

THE ROLE OF VOCAL COMMUNICATION IN THE BIOLOGY
OF FLEDGLING AND JUVENILE KEA (*Nestor notabilis*)
IN AORAKI/MOUNT COOK NATIONAL PARK

A thesis
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Photography: Gottlieb Braun-Elwert

“Long ago, the sun shone all the time and there was neither night nor cold. The land was covered by one enormous forest, and all the birds sang in harmony. There were rainbow parrots, tall moas, fantails so big they could catch dragonflies, ducks that flew with their feet - and Krikta the kea and his friends, who were always playing practical jokes on the other birds.”

-Philip Temple, The Legend of the Kea.

Abstract

The kea is the only parrot species in the world to include the true alpine environment as part of their habitat. Survival in these harsh alpine conditions has been hypothesised to be the cause of the generalist behaviour of kea, leading to their heightened explorative behaviour and curiosity. Kea are also widely regarded as being extraordinarily intelligent. It is their intelligence that suggests that kea may possess a sophisticated communication system.

I conducted a study exploring the potentially complex vocal repertoire of the kea. My study was conducted with wild population of banded juvenile and fledgling kea in Aoraki/Mount Cook National Park between February 2003 and April 2004. I obtained 449 vocalisations from 16 identified and several unidentified kea.

The results of this study confirmed that the vocal repertoire of the kea is exceptionally large for a parrot species, encompassing over 17 vocalisations. This study revealed five vocalisations previously undescribed in the kea repertoire and showed for the first time that vocal repertoire of immature kea may be different to the repertoire of adult kea. Two possible gender specific vocalisations were also revealed. The study of apparent vocal responses revealed that kea appear to be able to identify vocalisation types and respond accordingly using combinations of increasingly complex vocalisations. This is also the first study to take advantage of the similarity between human and parrot vocal systems for the kea, by utilizing powerful human speech analysis software. The results of this analysis allowed the identification of subtle differences in kea vocalisations, including the presence of graded signals, not identifiable by use of spectrogram analysis.

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Chapter 1

Introduction

The kea, Nestor notabilis

Parrots are among the most recognisable and diverse orders of birds with over 330 identified species (South and Pruett-Jones 2000). Of these, the kea is the only species to include the true alpine environment as part of their habitat (Johnston 2001). Survival in these harsh alpine conditions has been hypothesised to be the cause of the generalist behaviour of kea, leading to their heightened explorative behaviour and curiosity (Diamond and Bond 1991).

Endemic to the South Island of New Zealand, the habitat of the kea is dominated by, but not restricted to, mountain regions between 700 m-2000 m in altitude (Campbell 1976, Breejart 1988). During winter kea have been known to reach the coast in Nelson and Westland in search of more abundant food sources (Kinskey and Robertson 1987). The mountain habitat of the kea is predominantly southern beech (*Northofagus*) forest and alpine grasslands (Jackson 1960, Elliot and Kemp 1999).

Within this restricted habitat, the population size of the kea is small (1000 - 5000, Anderson 1986), and has declined dramatically since European arrival (Peat 1995). This decline is largely a result of persecution from high-country farmers, motivated by greatly exaggerated accusations of sheep killing (Anderson 1986). During 1860 - 1970 an estimated 150 000 kea were killed for bounty under the pretences of 'protection' of high country runs, yet many kea were killed in country where no sheep were present (Powell 1986). Although kea have been fully protected since 1986, there is no evidence of population increase (Peat 1995).

The kea is an opportunistic omnivore and is known to eat at least 89 plant species and 9 animal species in the wild (Campbell 1976). Beech species provide the base of the kea diet, but mast seeding makes this source unreliable (Breejart 1988). The unreliable presence of preferred food may account for the flexible feeding habits of the kea (Diamond and Bond 1999). This flexibility

is in turn the hallmark of ‘open programme’ animals (Mayer 1992) that specialise in learning (see Diamond and Bond 1999).

Described as ‘possibly the strangest bird in the world’ (Lint 1958) kea live in complex, stratified social systems and are perhaps best known for their playful and somewhat destructive nature. With over 40 distinct elements of behaviour described (Jackson 1963, Diamond and Bond 1991, Diamond and Bond 1999, Potts 1976 and 1977), kea are also widely regarded as being extraordinarily intelligent (Diamond and Bond 1999). It is their intelligence and their associated behavioural complexity that suggests that kea may possess a sophisticated communication system.

Despite the easy accessibility and high profile of the kea, there are huge gaps in the information available on all aspects of kea behaviour, ecology, distribution and population dynamics. This extends to the vocal communication of the kea which, is known to be well developed (Higgins 1990), yet has not been comprehensively described.

Previous work on kea vocalisations

Higgins (1990) published a list of kea calls and suggested the functions for these calls. However, there is currently no information on individual variation in kea vocalisations and no published studies on call function (see Higgins 1990). More recently Alan Bond and Judy Diamond (submitted) conducted a study on the function of kea vocalisations in which they identified the various vocalisations in the repertoire of populations of mostly adult kea. My objective was to extend this work by studying a population of mostly immature kea.

Rationale of thesis

Exchanging information and maintaining contact with specific individuals may be more challenging for individuals that are often separated in such a way that visual contact is inefficient. Many animals that are separated in such a way have been shown to use auditory signals in place of visual cues for the purposes of individual recognition (Maurello *et al* 2000). Examples include

cheetahs, several primate species, sea otters, wolves (Maurello *et al* 2000) and several parrot species (Fernandez-Juricic and Martella 2000). Using vocal communication, many animals can communicate specific messages accompanied by additional information about their motivation, sex, age or even identity (Sousa-Lima *et al* 2002). As kea often interact in situations where visual communication is impaired, it stands to reason that they too may use vocal communication for a large proportion of their information exchanges.

