^b	6.145	1	.000	-87.50	-47.75
	8	6.68	5.792	1	.899	-9.12	22.47
	10	91.67 ^b	4.508	1	.000	77.29	106.04
	11	100.59 ^b	4.712	1	.000	85.60	115.58
	12	42.14 ^b	4.881	1	.000	26.65	57.63
10	1	-50.28 ^b	3.764	1	.000	-62.90	-37.66
	2	-53.06 ^b	4.184	1	.000	-67.03	-39.09
	3	-49.81 ^b	3.667	1	.000	-61.98	-37.63
	4	-25.09 ^b	3.696	1	.000	-36.64	-13.53
	5	-65.27 ^b	3.904	1	.000	-78.04	-52.49
	6	-66.18 ^b	3.849	1	.000	-78.70	-53.66
	7	-159.29 ^b	5.443	1	.000	-176.86	-141.72
	8	-84.99 ^b	5.042	1	.000	-101.15	-68.83
	9	-91.67 ^b	4.508	1	.000	-106.04	-77.29
	11	8.92	3.752	1	.146	-1.45	19.30
	12	-49.53 ^b	3.962	1	.000	-62.06	-36.99
11	1	-59.21 ^b	4.007	1	.000	-72.62	-45.79
	2	-61.99 ^b	4.404	1	.000	-76.67	-47.30
	3	-58.73 ^b	3.916	1	.000	-71.71	-45.75
	4	-34.01 ^b	3.943	1	.000	-46.96	-21.06
	5	-74.19 ^b	4.139	1	.000	-87.71	-60.67
	6	-75.11 ^b	4.087	1	.000	-88.38	-61.83
	7	-168.21 ^b	5.614	1	.000	-186.29	-150.14

	8	-93.91 ^b	5.225	1	.000	-110.62	-77.20
	9	-100.59 ^b	4.712	1	.000	-115.58	-85.60
	10	-8.92	3.752	1	.146	-19.30	1.45
	12	-58.45 ^b	4.193	1	.000	-71.68	-45.22
12	1	-.76	4.204	1	.999	-11.11	9.59
	2	-3.53	4.584	1	.983	-15.83	8.76
	3	-.28	4.117	1	.999	-9.81	9.25
	4	24.44 ^b	4.144	1	.000	11.77	37.11
	5	-15.74 ^b	4.330	1	.004	-28.32	-3.15
	6	-16.65 ^b	4.280	1	.002	-29.43	-3.88
	7	-109.76 ^b	5.756	1	.000	-128.26	-91.27
	8	-35.46 ^b	5.378	1	.000	-52.16	-18.76
	9	-42.14 ^b	4.881	1	.000	-57.63	-26.65
	10	49.53 ^b	3.962	1	.000	36.99	62.06
	11	58.45 ^b	4.193	1	.000	45.22	71.68

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable
Syllables

- a. Confidence interval bounds are approximate.
b. The mean difference is significant at the .05 level.

Overall Test Results

Wald Chi-Square	df	Sig.
1650.418	11	.000

The Wald chi-square tests the effect of Month#.

This test is based on the linearly independent
pairwise comparisons among the estimated
marginal means.

Estimated Marginal Means 2: HourAfterSunset

Estimates

HourAfterSunset	Mean	Std. Error	95% Wald Confidence Interval
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			Lower	Upper
1	42.85	2.509	38.21	48.06
2	57.16	3.058	51.47	63.48
3	67.55	3.536	60.96	74.85
4	100.63	3.691	93.65	108.13
5	159.74	3.979	152.13	167.73
6	124.67	3.728	117.57	132.19
7	71.68	3.256	65.58	78.36
8	100.55	3.477	93.96	107.60
9	102.63	3.653	95.72	110.05
10	86.20	3.690	79.26	93.74
11	61.83	3.166	55.93	68.36
12	51.31	5.133	42.17	62.42
13	91.25	3.747	84.20	98.90
14	185.36	5.923	174.10	197.34

Pairwise Comparisons

(I)	(J)	Mean Difference (I-J)	Std. Error	df	Sequential Sidak Sig.	95% Wald Confidence Interval for Difference ^b	
						Lower	Upper
1	2	-14.30 ^a	3.956	1	.007	-26.45	-2.16
	3	-24.70 ^a	4.336	1	.000	-38.45	-10.94
	4	-57.78 ^a	4.463	1	.000	-73.17	-42.39
	5	-116.88 ^a	4.704	1	.000	-133.09	-100.68
	6	-81.82 ^a	4.494	1	.000	-97.29	-66.35
	7	-28.83 ^a	4.111	1	.000	-42.23	-15.43
	8	-57.69 ^a	4.288	1	.000	-72.44	-42.94
	9	-59.78 ^a	4.432	1	.000	-75.01	-44.55
	10	-43.35 ^a	4.462	1	.000	-58.67	-28.03
	11	-18.98 ^a	4.040	1	.000	-31.65	-6.30
	12	-8.45	5.713	1	.740	-24.25	7.35
	13	-48.40 ^a	4.510	1	.000	-63.87	-32.93
	14	-142.50 ^a	6.433	1	.000	-164.55	-120.46
2	1	14.30 ^a	3.956	1	.007	2.16	26.45
	3	-10.39	4.675	1	.329	-24.08	3.29
	4	-43.48 ^a	4.793	1	.000	-59.89	-27.06
	5	-102.58 ^a	5.018	1	.000	-119.75	-85.42
	6	-67.51 ^a	4.822	1	.000	-83.99	-51.04
	7	-14.53 ^a	4.467	1	.024	-28.07	-.99

	8	-43.39 ^a	4.631	1	.000	-59.20	-27.58
	9	-45.48 ^a	4.764	1	.000	-61.72	-29.23
	10	-29.04 ^a	4.793	1	.000	-44.40	-13.68
	11	-4.67	4.402	1	.908	-16.48	7.14
	12	5.85	5.975	1	.908	-9.91	21.61
	13	-34.10 ^a	4.837	1	.000	-49.89	-18.30
	14	-128.20 ^a	6.666	1	.000	-150.91	-105.49
3	1	24.70 ^a	4.336	1	.000	10.94	38.45
	2	10.39	4.675	1	.329	-3.29	24.08
	4	-33.08 ^a	5.111	1	.000	-49.65	-16.52
	5	-92.19 ^a	5.323	1	.000	-110.30	-74.07
	6	-57.12 ^a	5.138	1	.000	-74.59	-39.65
	7	-4.13	4.806	1	.908	-16.46	8.19
	8	-33.00 ^a	4.959	1	.000	-49.10	-16.89
	9	-35.08 ^a	5.084	1	.000	-51.62	-18.54
	10	-18.65 ^a	5.110	1	.007	-34.40	-2.89
	11	5.72	4.746	1	.874	-7.22	18.66
	12	16.24	6.233	1	.137	-2.13	34.62
	13	-23.71 ^a	5.152	1	.000	-39.81	-7.60
	14	-117.81 ^a	6.898	1	.000	-141.24	-94.38
4	1	57.78 ^a	4.463	1	.000	42.39	73.17
	2	43.48 ^a	4.793	1	.000	27.06	59.89
	3	33.08 ^a	5.111	1	.000	16.52	49.65
	5	-59.11 ^a	5.427	1	.000	-77.52	-40.70
	6	-24.04 ^a	5.246	1	.000	-40.39	-7.69
	7	28.95 ^a	4.922	1	.000	13.29	44.61
	8	.09	5.071	1	.987	-9.85	10.02
	9	-2.00	5.193	1	.967	-14.32	10.32
	10	14.43	5.219	1	.092	-1.05	29.91
	11	38.80 ^a	4.862	1	.000	22.81	54.80
	12	49.32 ^a	6.322	1	.000	28.60	70.05
	13	9.38	5.259	1	.577	-5.56	24.31
	14	-84.73 ^a	6.979	1	.000	-108.38	-61.08
5	1	116.88 ^a	4.704	1	.000	100.68	133.09
	2	102.58 ^a	5.018	1	.000	85.42	119.75
	3	92.19 ^a	5.323	1	.000	74.07	110.30
	4	59.11 ^a	5.427	1	.000	40.70	77.52
	6	35.07 ^a	5.452	1	.000	17.44	52.70
	7	88.05 ^a	5.141	1	.000	70.65	105.46
	8	59.19 ^a	5.284	1	.000	41.33	77.06
	9	57.11 ^a	5.401	1	.000	38.86	75.35

	10	73.54 ^a	5.426	1	.000	55.23	91.84
	11	97.91 ^a	5.085	1	.000	80.78	115.04
	12	108.43 ^a	6.494	1	.000	86.58	130.29
	13	68.48 ^a	5.465	1	.000	50.11	86.85
	14	-25.62 ^a	7.136	1	.008	-47.44	-3.80
6	1	81.82 ^a	4.494	1	.000	66.35	97.29
	2	67.51 ^a	4.822	1	.000	51.04	83.99
	3	57.12 ^a	5.138	1	.000	39.65	74.59
	4	24.04 ^a	5.246	1	.000	7.69	40.39
	5	-35.07 ^a	5.452	1	.000	-52.70	-17.44
	7	52.98 ^a	4.949	1	.000	36.37	69.60
	8	24.12 ^a	5.098	1	.000	8.08	40.16
	9	22.04 ^a	5.219	1	.001	5.83	38.25
	10	38.47 ^a	5.245	1	.000	21.31	55.63
	11	62.84 ^a	4.891	1	.000	46.44	79.23
	12	73.36 ^a	6.344	1	.000	52.12	94.60
	13	33.41 ^a	5.285	1	.000	16.35	50.48
	14	-60.69 ^a	6.999	1	.000	-84.09	-37.29
7	1	28.83 ^a	4.111	1	.000	15.43	42.23
	2	14.53 ^a	4.467	1	.024	.99	28.07
	3	4.13	4.806	1	.908	-8.19	16.46
	4	-28.95 ^a	4.922	1	.000	-44.61	-13.29
	5	-88.05 ^a	5.141	1	.000	-105.46	-70.65
	6	-52.98 ^a	4.949	1	.000	-69.60	-36.37
	8	-28.86 ^a	4.764	1	.000	-44.15	-13.57
	9	-30.95 ^a	4.893	1	.000	-46.74	-15.16
	10	-14.51	4.921	1	.059	-29.28	.25
	11	9.85	4.541	1	.344	-3.36	23.07
	12	20.38 ^a	6.078	1	.017	1.87	38.88
	13	-19.57 ^a	4.964	1	.002	-34.93	-4.21
	14	-113.67 ^a	6.759	1	.000	-136.24	-91.10
8	1	57.69 ^a	4.288	1	.000	42.94	72.44
	2	43.39 ^a	4.631	1	.000	27.58	59.20
	3	33.00 ^a	4.959	1	.000	16.89	49.10
	4	-.09	5.071	1	.987	-10.02	9.85
	5	-59.19 ^a	5.284	1	.000	-77.06	-41.33
	6	-24.12 ^a	5.098	1	.000	-40.16	-8.08
	7	28.86 ^a	4.764	1	.000	13.57	44.15
	9	-2.09	5.043	1	.967	-14.13	9.96
	10	14.35	5.070	1	.081	-.78	29.48
	11	38.72 ^a	4.702	1	.000	23.20	54.23

	12	49.24 ^a	6.200	1	.000	28.88	69.60
	13	9.29	5.112	1	.577	-5.32	23.90
	14	-84.81 ^a	6.869	1	.000	-107.71	-61.91
9	1	59.78 ^a	4.432	1	.000	44.55	75.01
	2	45.48 ^a	4.764	1	.000	29.23	61.72
	3	35.08 ^a	5.084	1	.000	18.54	51.62
	4	2.00	5.193	1	.967	-10.32	14.32
	5	-57.11 ^a	5.401	1	.000	-75.35	-38.86
	6	-22.04 ^a	5.219	1	.001	-38.25	-5.83
	7	30.95 ^a	4.893	1	.000	15.16	46.74
	8	2.09	5.043	1	.967	-9.96	14.13
	10	16.43 ^a	5.192	1	.031	.77	32.09
	11	40.80 ^a	4.834	1	.000	24.71	56.90
	12	51.33 ^a	6.300	1	.000	30.57	72.08
	13	11.38	5.233	1	.344	-3.83	26.59
	14	-82.73 ^a	6.959	1	.000	-105.87	-59.59
10	1	43.35 ^a	4.462	1	.000	28.03	58.67
	2	29.04 ^a	4.793	1	.000	13.68	44.40
	3	18.65 ^a	5.110	1	.007	2.89	34.40
	4	-14.43	5.219	1	.092	-29.91	1.05
	5	-73.54 ^a	5.426	1	.000	-91.84	-55.23
	6	-38.47 ^a	5.245	1	.000	-55.63	-21.31
	7	14.51	4.921	1	.059	-.25	29.28
	8	-14.35	5.070	1	.081	-29.48	.78
	9	-16.43 ^a	5.192	1	.031	-32.09	-.77
	11	24.37 ^a	4.862	1	.000	9.03	39.71
	12	34.89 ^a	6.321	1	.000	14.89	54.90
	13	-5.06	5.259	1	.908	-18.87	8.76
	14	-99.16 ^a	6.979	1	.000	-122.33	-75.99
11	1	18.98 ^a	4.040	1	.000	6.30	31.65
	2	4.67	4.402	1	.908	-7.14	16.48
	3	-5.72	4.746	1	.874	-18.66	7.22
	4	-38.80 ^a	4.862	1	.000	-54.80	-22.81
	5	-97.91 ^a	5.085	1	.000	-115.04	-80.78
	6	-62.84 ^a	4.891	1	.000	-79.23	-46.44
	7	-9.85	4.541	1	.344	-23.07	3.36
	8	-38.72 ^a	4.702	1	.000	-54.23	-23.20
	9	-40.80 ^a	4.834	1	.000	-56.90	-24.71
	10	-24.37 ^a	4.862	1	.000	-39.71	-9.03
	12	10.52	6.031	1	.577	-6.44	27.48
	13	-29.43 ^a	4.905	1	.000	-45.07	-13.78