It is widely accepted that all animal species have at least some rudimentary means to communicate with conspecifics, and in some species communication is elaborate. The sensory modalities used by animals vary greatly. The level of flexibility found in communication systems also varies, with human verbal language providing a more flexible form of communication compared to most other species' means of communicating. Human language has been a key component in enabling our species to exchange information and to formulate ideas on an arguably unparalleled scale. The acquisition of human language has been argued to be the defining factor between human and animal intelligence (Macphail & Bolhuis 2001).

Kea are widely regarded as being exceptionally intelligent birds, but this consensus view is based largely on anecdotes. In particular, little is known about the potential relationship between communication and intelligence in the kea. McPhail (1995) argues that being long-lived, having frequent interactions and remaining in the same area for years, creates potential for complex social relationships which could result in selection for a relatively complex vocal repertoire. Kea meet each of McPhail's (1995) criteria, suggesting that the kea may demonstrate an elaborate and complex vocal repertoire. This possibility has been supported by recent work by Bond and Diamond (submitted) which suggests that kea vocal communication may be elaborate and variable. My goal was to build on the work of Diamond and Bond by carrying out an in-depth study of kea vocalisations. This is a step towards the long term goal of understanding the relationship between animal intelligence and communication systems.

The role of complex communication systems in animal intelligence

There has been a lot of interest in the capability of animals to imitate (Akins *et al* 2002, Stoinski *et al* 2001, Blackmore 1999, Heyes 1996, Heyes 1993) and this ability is often envisaged as an indication of exceptional intelligence. Primates (Byrne 1995) and kea (Huber *et al* 2001) often do not perform well in laboratory experiments designed to test for imitation. Humphrey (1988; see Byrne 1995) proposed that the reason for primates often not emerging as better than other animals in laboratory intelligence tests, including tests for imitation, is that these species have evolved the skills of compromise required for social living . This tendency to compromise maximises individual gains and yet retains the benefits obtained by the individual from the group, which results in laboratory tests being ineffective at revealing the intelligence of these animals. The lives of primates in nature often appear unchallenging when we only look at environmental problems. Primate intelligence often appears surplus to requirements. Humphrey (1988; see Byrne 1995) argued that this is because the really tough problems for primates are the social ones. This argument may also be applicable to other intelligent social animals, such as the kea. If language complexity can be related to intelligence, communication may provide an alternative avenue for understanding the intelligence of species that do not perform well in many laboratory experiments.

Although this study will not be adequate to answer whether or not kea, or any animals, are capable of language and what this capability implies about cognition, it will provide a stepping stone towards the identification and understanding of possible animal languages and the cognitive significance of complicated animal communication

Conservation implications

There may also be conservation implications to a better understanding of the vocal communication system of the kea. Since 1600, over 1100 recorded plant and animal species have been lost to extinction worldwide. Historically, conservation efforts have been defeated by the reluctance of wild animals to breed in captivity. However, more recent intensive behavioural research and biotechnological advancements have all but eliminated this conservation hurdle. The biggest remaining challenge for conservation by captive breeding currently is reestablishment

into the wild. Captive breeding has had only limited success in protecting threatened species, because only 11% of attempted reestablishments have succeeded (Ebenhard 1995). Animals reared in captivity often appear to have difficulty selecting mates, or else they are less attractive to potential mates, and they can fail to develop the foraging ability and the social skills required for survival in groups. Social-skill failure is largely attributed to lack of ‘cultural’ development in captive animals. Animal communication may often be a crucial part of animal ‘culture’. There are many examples to show that loss of culture is a major cause of reintroduction failure in captive breeding programmes. One such example was provided by van Heezik & Seddon (2001), who showed that hand-reared male partridges, when released, were not only lacking in basic survival skills, but were also less attractive to females than wild birds. Understanding how animals communicate therefore appears to be important for captive breeding success.

Although there are currently no captive breeding programmes for kea active in New Zealand, the kea population is low (less than 5,000 individuals) with no indication of increase (Peat 1995). Information on cultural transmission in kea populations may prove invaluable if the kea population does not increase and captive breeding becomes necessary.

Thesis organisation

This thesis consists of extensive analysis of kea vocalisations recorded from a single population in one region. Because the same set of 448 vocalisations were analysed in each chapter using the same primary analysis, with the exception of the complex analysis required in Chapter 7, all the methods have been presented together in Chapter 2. To further minimise repetition, the references are all presented in one section at the end of the thesis.

Objectives

This study is largely focused on fledgling, juvenile and sub-adult kea. The goal is to further extend the recent work of Bond and Diamond (submitted) on a population of mostly adult kea. My primary objectives were to identify any further vocalisations in immature kea not observed in Bond and Diamond’s (submitted) study, examine the complexity of vocal exchanges, determine

if the functions of kea vocalisations can be inferred by behavioural context, identify any gender specific vocalisations and determine the extent and role of intra-individual variation in kea vocalisations.

Chapter 2

Methods

I studied a wild population of banded, immature kea (*Nestor notabilis*) in Aoraki/Mount Cook National Park between February 2003 and April 2004. The banding of the kea was conducted by the Vienna University Kea Research Group (Werdenich 2003 pers. comm.)^{*}. Recordings were made using two types of equipment. Most of the recordings were made with a Sony mini DV digital handycam, model DCR-TRV 18E and an AKG D109/200 NR95118 external microphone mounted in a 30 cm parabolic reflector on Sony mini DV DMV60 tapes. Some recordings were made using an E'lite portable cassette recorder on TDK 90 min cassette tapes. The same external microphone and parabolic reflector were used with the tape deck to ensure sound artefacts created by the parabolic reflector were consistent across the study.

Age categories

Age categories of kea are easily determined in the field by the changing colour patterns in plumage, eye ring, cere and lower mandible of the kea. In this study I have followed the kea age category definitions given by Diamond and Bond (1999). Fledglings were defined as kea in their first summer since emergence from the nest. They were identified by a light yellow cast to the plumage around the crown and bright orange-yellow eye rings, with a similarly coloured cere and lower mandible. Juveniles were kea in their second summer. They had lost the lighter feathers on the crown, but maintained a light yellow eye ring, cere and lower mandible. They also often appeared to have dull, worn feathers as they had not yet undergone a moult. Sub-adults were kea in their third or fourth summer. They had an incomplete yellow eye ring. Sub-adults may still show traces of yellow in their ceres, but their mandibles have become dark. It is during the sub-adult phase that the largest changes in kea social behaviour occur (Diamond and Bond 1999). Adult kea are identified by dark brown-grey cere, eye ring and bill.

^{*} Authorised by the Department of Conservation, funded by a grant from Austrian Science Foundation.

Frequency response of the parabolic microphone

In order to determine what frequencies were not recorded by the parabolic microphone used in this study, it was necessary to produce a frequency response curve of the microphones performance.

To do this a white noise generator was connected to an amplifier (a tape recorder line in) and the signal was fed out to a high quality speaker. The output from the white noise generator was sent to a spectrum analyser (using a program called "SpectrumAnalyzer" that was run on an iMAC computer). The speaker's white noise output was then recorded with the parabolic reflector microphone used in this study from a distance of approximately 1 m, the microphone signal was then sent to the same spectrum analyser. Both spectrums were compared by measuring the difference between the speaker output level and the microphone output at 26 points. Using these measurements a curve that is comparable to a frequency response curve (Fig. 1) was produced.

As expected, with using a parabolic reflector there were significant losses in response at very low and very high frequencies with some variation in response at 200 Hz. Thus the reflector may be thought of as a 20 dB amplifier with a high-pass filter network that cuts off at 1 kHz (Scott 1964). However, the response was remarkably level through the 1-4 kHz range where the bulk of the usable information analysed in my recordings occurred. Although the fundamental frequencies in the vocalisations were below 1 kHz, all of the recordings were made with the same parabolic reflector, so any sound losses were consistent. As these characteristics were constant throughout all recordings in the study I regard it appropriate to consider that microphone response is not a significant factor in the analysis of my results.

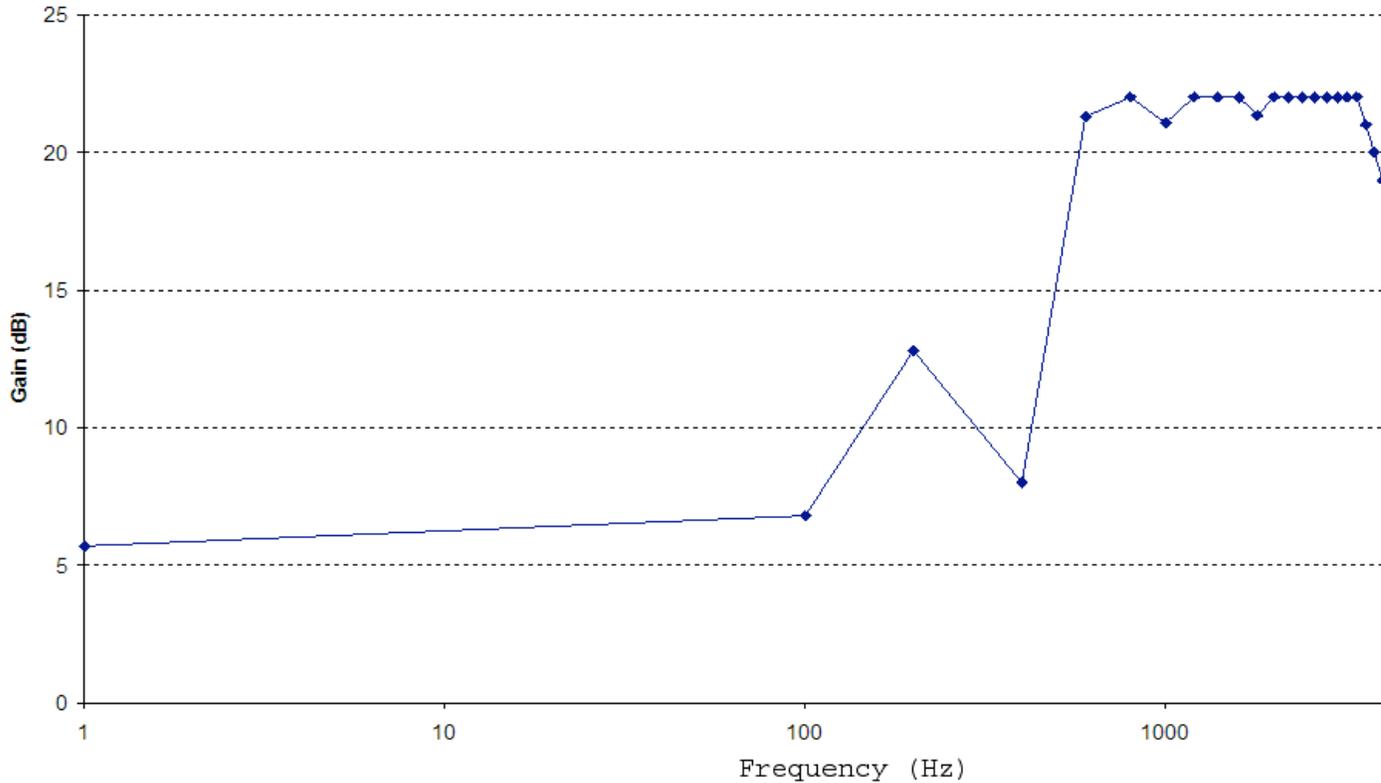


Figure 1. Indicative frequency response of Parabolic Microphone

Recording locations and times

the kea have become habituated to congregating in this location through other studies being conducted there (Werdenich 2003 pers. comm.*). Whitehorse Hill (917 m altitude) was selected because it is an area known to be frequented by immature kea, and is occasionally visited by adults. This site is a moraine hill created by glacial movement and is now vegetated predominantly with shrub species. Sealy Tarns (1300 m altitude) are located approximately halfway up the Northwest side of the Sealy Range below Mt. Ollivier. They were selected as a location because aside from being an area frequented by kea, there is an active nest site nearby giving the opportunity to record nesting related vocalisations. Recordings were also obtained from areas with high levels of human activity such as the ‘rubbish corner’ (see map, Fig. 2) and carparks at the Hermitage Hotel (see map, Fig. 2). Kea are present in these locations because they have become conditioned to congregating in human habituated areas to forage on food scraps and rubbish. The rubbish corner was infrequently used as a site for this study due to high levels of background noise from the hotel interfering with recording quality.