	14	-123.53 ^a	6.716	1	.000	-145.79	-101.26
12	1	8.45	5.713	1	.740	-7.35	24.25
	2	-5.85	5.975	1	.908	-21.61	9.91
	3	-16.24	6.233	1	.137	-34.62	2.13
	4	-49.32 ^a	6.322	1	.000	-70.05	-28.60
	5	-108.43 ^a	6.494	1	.000	-130.29	-86.58
	6	-73.36 ^a	6.344	1	.000	-94.60	-52.12
	7	-20.38 ^a	6.078	1	.017	-38.88	-1.87
	8	-49.24 ^a	6.200	1	.000	-69.60	-28.88
	9	-51.33 ^a	6.300	1	.000	-72.08	-30.57
	10	-34.89 ^a	6.321	1	.000	-54.90	-14.89
	11	-10.52	6.031	1	.577	-27.48	6.44
	13	-39.95 ^a	6.355	1	.000	-60.37	-19.53
	14	-134.05 ^a	7.838	1	.000	-160.00	-108.11
13	1	48.40 ^a	4.510	1	.000	32.93	63.87
	2	34.10 ^a	4.837	1	.000	18.30	49.89
	3	23.71 ^a	5.152	1	.000	7.60	39.81
	4	-9.38	5.259	1	.577	-24.31	5.56
	5	-68.48 ^a	5.465	1	.000	-86.85	-50.11
	6	-33.41 ^a	5.285	1	.000	-50.48	-16.35
	7	19.57 ^a	4.964	1	.002	4.21	34.93
	8	-9.29	5.112	1	.577	-23.90	5.32
	9	-11.38	5.233	1	.344	-26.59	3.83
	10	5.06	5.259	1	.908	-8.76	18.87
	11	29.43 ^a	4.905	1	.000	13.78	45.07
	12	39.95 ^a	6.355	1	.000	19.53	60.37
	14	-94.10 ^a	7.009	1	.000	-117.27	-70.94
14	1	142.50 ^a	6.433	1	.000	120.46	164.55
	2	128.20 ^a	6.666	1	.000	105.49	150.91
	3	117.81 ^a	6.898	1	.000	94.38	141.24
	4	84.73 ^a	6.979	1	.000	61.08	108.38
	5	25.62 ^a	7.136	1	.008	3.80	47.44
	6	60.69 ^a	6.999	1	.000	37.29	84.09
	7	113.67 ^a	6.759	1	.000	91.10	136.24
	8	84.81 ^a	6.869	1	.000	61.91	107.71
	9	82.73 ^a	6.959	1	.000	59.59	105.87
	10	99.16 ^a	6.979	1	.000	75.99	122.33
	11	123.53 ^a	6.716	1	.000	101.26	145.79
	12	134.05 ^a	7.838	1	.000	108.11	160.00
	13	94.10 ^a	7.009	1	.000	70.94	117.27

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable
Syllables

- a. The mean difference is significant at the .05 level.
- b. Confidence interval bounds are approximate.

Overall Test Results

Wald Chi-Square	df	Sig.
1318.702	13	.000

The Wald chi-square tests the effect of
HourAfterSunset. This test is based on the linearly
independent pairwise comparisons among the
estimated marginal means.

```

* Generalized Linear Models.
GENLIN Syllables BY Month# (ORDER=ASCENDING)
  /MODEL Month# INTERCEPT=YES
  DISTRIBUTION=POISSON LINK=LOG
  /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100
  MAXSTEPHALVING=5 PCONVERGE=1E-006 (ABSOLUTE) SINGULAR=1E-012
  ANALYSISTYPE=3 (WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL
  /EMMEANS TABLES=Month# SCALE=ORIGINAL COMPARE=Month#
  CONTRAST=PAIRWISE PADJUST=SEQSIDAK
  /MISSING CLASSMISSING=EXCLUDE
  /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.

```

Generalized Linear Models MONTH SEQUENTIAL SIDAK ADJUSTMENT

Notes

Output Created		15-MAR-2015 23:26:53
Comments		
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	Active	DataSet2
	Dataset	
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	Weight	<none>
	Split File	<none>
	N of Rows in Working Data	157
	File	
Missing Value	Definition of Missing	User-defined missing values for factor, subject and within-subject variables are treated as missing.
Handling	Cases Used	Statistics are based on cases with valid data for all variables in the model.
Weight Handling		not applicable

Syntax	GENLIN Syllables BY Month# (ORDER=ASCENDING) /MODEL Month# INTERCEPT=YES DISTRIBUTION=POISSON LINK=LOG /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100 MAXSTEPHALVING=5 PCONVERGE=1E-006(ABSOLUTE) SINGULAR=1E-012 ANALYSISTYPE=3(WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL /EMMEANS TABLES=Month# SCALE=ORIGINAL COMPARE=Month# CONTRAST=PAIRWISE PADJUST=SEQSIDAK /MISSING CLASSMISSING=EXCLUDE /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.	
Resources	Processor	00:00:00.36
	Time	
	Elapsed Time	00:00:00.43

Model Information

Dependent Variable	Syllables
Probability Distribution	Poisson
Link Function	Log

Case Processing Summary

	N	Percent
Included	156	99.4%
Excluded	1	0.6%
Total	157	100.0%

Categorical Variable Information

			N	Percent
Factor	Month#	1	14	9.0%
		2	14	9.0%
		3	14	9.0%
		4	14	9.0%
		5	14	9.0%
		6	13	8.3%
		7	12	7.7%
		8	11	7.1%
		9	12	7.7%
		10	11	7.1%
		11	13	8.3%
		12	14	9.0%
		Total	156	100.0%

Continuous Variable Information

		N	Minimum	Maximum	Mean	Std. Deviation
Dependent Variable	Syllables	156	1	510	125.42	99.046

Goodness of Fit^a

	Value	df	Value/df
Deviance	9807.522	144	68.108
Scaled Deviance	9807.522	144	
Pearson Chi-Square	10436.155	144	72.473
Scaled Pearson Chi-Square	10436.155	144	
Log Likelihood ^b	-5392.703		
Akaike's Information Criterion (AIC)	10809.406		
Finite Sample Corrected AIC (AICC)	10811.587		
Bayesian Information Criterion (BIC)	10846.004		
Consistent AIC (CAIC)	10858.004		

Dependent Variable: Syllables

Model: (Intercept), Month#^a

a. Information criteria are in smaller-is-better form.

b. The full log likelihood function is displayed and used in computing information criteria.