A camera was also placed in a kea nest that was believed to be active. This was done in conjunction with a Department of Conservation (DOC) study (Weston, pers. comm. 2003). Images from this camera were transmitted to a 24-hour video link in the DOC. Area Office, Aoraki/Mount Cook National Park. Unfortunately due to nesting failure there were no vocalisations obtained.

Recording methods

I selected one individual per recording session and recorded all behaviours and interactions made by that individual. With each call, where possible I recorded the identity of the individual that gave the call, the behaviour of the individual before, during and after the vocalisation, the number of individuals present, the presence of other birds in flight or vocalising from a distance, the distance of the individual from the microphone and any response of other individuals to the call. I collected 449 calls encompassing 24 hours of recorded data.

Spectrum analysis

Calls were then digitised using Canary 1.2.1 software on a Macintosh G3 computer at a

* University of Vienna kea research group, funded by the Austrian Science Fund.

sampling rate of 31.25 kHz. Spectrograms were made using a Hamming window, logarithmic display amplitude, filter bandwidth 507.5 Hz, frame length 256 points, grid resolution frequency 31.25 Hz, FFT size 1024 points with 50% overlap. Vocalisations were then catalogued according to which kea they were given by and then further by the sound of each vocalisation. Spectrograms, spectra and waveforms of each call were constructed and categorisation of the vocalisations was finalised visually into ten distinct groups (*ahh*, *kee-ah*, *ke-ee-ee-ah*, *aww*, *ke-eh-eh*, *squeal*, *growl*, *ehh*, *ah-ah-ah* and *ahh-ahh*). I then used the Canary measurement panel to derive the peak frequency, call duration, change in frequency, peak time, number of harmonics, dominant harmonic, amplitude ceiling and average intensity of each vocalisation. These measurements were then used in a cluster analysis, which confirmed the call groupings (see Chapter 3, Fig. 2). Only recordings with minimal background noise and no call overlap, or those that could be accurately filtered with no overlapping harmonics were used for further analysis.

Cluster analysis: Hierarchical cluster analysis (using the nearest-neighbour method (Terhune *et al* 1992) was conducted using SPSS software (© 2004, SPSS inc.) and used to test the classifications of the vocalisations I had hypothesised. Ten different aspects (call duration, number of syllables, peak frequency, number of harmonics, number of modulations, peak period, dominant harmonic, harmonic shift, terminal compression, onset peaks, portion unmodulated, modulation direction and peak direction) of the call morphology were measured for each vocalisation. The geometric distance was then calculated and presented in a dendrogram (Chapter 3, Fig. 2).

Additional methods applied in each chapter

Response sequences: To determine what vocalisations were used in response sequences, I compiled tables showing the initial vocalisation and the vocalisations that appeared to be given in response. Spectrograms were compiled for vocalisations were given within one second after another vocalisation from a different kea. Both the initial vocalisation and apparent response vocalisation were illustrated on the same spectrogram. The percentage of time each vocalisation appeared to receive another vocalisation in response was then calculated. This information was then presented on a separate table for each of the vocalisations that appeared

to incite responses. For ease of comparison between vocalisations this data was also presented on a bar graph.

Behavioural context: To determine if vocalisations have specific behavioural functions I recorded the behaviours that were associated with each vocalisation. Using digital video sequences, I made notes on the behaviours that occurred before, during and after each vocalisation. I also noted any apparent responses to the vocalisations given by other individuals. I then compared all the noted behaviours associated with each vocalisation type. This was done by calculating the percentage of time each behavioural category and type was associated with each vocalisation. During each apparent response, the behaviour of the kea giving the initial vocalisation was recorded. I then calculated the percentage of time each vocalisation seemed to gain a response when associated with each behavioural context. I presented the results in tables illustrating the percentage of time a vocalisation was given in each behavioural contexts and the percentage of time each vocalisation seemed to gain a response during each behavioural context. This data was presented in separate tables for each vocalisation. The analysis of apparent responses in this chapter differ from the analyses of responses in Chapter 4 in that the behaviour of the initial sender was recorded, not the vocalisation type of the apparent response.

Gender specificity

Using previously constructed tables of the vocalisations recorded from each kea I divided the recordings from identified kea into two groups based on the gender of the kea that gave the vocalisation. A total of 429 vocalisations were compared. I then calculated the percentage of time each vocalisation was given by each gender of kea and presented the data in a chart and bar graph. I then selected any vocalisations made by only males or only females and conducted a chi-squared of goodness of fit test for vocalisations with an adequate sample size. Gender in kea may be determined by observation (Chapter 6, Fig. 1). For this study these observational identifications of gender were supported with DNA sexing based on blood samples taken by the Vienna University Kea Research Group (Werdenich 2003 pers. comm.). The blood samples were analysed using DNA fingerprinting by Bruce Robertson at the University of Canterbury (2003).

Intra-individual variation

I divided all the samples of each vocalisation type from each identified individual into behavioural contexts (429 recordings in total). Comparing the spectrogram images I then identified consistent differences in call morphology for each of the vocalisation types. This was done by comparing the call morphology between recordings of the same vocalisation from the same kea in two different behavioural contexts. Of these variations only those differences that were consistent across all the recordings of the same call type in different behavioural context for each bird studied were analysed. I then further selected only the variation that was consistent across all the birds. This was to eliminate the possibility of some variations being due to inter-individual variation between different kea.

Roberts (1996) claimed that in some parrot species spectrograms were not accurate enough to identify inter-individual variation. As intra-individual variation would be expected to be equally difficult to detect, I conducted further analysis on the *ahh*, *kee-ah* and *ke-ee-ee-ah* vocalisations using SpeechStation 2 software (Sensimetrics corporation) on a PC. This analysis technique was initially designed for human speech analysis. However, the similarities in parrot vocal tracts and the sounds produced by parrots to those of humans (see Chapter 7) suggest this technique could potentially be a new method of sound analysis for parrots. This technique may be a powerful tool in detecting and identifying any subtle intra-individual variation in parrot vocalisations that are not identifiable in spectrograms. This analysis procedure also allows for the identification of the physiological causes of variations in the vocalisations, possibly giving some insight to the function of the variation. In order to apply this technique files first had to be converted from Macintosh formatted AIFF files to PC formatted WAVE files. This was done using RiverPast file conversion software on a PC. Vocalisations of birds may change with the time of year or the age of the bird. To eliminate possible variations caused by these influences, I only conducted this analysis on vocalisations that were given by the same bird, in the same season during the same year in two different behavioural contexts. This exclusion limited this section of the study to three vocalisation types, *ahh*, *kee-ahh* and *ke-ee-ee-ah*. Analysis of the fundamental frequency, acoustic energy levels and frequency variations in the first and second formants were conducted. A detailed explanation of each of these analyses is

presented in Chapter 7.

Fundamental frequency analysis settings: The fundamental frequency was automatically plotted on a spectrogram using the ‘pitch plotting’ option in SpeechStation. This was set to display the fundamental frequency at ten times the actual frequency to allow for easier comparisons.

Acoustic energy analysis; waterfall plot setting: Shaded plots were produced with the clipping level of 90 dB, the range of 40 dB, a plot height of 50 was selected and resolution was set at 257.

Formant analysis; vowel space plots: Data plots were created with an interval sampling rate of four.

Each of these techniques were examined for plotting accuracy by re-plotting randomly selected vocalisations and comparing the results.

In a study of the parrot species *Amazona aestiva* (the blue fronted amazon), Fernandez-Juricic and Martella (2000) found that inter-individual variation in guttural call duration and in the lowest frequency was greater for flocks larger than four individuals than for single individuals. This suggests there would also be a reduction in intra-individual variation. Increased vocal variation in groups compared to solitary individuals may suggest that the variation has a social function. When assessing the level of intra-individual variation present between behavioural contexts the number of kea present was considered. Where possible I have compared vocalisations with the same number of kea present. Where this was not possible the variations in group size was noted.

Armstrong (1992) showed that sounds with high-frequency characteristics are unreliable because of the more rapid degradation rate of high frequencies compared to low frequencies over long distance. Artefacts are created and these are difficult to identify from notes. Therefore I have compared calls obtained from a long distance separately from calls obtained

in close proximity. This procedure minimised the problem of sound artefacts biasing the results. I have also focused most of my study on the lower frequency sounds.

Playback experiment

I used a playback experiment to determine whether receivers can detect, and discriminate against, intra-individual variation in vocalisations. This experiment was conducted with the same wild population the vocalisations were recorded from. There are over 78 banded kea in Aoraki/Mount Cook National Park. However, only a small proportion of these frequent the study site. Use of the wild population effectively removed the problem of atypical results due to artificial environments which may occur in laboratory experiments (Falls 1982). To ensure conditions were kept as natural as possible, the playback experiments were conducted at the same time of day as the calls were obtained (within 3 hours of sunrise), in the same location (behind the Hermitage Hotel, midway up the water stopbank (see map, Fig. 2) and played at an estimated amplitude similar to what the vocalisations would have been given (Falls 1982).

The *kee-ah* vocalisation obtained from the kea with the band combination left plastic white green was used. This vocalisation was selected because Bond and Diamond (submitted) found they gained the highest proportion of apparent responses during playback of this vocalisation. Two vocalisations that sound the same to the human ear, but were recorded during different behavioural contexts were selected. The first vocalisation was given during an aggressive interaction (for definition see Chapter 5). This vocalisation was given immediately after white green had been bitten and displaced by another kea, white green turned towards the attacking kea and gave the *kee-ah* vocalisation before departing the study site. The second vocalisation was given during altruistic physical contact (head-bill touch) with another kea. This vocalisation appeared to gain responses from other kea in Governor's Bush. Background noise was removed from the calls using Canary's editing software to ensure the strongest possible signal to noise ratio.

Both of the vocalisations were recorded at the same time of year (autumn 2003) to eliminate

possible season related variations in response. However, it was not possible to play the vocalisations back during the same time of year that they were recorded. Vocalisations were played using a purpose built animal caller with a 'play' compact disc player. The loud speaker was concealed from view of the receivers by attaching it to the side of a perching post, behind a mesh fence running the length of the stopbank that the kea infrequently cross (see map, Fig. 2). The speaker was placed at the height that the original vocalisations were recorded from (Phillmore *et al* 2002), which was approximately 45 cm from the ground, the height of a standing kea.

Cheney and Seyfarth (1990) stated that before beginning a playback experiment the predicted purpose of the vocalisation should not present to influence the behaviour of the receivers. For example, if a vocalisation thought to signal aerial predators was to be played, then there must be no aerial predators present. This is to eliminate the possibility of the receivers responding to the actual cue instead of the playback stimulus. For this experiment the only obvious cue to the vocalisations was the behavioural context and the vocalising individual. Therefore, I ensured that the kea 'white green' was not present at the study site during the experiment. Video and audio recording of the receiver began 10 seconds before the playback to ensure there were no abnormalities in the receiver behaviour before the playback that may affect the results (Cheney and Seyfarth 1990). Since birds habituate quickly to individual vocalisations and the playback protocol rapidly during playback experiments (Phillmore *et al* 2002), I conducted a large amount of playback over a short period of time as opposed to one or two per day over a long period of time. This was to ensure that if the kea were to become habituated, it would be obvious early on in the study. Short sequences were used to minimise lasting changes in response (Falls 1982) and there was a 15 minute pause between each repeat. I played both vocalisation types in each session alternating between the two vocalisations. The number and identification of receivers was noted to assess if there was any variation in receiver response due to the structure of the receiver group. Only the initial response was assessed because the initial response is most likely to reflect natural behaviour than prolonged encounters with an unresponsive sound source. The playback was repeated until the kea terminated the experiment by vacating the experimental area.