Omnibus Test^a

Likelihood Ratio		
Chi-Square	df	Sig.
1890.482	11	.000

Dependent Variable: Syllables

Model: (Intercept), Month#^a

a. Compares the fitted model against the intercept-only model.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	400818.275	1	.000
Month#	1895.371	11	.000

Dependent Variable: Syllables

Model: (Intercept), Month#

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	4.781	.0245	4.733	4.829	38148.702	1	.000
[Month#=1]	-3.035E-16	.0346	-.068	.068	.000	1	1.000
[Month#=2]	.155	.0334	.089	.220	21.478	1	.000
[Month#=3]	-.133	.0358	-.203	-.063	13.802	1	.000
[Month#=4]	-.222	.0367	-.294	-.150	36.518	1	.000
[Month#=5]	.010	.0345	-.058	.078	.086	1	.769
[Month#=6]	-.047	.0357	-.117	.023	1.714	1	.190
[Month#=7]	.641	.0311	.580	.702	424.863	1	.000
[Month#=8]	.282	.0343	.215	.349	67.845	1	.000
[Month#=9]	.365	.0329	.300	.429	122.586	1	.000
[Month#=10]	-.682	.0459	-.772	-.592	220.732	1	.000
[Month#=11]	-.309	.0384	-.384	-.233	64.541	1	.000
[Month#=12]	0 ^a
(Scale)	1 ^b						

Dependent Variable: Syllables

Model: (Intercept), Month#

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Estimated Marginal Means: Month#

Estimates

Month#	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
1	119.21	2.918	113.63	125.07
2	139.14	3.153	133.10	145.46
3	104.36	2.730	99.14	109.85
4	95.50	2.612	90.52	100.76
5	120.43	2.933	114.82	126.32
6	113.77	2.958	108.12	119.72
7	226.33	4.343	217.98	235.01
8	158.09	3.791	150.83	165.70
9	171.67	3.782	164.41	179.24
10	60.27	2.341	55.86	65.04
11	87.54	2.595	82.60	92.78
12	119.21	2.918	113.63	125.07

Pairwise Comparisons

(I) Month#	(J) Month#	Mean Difference (I-J)	Std. Error	df	Sequential Sidak Sig.	95% Wald Confidence Interval for Difference ^b	
						Lower	Upper
1	2	-19.93 ^a	4.296	1	.000	-32.82	-7.04
	3	14.86 ^a	3.996	1	.002	3.44	26.28
	4	23.71 ^a	3.916	1	.000	11.79	35.64
	5	-1.21	4.137	1	.988	-11.12	8.69
	6	5.45	4.155	1	.651	-5.26	16.15
	7	-107.12 ^a	5.232	1	.000	-124.70	-89.53
	8	-38.88 ^a	4.784	1	.000	-53.93	-23.82
	9	-52.45 ^a	4.777	1	.000	-68.49	-36.42
	10	58.94 ^a	3.741	1	.000	46.40	71.48
	11	31.68 ^a	3.905	1	.000	19.36	43.99
	12	.00	4.127	1	1.000	-8.09	8.09
2	1	19.93 ^a	4.296	1	.000	7.04	32.82
	3	34.79 ^a	4.170	1	.000	21.63	47.95
	4	43.64 ^a	4.094	1	.000	29.94	57.35

	5	18.71 ^a	4.306	1	.000	6.11	31.32
	6	25.37 ^a	4.323	1	.000	12.33	38.41
	7	-87.19 ^a	5.367	1	.000	-105.13	-69.25
	8	-18.95 ^a	4.931	1	.002	-33.16	-4.73
	9	-32.52 ^a	4.924	1	.000	-47.64	-17.40
	10	78.87 ^a	3.927	1	.000	65.76	91.98
	11	51.60 ^a	4.083	1	.000	37.99	65.22
	12	19.93 ^a	4.296	1	.000	7.01	32.85
3	1	-14.86 ^a	3.996	1	.002	-26.28	-3.44
	2	-34.79 ^a	4.170	1	.000	-47.95	-21.63
	4	8.86	3.778	1	.159	-1.59	19.31
	5	-16.07 ^a	4.007	1	.001	-27.72	-4.43
	6	-9.41	4.026	1	.159	-20.55	1.73
	7	-121.98 ^a	5.130	1	.000	-139.06	-104.89
	8	-53.73 ^a	4.672	1	.000	-69.27	-38.20
	9	-67.31 ^a	4.665	1	.000	-82.80	-51.82
	10	44.08 ^a	3.596	1	.000	32.16	56.01
	11	16.82 ^a	3.767	1	.000	5.72	27.92
	12	-14.86 ^a	3.996	1	.002	-26.31	-3.41
4	1	-23.71 ^a	3.916	1	.000	-35.64	-11.79
	2	-43.64 ^a	4.094	1	.000	-57.35	-29.94
	3	-8.86	3.778	1	.159	-19.31	1.59
	5	-24.93 ^a	3.927	1	.000	-36.94	-12.92
	6	-18.27 ^a	3.946	1	.000	-30.08	-6.46
	7	-130.83 ^a	5.068	1	.000	-147.61	-114.06
	8	-62.59 ^a	4.604	1	.000	-77.81	-47.38
	9	-76.17 ^a	4.596	1	.000	-91.33	-61.00
	10	35.23 ^a	3.507	1	.000	23.67	46.78
	11	7.96	3.682	1	.195	-1.92	17.84
	12	-23.71 ^a	3.916	1	.000	-35.67	-11.76
5	1	1.21	4.137	1	.988	-8.69	11.12
	2	-18.71 ^a	4.306	1	.000	-31.32	-6.11
	3	16.07 ^a	4.007	1	.001	4.43	27.72
	4	24.93 ^a	3.927	1	.000	12.92	36.94
	6	6.66	4.166	1	.503	-4.30	17.62
	7	-105.90 ^a	5.241	1	.000	-123.14	-88.67
	8	-37.66 ^a	4.793	1	.000	-52.55	-22.78
	9	-51.24 ^a	4.786	1	.000	-66.95	-35.52
	10	60.16 ^a	3.753	1	.000	47.86	72.46
	11	32.89 ^a	3.916	1	.000	20.08	45.70
	12	1.21	4.137	1	.988	-8.66	11.09

6	1	-5.45	4.155	1	.651	-16.15	5.26
	2	-25.37 ^a	4.323	1	.000	-38.41	-12.33
	3	9.41	4.026	1	.159	-1.73	20.55
	4	18.27 ^a	3.946	1	.000	6.46	30.08
	5	-6.66	4.166	1	.503	-17.62	4.30
	7	-112.56 ^a	5.255	1	.000	-129.73	-95.40
	8	-44.32 ^a	4.809	1	.000	-60.00	-28.65
	9	-57.90 ^a	4.802	1	.000	-73.52	-42.27
	10	53.50 ^a	3.772	1	.000	41.25	65.75
	11	26.23 ^a	3.935	1	.000	14.10	38.36
	12	-5.45	4.155	1	.651	-16.12	5.23
7	1	107.12 ^a	5.232	1	.000	89.53	124.70
	2	87.19 ^a	5.367	1	.000	69.25	105.13
	3	121.98 ^a	5.130	1	.000	104.89	139.06
	4	130.83 ^a	5.068	1	.000	114.06	147.61
	5	105.90 ^a	5.241	1	.000	88.67	123.14
	6	112.56 ^a	5.255	1	.000	95.40	129.73
	8	68.24 ^a	5.765	1	.000	49.56	86.92
	9	54.67 ^a	5.759	1	.000	36.04	73.29
	10	166.06 ^a	4.934	1	.000	150.14	181.98
	11	138.79 ^a	5.059	1	.000	122.50	155.09
	12	107.12 ^a	5.232	1	.000	90.31	123.93
8	1	38.88 ^a	4.784	1	.000	23.82	53.93
	2	18.95 ^a	4.931	1	.002	4.73	33.16
	3	53.73 ^a	4.672	1	.000	38.20	69.27
	4	62.59 ^a	4.604	1	.000	47.38	77.81
	5	37.66 ^a	4.793	1	.000	22.78	52.55
	6	44.32 ^a	4.809	1	.000	28.65	60.00
	7	-68.24 ^a	5.765	1	.000	-86.92	-49.56
	9	-13.58	5.355	1	.107	-28.57	1.42
	10	97.82 ^a	4.455	1	.000	83.54	112.10
	11	70.55 ^a	4.594	1	.000	55.86	85.24
	12	38.88 ^a	4.784	1	.000	23.79	53.96
9	1	52.45 ^a	4.777	1	.000	36.42	68.49
	2	32.52 ^a	4.924	1	.000	17.40	47.64
	3	67.31 ^a	4.665	1	.000	51.82	82.80
	4	76.17 ^a	4.596	1	.000	61.00	91.33
	5	51.24 ^a	4.786	1	.000	35.52	66.95
	6	57.90 ^a	4.802	1	.000	42.27	73.52
	7	-54.67 ^a	5.759	1	.000	-73.29	-36.04
	8	13.58	5.355	1	.107	-1.42	28.57

	10	111.39 ^a	4.448	1	.000	97.21	125.58
	11	84.13 ^a	4.587	1	.000	69.53	98.72
	12	52.45 ^a	4.777	1	.000	37.29	67.61
10	1	-58.94 ^a	3.741	1	.000	-71.48	-46.40
	2	-78.87 ^a	3.927	1	.000	-91.98	-65.76
	3	-44.08 ^a	3.596	1	.000	-56.01	-32.16
	4	-35.23 ^a	3.507	1	.000	-46.78	-23.67
	5	-60.16 ^a	3.753	1	.000	-72.46	-47.86
	6	-53.50 ^a	3.772	1	.000	-65.75	-41.25
	7	-166.06 ^a	4.934	1	.000	-181.98	-150.14
	8	-97.82 ^a	4.455	1	.000	-112.10	-83.54
	9	-111.39 ^a	4.448	1	.000	-125.58	-97.21
	11	-27.27 ^a	3.495	1	.000	-38.08	-16.45
	12	-58.94 ^a	3.741	1	.000	-70.78	-47.10
11	1	-31.68 ^a	3.905	1	.000	-43.99	-19.36
	2	-51.60 ^a	4.083	1	.000	-65.22	-37.99
	3	-16.82 ^a	3.767	1	.000	-27.92	-5.72
	4	-7.96	3.682	1	.195	-17.84	1.92
	5	-32.89 ^a	3.916	1	.000	-45.70	-20.08
	6	-26.23 ^a	3.935	1	.000	-38.36	-14.10
	7	-138.79 ^a	5.059	1	.000	-155.09	-122.50
	8	-70.55 ^a	4.594	1	.000	-85.24	-55.86
	9	-84.13 ^a	4.587	1	.000	-98.72	-69.53
	10	27.27 ^a	3.495	1	.000	16.45	38.08
	12	-31.68 ^a	3.905	1	.000	-43.99	-19.36
12	1	.00	4.127	1	1.000	-8.09	8.09
	2	-19.93 ^a	4.296	1	.000	-32.85	-7.01
	3	14.86 ^a	3.996	1	.002	3.41	26.31
	4	23.71 ^a	3.916	1	.000	11.76	35.67
	5	-1.21	4.137	1	.988	-11.09	8.66
	6	5.45	4.155	1	.651	-5.23	16.12
	7	-107.12 ^a	5.232	1	.000	-123.93	-90.31
	8	-38.88 ^a	4.784	1	.000	-53.96	-23.79
	9	-52.45 ^a	4.777	1	.000	-67.61	-37.29
	10	58.94 ^a	3.741	1	.000	47.10	70.78
	11	31.68 ^a	3.905	1	.000	19.36	43.99

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable
Syllables

a. The mean difference is significant at the .05 level.

b. Confidence interval bounds are approximate.

Overall Test Results

Wald Chi-Square	df	Sig.
1804.981	11	.000

The Wald chi-square tests the effect of Month#.