Study site

Aoraki/Mount Cook National Park was formally declared a national park in 1953. It spans approximately 70 111 hectares and encompasses 65 km of the Southern Alps with 40% of the park covered by glaciers (Department of Conservation 2004). The park has an average annual rainfall of 4000 mm/year with 149 rain days per year (Department of Conservation 2004). On average the area has 21 days of snow on the ground per year. Temperatures range from -10°C to 30°C (Department of Conservation, 2004).

The flora of Aoraki/Mount Cook National Park includes over 400 native higher plant species, numerous species of native lower plants (for example mosses and lichens) and approximately 100 exotic plant species (Department of Lands and Survey 1986). Approximately 30% of the native flowering plant, conifer and fern species found in Aoraki/Mount Cook and Westland National Parks grow mainly above 1000 m (Department of Lands and Survey 1986). There are two main forest types in the region, one is predominantly silver beech (*Northofagus menisci*), and the other is predominantly thin-barked totora (*Podocarpus hallii*). However, forested areas in the park are scarce due to the elevated, unstable, eroding landscape limiting areas where forest can grow and much of the forest which was able to grow having been burnt so that only remnants remain (Department of Lands and Survey 1986).

The park also provides habitat for many animal species. Amongst these are three lizard species, including the rare jewelled gecko (*Heteropholis gemmeus*), over 670 insect and spider species and several species of fish (Department of Lands and Survey 1986). Approximately 35 bird species either inhabit Aoraki/Mount Cook National Park or are regular visitors (Department of Lands and Survey 1986) (including the kea, rock wren (*Xenicus gilviventris*), paradise shelduck (*Tadoma variegata*), morepork (*Ninox novaeseelandiae*), the rifleman (*Acanthisitta chloris*) and the New Zealand falcon (*Falco novaeseelandiae*). Although this appears to be a large number of species capable of inhabiting such a harsh habitat, there has been a decline in the number of bird species since the arrival of humans. One of the first Europeans to explore the park was Julius von Haast in 1862. He reported vast numbers of wekas (*Gallirallus australis*), kakas (*N. meridionalis*), whio/blue ducks (*Hymenolaimus malacarrhunchos*) and piopio (*Turnagra capensis*) being present (Department of Lands and Survey 1986). Now all of

these birds are gone from the park and the piopio is extinct (Department of Lands and Survey 1986). This loss of bird species in the area occurred with the arrival of humans and is most probably due to destruction of habitat for farming and human-introduced predators (Department of Lands and Survey 1986).

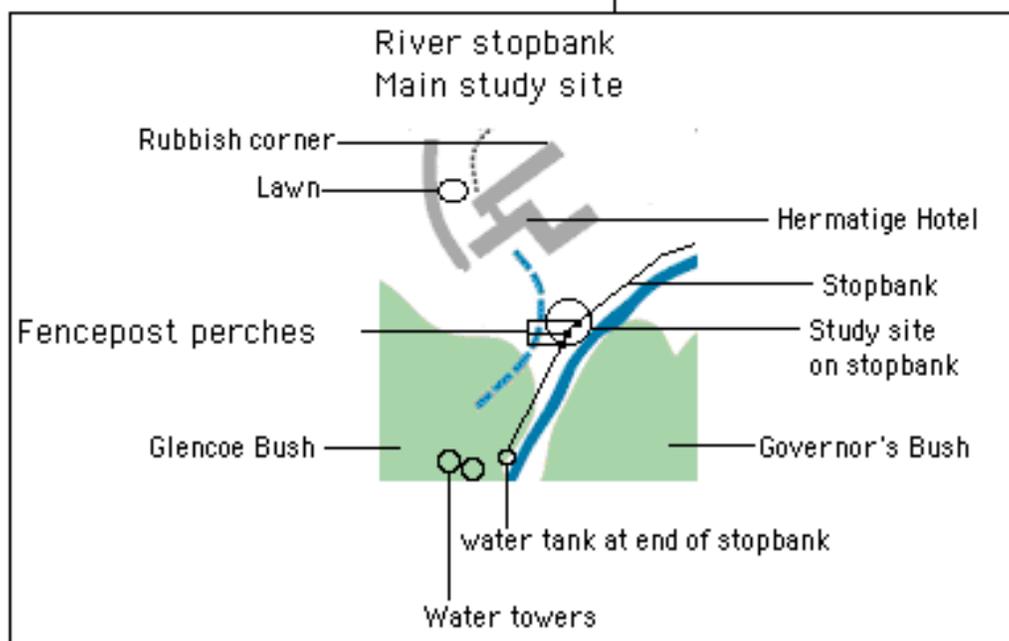
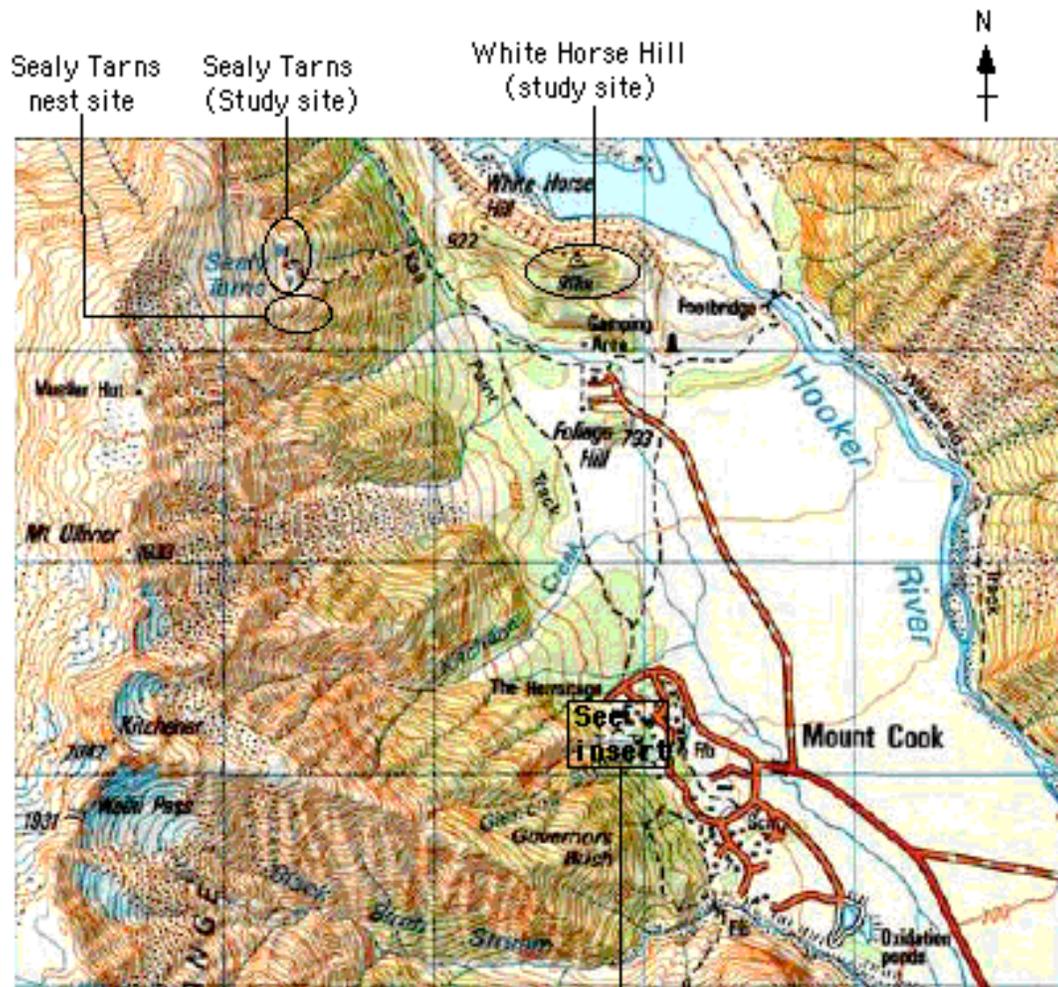