This test is based on the linearly independent pairwise comparisons among the estimated marginal means.


```

* Generalized Linear Models.
GENLIN Syllables BY HourAfterSunset (ORDER=ASCENDING)
  /MODEL HourAfterSunset INTERCEPT=YES
  DISTRIBUTION=POISSON LINK=LOG
  /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100
  MAXSTEPHALVING=5 PCONVERGE=1E-006 (ABSOLUTE) SINGULAR=1E-012
  ANALYSISTYPE=3 (WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL
  /EMMEANS TABLES=HourAfterSunset SCALE=ORIGINAL
  COMPARE=HourAfterSunset CONTRAST=PAIRWISE PADJUST=SEQSIDAK
  /MISSING CLASSMISSING=EXCLUDE
  /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.

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Generalized Linear Models HOUR SEQUENTIAL SIDAK

Notes		
Output Created		15-MAR-2015 23:35:23
Comments		
Input	Data	F:\Morepork MSc\Morepork Recordings\Chapter 3 - Temporal\CURRENT\SUMS DATA.sav
	Active	
	Dataset	DataSet2
	Filter	<none>
	Weight	<none>
	Split File	<none>
	N of Rows in Working Data	157
	File	
Missing	Definition of	User-defined missing values for factor, subject and within-subject
Value	Missing	variables are treated as missing.
Handling	Cases Used	Statistics are based on cases with valid data for all variables in the model.
Weight Handling		not applicable

Syntax	GENLIN Syllables BY HourAfterSunset (ORDER=ASCENDING) /MODEL HourAfterSunset INTERCEPT=YES DISTRIBUTION=POISSON LINK=LOG /CRITERIA METHOD=FISHER(1) SCALE=1 COVB=MODEL MAXITERATIONS=100 MAXSTEPHALVING=5 PCONVERGE=1E-006(ABSOLUTE) SINGULAR=1E-012 ANALYSISTYPE=3(WALD) CILEVEL=95 CITYPE=WALD LIKELIHOOD=FULL /EMMEANS TABLES=HourAfterSunset SCALE=ORIGINAL COMPARE=HourAfterSunset CONTRAST=PAIRWISE PADJUST=SEQSIDAK /MISSING CLASSMISSING=EXCLUDE /PRINT CPS DESCRIPTIVES MODELINFO FIT SUMMARY SOLUTION.	
Resources	Processor	00:00:00.36
	Time	
	Elapsed Time	00:00:00.39

Model Information

Dependent Variable	Syllables
Probability Distribution	Poisson
Link Function	Log

Case Processing Summary

	N	Percent
Included	156	99.4%
Excluded	1	0.6%
Total	157	100.0%

Categorical Variable Information

			N	Percent
Factor	HourAfterSunset	1	11	7.1%
		2	12	7.7%
		3	12	7.7%
		4	12	7.7%
		5	12	7.7%
		6	12	7.7%
		7	12	7.7%
		8	12	7.7%
		9	12	7.7%
		10	12	7.7%
		11	12	7.7%
		12	11	7.1%
	13	8	5.1%	
	14	6	3.8%	
	Total		156	100.0%

Continuous Variable Information

		N	Minimum	Maximum	Mean	Std. Deviation
Dependent Variable	Syllables	156	1	510	125.42	99.046

Goodness of Fit^a

	Value	df	Value/df
Deviance	10230.905	142	72.049
Scaled Deviance	10230.905	142	
Pearson Chi-Square	10606.263	142	74.692
Scaled Pearson Chi-Square	10606.263	142	
Log Likelihood ^b	-5604.395		
Akaike's Information Criterion (AIC)	11236.789		
Finite Sample Corrected AIC (AICC)	11239.768		
Bayesian Information Criterion (BIC)	11279.487		
Consistent AIC (CAIC)	11293.487		

Dependent Variable: Syllables

Model: (Intercept), HourAfterSunset^a

a. Information criteria are in smaller-is-better form.

b. The full log likelihood function is displayed and used in computing information criteria.

Omnibus Test^a

Likelihood Ratio Chi-Square	df	Sig.
1467.098	13	.000

Dependent Variable: Syllables

Model: (Intercept), HourAfterSunset^a

a. Compares the fitted model against the intercept-only model.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	417601.736	1	.000
HourAfterSunset	1447.606	13	.000

Dependent Variable: Syllables

Model: (Intercept), HourAfterSunset

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	5.378	.0277	5.323	5.432	37565.106	1	.000
[HourAfterSunset=1]	-1.174	.0461	-1.265	-1.084	647.810	1	.000
[HourAfterSunset=2]	-.971	.0423	-1.054	-.888	527.742	1	.000
[HourAfterSunset=3]	-.686	.0392	-.763	-.609	306.924	1	.000
[HourAfterSunset=4]	-.499	.0375	-.572	-.425	177.114	1	.000
[HourAfterSunset=5]	-.143	.0348	-.212	-.075	16.930	1	.000
[HourAfterSunset=6]	-.302	.0359	-.373	-.232	70.860	1	.000
[HourAfterSunset=7]	-.581	.0382	-.656	-.506	231.604	1	.000
[HourAfterSunset=8]	-.542	.0378	-.616	-.468	205.172	1	.000
[HourAfterSunset=9]	-.457	.0371	-.530	-.384	151.591	1	.000
[HourAfterSunset=10]	-.506	.0375	-.579	-.432	181.543	1	.000
[HourAfterSunset=11]	-.749	.0398	-.827	-.671	353.847	1	.000
[HourAfterSunset=12]	-.732	.0405	-.812	-.653	326.379	1	.000
[HourAfterSunset=13]	-.612	.0428	-.696	-.528	204.280	1	.000
[HourAfterSunset=14]	0 ^a
(Scale)	1 ^b

Dependent Variable: Syllables

Model: (Intercept), HourAfterSunset

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Estimated Marginal Means: HourAfterSunset

Estimates				
HourAfterSunset	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
1	66.91	2.466	62.25	71.92
2	82.00	2.614	77.03	87.29
3	109.00	3.014	103.25	115.07
4	131.50	3.310	125.17	138.15
5	187.58	3.954	179.99	195.49
6	160.00	3.651	153.00	167.32
7	121.08	3.177	115.01	127.47
8	125.92	3.239	119.73	132.43
9	137.08	3.380	130.62	143.87
10	130.58	3.299	124.28	137.21
11	102.42	2.921	96.85	108.31
12	104.09	3.076	98.23	110.30
13	117.38	3.830	110.10	125.13
14	216.50	6.007	205.04	228.60

Pairwise Comparisons							
(I) HourAfterSunset	(J) HourAfterSunset	Mean Difference (I- J)	Std. Error	df	Sequential Sidak Sig.	95% Wald Confidence Interval for Difference ^b	
						Lower	Upper
1	2	-15.09 ^a	3.594	1	.001	-26.21	-3.97
	3	-42.09 ^a	3.894	1	.000	-55.52	-28.66
	4	-64.59 ^a	4.128	1	.000	-78.81	-50.37
	5	-120.67 ^a	4.660	1	.000	-136.72	-104.63
	6	-93.09 ^a	4.406	1	.000	-108.25	-77.94
	7	-54.17 ^a	4.022	1	.000	-67.99	-40.35
	8	-59.01 ^a	4.071	1	.000	-72.99	-45.03
	9	-70.17 ^a	4.184	1	.000	-84.53	-55.82
	10	-63.67 ^a	4.119	1	.000	-77.79	-49.56
	11	-35.51 ^a	3.823	1	.000	-48.60	-22.42
	12	-37.18 ^a	3.943	1	.000	-50.67	-23.70
	13	-50.47 ^a	4.556	1	.000	-66.03	-34.90
	14	-149.59 ^a	6.494	1	.000	-171.76	-127.42

2	1	15.09 ^a	3.594	1	.001	3.97	26.21
	3	-27.00 ^a	3.990	1	.000	-39.93	-14.07
	4	-49.50 ^a	4.218	1	.000	-63.88	-35.12
	5	-105.58 ^a	4.740	1	.000	-121.73	-89.44
	6	-78.00 ^a	4.491	1	.000	-93.28	-62.72
	7	-39.08 ^a	4.114	1	.000	-53.07	-25.10
	8	-43.92 ^a	4.162	1	.000	-58.05	-29.78
	9	-55.08 ^a	4.273	1	.000	-69.58	-40.59
	10	-48.58 ^a	4.209	1	.000	-62.85	-34.32
	11	-20.42 ^a	3.920	1	.000	-32.82	-8.01
	12	-22.09 ^a	4.037	1	.000	-34.93	-9.25
	13	-35.37 ^a	4.637	1	.000	-50.49	-20.26
	14	-134.50 ^a	6.551	1	.000	-156.67	-112.33
3	1	42.09 ^a	3.894	1	.000	28.66	55.52
	2	27.00 ^a	3.990	1	.000	14.07	39.93
	4	-22.50 ^a	4.477	1	.000	-36.59	-8.41
	5	-78.58 ^a	4.971	1	.000	-95.39	-61.77
	6	-51.00 ^a	4.735	1	.000	-66.99	-35.01
	7	-12.08	4.379	1	.099	-25.15	.98
	8	-16.92 ^a	4.425	1	.003	-30.39	-3.45
	9	-28.08 ^a	4.528	1	.000	-42.67	-13.50
	10	-21.58 ^a	4.468	1	.000	-35.55	-7.61
	11	6.58	4.197	1	.711	-5.17	18.33
	12	4.91	4.307	1	.874	-6.69	16.51
	13	-8.37	4.874	1	.659	-22.30	5.55
	14	-107.50 ^a	6.721	1	.000	-130.17	-84.83
4	1	64.59 ^a	4.128	1	.000	50.37	78.81
	2	49.50 ^a	4.218	1	.000	35.12	63.88
	3	22.50 ^a	4.477	1	.000	8.41	36.59
	5	-56.08 ^a	5.157	1	.000	-73.46	-38.71
	6	-28.50 ^a	4.929	1	.000	-44.22	-12.78
	7	10.42	4.588	1	.280	-2.92	23.75
	8	5.58	4.632	1	.874	-7.05	18.21
	9	-5.58	4.731	1	.874	-18.44	7.28
	10	.92	4.673	1	.906	-8.71	10.54
	11	29.08 ^a	4.415	1	.000	14.80	43.36
	12	27.41 ^a	4.519	1	.000	12.89	41.93
	13	14.12	5.063	1	.096	-1.07	29.32
	14	-85.00 ^a	6.859	1	.000	-108.08	-61.92
5	1	120.67 ^a	4.660	1	.000	104.63	136.72
	2	105.58 ^a	4.740	1	.000	89.44	121.73

	3	78.58 ^a	4.971	1	.000	61.77	95.39
	4	56.08 ^a	5.157	1	.000	38.71	73.46
	6	27.58 ^a	5.382	1	.000	10.60	44.57
	7	66.50 ^a	5.072	1	.000	49.45	83.55
	8	61.67 ^a	5.111	1	.000	44.51	78.82
	9	50.50 ^a	5.201	1	.000	33.06	67.94
	10	57.00 ^a	5.149	1	.000	39.76	74.24
	11	85.17 ^a	4.916	1	.000	68.73	101.60
	12	83.49 ^a	5.009	1	.000	66.77	100.22
	13	70.21 ^a	5.505	1	.000	51.85	88.56
	14	-28.92 ^a	7.191	1	.001	-51.09	-6.75
6	1	93.09 ^a	4.406	1	.000	77.94	108.25
	2	78.00 ^a	4.491	1	.000	62.72	93.28
	3	51.00 ^a	4.735	1	.000	35.01	66.99
	4	28.50 ^a	4.929	1	.000	12.78	44.22
	5	-27.58 ^a	5.382	1	.000	-44.57	-10.60
	7	38.92 ^a	4.840	1	.000	23.05	54.78
	8	34.08 ^a	4.881	1	.000	18.23	49.93
	9	22.92 ^a	4.976	1	.000	7.41	38.42
	10	29.42 ^a	4.921	1	.000	13.64	45.19
	11	57.58 ^a	4.676	1	.000	42.01	73.15
	12	55.91 ^a	4.775	1	.000	40.03	71.78
	13	42.62 ^a	5.292	1	.000	25.25	60.00
	14	-56.50 ^a	7.030	1	.000	-79.59	-33.41
7	1	54.17 ^a	4.022	1	.000	40.35	67.99
	2	39.08 ^a	4.114	1	.000	25.10	53.07
	3	12.08	4.379	1	.099	-.98	25.15
	4	-10.42	4.588	1	.280	-23.75	2.92