Figure 2. Topographical map showing the study site locations in and around Mount Cook Village. The insert shows locations mentioned throughout this thesis.

Chapter 3

Repertoire

Introduction

Many parrot species are social, with vocal communication playing an important role in group coordination (Saunders 1983). The important role of vocal communication has led to complex vocal repertoires in many social parrot species (Farabaugh and Dooling 1996). For example, Pidgeon (1981) found 12 functionally distinct calls in the galah (*Cacatua roseicapilla*), described seven calls in the cockatiel (*Nymphicus hollandicus*) and 15 calls in the red-rumped parrot (*Psephotus haematonotus*). Fernandez-Juricic *et al* (1997) identified nine calls in the blue fronted Amazon (*Amazona aestiva*), Saunders (1983) described 15 call types in the short-billed white-tailed cockatoo (*Calyptorhynchus funereus latirostris* Carnaby) and eight distinct calls in the budgerigar (*Melopsittacus undulates*) including a song between mated pairs. Despite the importance and complexity of parrot vocal communication, in comparison to passerines, there have been few studies on parrot vocal systems (Farabaugh and Dooling 1996). Although there have been comprehensive studies on the communication of a few parrot species including the grey parrot (*Psittacus erithacus*) (Cruickshank *et al* 1993, Pepperberg 1990, 2002, Pepperberg and Shive 2001) and the budgerigar (Brockway 1969, Brown *et al* 1988, Dooling 1986, Dooling *et al* 1990 and 1996, Farabaugh and Dooling 1996, Farabaugh *et al* 1994, Gramza 1970, Manabe *et al* 1997) most of the studies on parrot vocalisations have been parts of broader studies on ecology, behaviour or both (for example Powesland *et al* 1992, Saunders 1983). Saunders (1983) argued that the high levels of intra-individual variation in parrot calls make studying the vocal complexity of parrot vocalisations especially time consuming and he suggested that this may limit broader studies. Saunders (1983) claims this may have resulted in understating the complexity of parrot vocal systems.

There is little information on the vocalisations of the kea, and most of this is somewhat anecdotal. Falla *et al* (1981) described a *keaa* call given mainly in flight. This is probably the same flight call as described by Chambers (1989; *kee-aa kee-aa kee-aa*), Moon (1995; *kee-aa*)

and Jackson (1960; *kuer*). Jackson (1960) described a *kua-ua-ua* call given when another kea is sighted. Jackson (1962) also described a soft cooing vocalisation given by the male from outside the nest to chicks inside. Bond and Diamond (1991) identified a *bleat-trill* call, a *scream* (described as a series of continuous high-intensity shrieks without modulations) and a *squeal* which is described as a high intensity, modulated sound given during aggressive interactions. Higgins (1990) suggested that the squeal may be the rasping sound Potts (1977) reported as preceding lunging or run-rushing. Bond and Diamond (1989) also described a *wa-wa-wa* sound produced by a solitary captive interacting with mirror. They also describe a *gurgle* call and a *meow* call given when sitting alone. Although various other aspects of the biology of the kea have been described, there have been no published studies of function of calls, period of calling, sexual vocal dimorphism, regional or individual vocal variation. Nor have there been adequate basic descriptions of kea vocalisations (see Higgins 1990).

In a recently completed study, Bond and Diamond (submitted) documented the vocal repertoire of the kea, along with presenting data on functional significance and geographical variation. They identified 13 distinct call types: three distant contact calls, two lower intensity contact calls, two pair vocalisations, two antagonistic calls and assorted alarm, solicitation and other special purpose vocalisations.