	5	-66.50 ^a	5.072	1	.000	-83.55	-49.45
	6	-38.92 ^a	4.840	1	.000	-54.78	-23.05
	8	-4.83	4.537	1	.874	-16.84	7.17
	9	-16.00 ^a	4.638	1	.012	-30.06	-1.94
	10	-9.50	4.580	1	.396	-22.70	3.70
	11	18.67 ^a	4.316	1	.000	5.26	32.07
	12	16.99 ^a	4.422	1	.003	3.47	30.51
	13	3.71	4.976	1	.874	-8.43	15.85
	14	-95.42 ^a	6.795	1	.000	-117.98	-72.86
8	1	59.01 ^a	4.071	1	.000	45.03	72.99
	2	43.92 ^a	4.162	1	.000	29.78	58.05
	3	16.92 ^a	4.425	1	.003	3.45	30.39
	4	-5.58	4.632	1	.874	-18.21	7.05

	5	-61.67 ^a	5.111	1	.000	-78.82	-44.51
	6	-34.08 ^a	4.881	1	.000	-49.93	-18.23
	7	4.83	4.537	1	.874	-7.17	16.84
	9	-11.17	4.682	1	.228	-24.87	2.54
	10	-4.67	4.623	1	.874	-16.73	7.40
	11	23.50 ^a	4.362	1	.000	9.66	37.34
	12	21.83 ^a	4.467	1	.000	7.81	35.84
	13	8.54	5.016	1	.659	-5.78	22.86
	14	-90.58 ^a	6.825	1	.000	-113.21	-67.96
9	1	70.17 ^a	4.184	1	.000	55.82	84.53
	2	55.08 ^a	4.273	1	.000	40.59	69.58
	3	28.08 ^a	4.528	1	.000	13.50	42.67
	4	5.58	4.731	1	.874	-7.28	18.44
	5	-50.50 ^a	5.201	1	.000	-67.94	-33.06
	6	-22.92 ^a	4.976	1	.000	-38.42	-7.41
	7	16.00 ^a	4.638	1	.012	1.94	30.06
	8	11.17	4.682	1	.228	-2.54	24.87
	10	6.50	4.723	1	.810	-6.56	19.56
	11	34.67 ^a	4.467	1	.000	20.08	49.26
	12	32.99 ^a	4.570	1	.000	18.12	47.86
	13	19.71 ^a	5.108	1	.003	4.02	35.40
	14	-79.42 ^a	6.893	1	.000	-102.23	-56.60
10	1	63.67 ^a	4.119	1	.000	49.56	77.79
	2	48.58 ^a	4.209	1	.000	34.32	62.85
	3	21.58 ^a	4.468	1	.000	7.61	35.55
	4	-.92	4.673	1	.906	-10.54	8.71
	5	-57.00 ^a	5.149	1	.000	-74.24	-39.76
	6	-29.42 ^a	4.921	1	.000	-45.19	-13.64
	7	9.50	4.580	1	.396	-3.70	22.70
	8	4.67	4.623	1	.874	-7.40	16.73
	9	-6.50	4.723	1	.810	-19.56	6.56
	11	28.17 ^a	4.406	1	.000	13.95	42.39
	12	26.49 ^a	4.511	1	.000	12.07	40.92
	13	13.21	5.055	1	.134	-1.69	28.11
	14	-85.92 ^a	6.853	1	.000	-108.57	-63.27
11	1	35.51 ^a	3.823	1	.000	22.42	48.60
	2	20.42 ^a	3.920	1	.000	8.01	32.82
	3	-6.58	4.197	1	.711	-18.33	5.17
	4	-29.08 ^a	4.415	1	.000	-43.36	-14.80
	5	-85.17 ^a	4.916	1	.000	-101.60	-68.73
	6	-57.58 ^a	4.676	1	.000	-73.15	-42.01

	7	-18.67 ^a	4.316	1	.000	-32.07	-5.26
	8	-23.50 ^a	4.362	1	.000	-37.34	-9.66
	9	-34.67 ^a	4.467	1	.000	-49.26	-20.08
	10	-28.17 ^a	4.406	1	.000	-42.39	-13.95
	12	-1.67	4.242	1	.906	-11.16	7.81
	13	-14.96 ^a	4.817	1	.037	-29.49	-.43
	14	-114.08 ^a	6.680	1	.000	-136.13	-92.04
12	1	37.18 ^a	3.943	1	.000	23.70	50.67
	2	22.09 ^a	4.037	1	.000	9.25	34.93
	3	-4.91	4.307	1	.874	-16.51	6.69
	4	-27.41 ^a	4.519	1	.000	-41.93	-12.89
	5	-83.49 ^a	5.009	1	.000	-100.22	-66.77
	6	-55.91 ^a	4.775	1	.000	-71.78	-40.03
	7	-16.99 ^a	4.422	1	.003	-30.51	-3.47
	8	-21.83 ^a	4.467	1	.000	-35.84	-7.81
	9	-32.99 ^a	4.570	1	.000	-47.86	-18.12
	10	-26.49 ^a	4.511	1	.000	-40.92	-12.07
	11	1.67	4.242	1	.906	-7.81	11.16
	13	-13.28	4.913	1	.110	-27.86	1.29
	14	-112.41 ^a	6.749	1	.000	-134.64	-90.18
13	1	50.47 ^a	4.556	1	.000	34.90	66.03
	2	35.37 ^a	4.637	1	.000	20.26	50.49
	3	8.37	4.874	1	.659	-5.55	22.30
	4	-14.12	5.063	1	.096	-29.32	1.07
	5	-70.21 ^a	5.505	1	.000	-88.56	-51.85
	6	-42.62 ^a	5.292	1	.000	-60.00	-25.25
	7	-3.71	4.976	1	.874	-15.85	8.43
	8	-8.54	5.016	1	.659	-22.86	5.78
	9	-19.71 ^a	5.108	1	.003	-35.40	-4.02
	10	-13.21	5.055	1	.134	-28.11	1.69
	11	14.96 ^a	4.817	1	.037	.43	29.49
	12	13.28	4.913	1	.110	-1.29	27.86
	14	-99.12 ^a	7.124	1	.000	-122.56	-75.69
14	1	149.59 ^a	6.494	1	.000	127.42	171.76
	2	134.50 ^a	6.551	1	.000	112.33	156.67
	3	107.50 ^a	6.721	1	.000	84.83	130.17
	4	85.00 ^a	6.859	1	.000	61.92	108.08
	5	28.92 ^a	7.191	1	.001	6.75	51.09
	6	56.50 ^a	7.030	1	.000	33.41	79.59
	7	95.42 ^a	6.795	1	.000	72.86	117.98

8	90.58 ^a	6.825	1	.000	67.96	113.21
9	79.42 ^a	6.893	1	.000	56.60	102.23
10	85.92 ^a	6.853	1	.000	63.27	108.57
11	114.08 ^a	6.680	1	.000	92.04	136.13
12	112.41 ^a	6.749	1	.000	90.18	134.64
13	99.12 ^a	7.124	1	.000	75.69	122.56

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable
Syllables

- a. The mean difference is significant at the .05 level.
- b. Confidence interval bounds are approximate.

Overall Test Results

Wald Chi-Square	df	Sig.
1452.709	13	.000

The Wald chi-square tests the effect of
HourAfterSunset. This test is based on the linearly
independent pairwise comparisons among the
estimated marginal means.