When I began my thesis work, the work of Bond and Diamond had not been analysed. None of the details were available to me at that time. However, this study differs from that of Bond and Diamonds in two main areas. Firstly the number of locations, my study was an in-depth study limited to a kea population in one location, Aoraki/Mount Cook National Park. Bond and Diamonds study included analysis of the levels of geographical variation in kea populations, so their study was conducted in six different locations throughout the South Island. Secondly, the population dynamics of recorded kea populations differed. Recordings for my study were obtained mostly from fledglings, juveniles and sub-adults (94%), whereas Bond and Diamonds recordings consisted of approximately 50% adults and 50% immatures. It is possible that the juvenile kea may have a different vocal repertoire to the adult. Because it is essential to identify

the vocal repertoire of a species before further analysis on the vocalisations can be conducted, I have also conducted a study on the vocal repertoire of the kea. Although the Bond and Diamond paper is currently submitted, the authors have kindly shared their results to allow for consistency across the studies.

Materials and methods

From 449 recordings from 17 banded birds (eight fledglings, seven juveniles, one sub-adult and one adult) and numerous unbanded birds, I have identified and described ten distinct call types: *ke-ee-ee-ah*, *kee-ah*, *growl*, *squeal*, *aww*, *ehhh*, *ah-ah-ah*, *ahh-ahh*, *ke-eh-eh* and *ahh*. I have included spectrograms of each vocalisation as well as descriptions of the call morphology. To keep terminology consistent across the studies, where applicable I have used the same names for vocalisations as Bond and Diamond (submitted) (For the full description of recording and analysis methodology refer to methods, Chapter 2).

General call structure and terms used

There are substantive differences in oral structure of parrots and passerine birds. These have a strong influence on how parrot vocalisations differ from those of passerines. Passerine birds communicate largely in notes in the form of a song (Roberts 1996), which may also include a large variety of fricatives in forms such as clicks, buzzes and ticks. Parrots communicate with more vowel-like vocalisations such as the *ehh* and *ahh* of the kea. Unlike passerines, parrots use vocal communication consisting of calls and call sequences which have striking resemblance to the word-sentence structure of human speech (Roberts 1996).

Based on morphology, kea vocalisations fall into several broad groupings: smoothly modulated vocalisations, oscillatory vocalisations, regularly modulated vocalisations, irregularly modulated vocalisations (Bond and Diamond, submitted) and un-modulated vocalisations. Several of the vocalisations of the kea are characteristic of vocal communication signals in forest dwelling bird species (*Kee-ah*, *ahh*, *ahh-ahh* and *aww*). They have low pitch (i.e., they are based on low frequencies) and a narrow frequency range consisting of long, simple notes (Slabbekoorn *et al* 2002). Kea also have vocalisations displaying characteristics specific to short range

communication, sudden onset, wide bandwidth and low intensity (*ahh-ahh, ah-ah-ah*) (Fernandez-Juricic and Martella 2000).

Figure 1. a. *Ke-ee-ee-ah* vocalization, illustrating features and terms used in this thesis (frequency, Increase-decrease phase, oscillation, modulation, oscillation period, formants, terminal drop, terminal compression, frequency change, fundamental, dominant harmonic, third harmonic, time change and dominant shift.)

b. A smoothly modulated frequency. **c.** 20 ms flick present in some *kee-ah* and *ahh* vocalisations.

This section provides definitions of the terminology used in this thesis. Each term used is labelled on the spectrogram in Fig. 1a. The *frequency* is the number of cycles of vibration per second given in Hz or kHz (Seikel *et al* 1997). Δ *Frequency* gives the difference between the upper and lower frequency limits of the vocalisation (Charif *et al* 1995). Δ *Time* gives the duration of the vocalisation (Charif *et al* 1995). The *fundamental frequency* is the lowest frequency of vibration of the vocal folds or of a harmonic series (Seikel *et al* 1997). *Harmonics* are tones produced when the energy forming the fundamental or carrier frequency evokes structural vibrations at multiples of the fundamental: half, quarter, eighth, etc. of the fundamental wavelengths (Bailey 1991). *Formants* are harmonics amplified by resonance in parts of the vocal tract. The *dominant harmonic* is the harmonic with the highest energy concentration. In Fig. 1a, the dominant is the second harmonic. When this concentrated energy shifts from one harmonic to another, it has been called *dominant shift*. The *high frequency* is the upper frequency limit of the signal (Charif *et al* 1995), with *low frequency* being the lower frequency limit of the signal (Charif *et al* 1995). The *peak frequency* is the frequency at which the highest amplitude in a vocalisation occurs (Charif *et al* 1995). *Peak time* is the time (from the beginning of the signal) at which the highest amplitude in the vocalisation occurs (Charif *et al* 1995). *Oscillations* are repeated sudden shifts of call harmonics between two frequency levels. Each frequency peak of sequential cycles may be separated by a short silent period. *Oscillation period* is the period of

time from the onset of one oscillation to the onset of the next oscillation. The *increase-decrease phase* is where there is a sharp increase then decrease in frequency, giving the harmonics ‘peaks’. The *terminal drop* is the drop in the frequency of harmonics at the end of a signal. *Terminal compression* is the compression of the harmonics at the end of a signal. *Modulations* are a repeated, graded shifting of call harmonics between frequency levels.

Cluster analysis

Hierarchical cluster analysis was used to test the groupings of the kea vocalisations I had hypothesised (Fig. 2). Ten different aspects of the morphology of each vocalisation were measured (see methods, Chapter 2) and then the geometric distance in the multidimensional space using Euclidean distance was calculated. The cluster analysis confirms the classification of the kea vocalisations into ten distinct categories and illustrates how closely related each of the vocalisations are.

Figure 2. Hierarchical cluster analysis showing the ten distinct categories of kea vocalisations and how closely related each of the vocalisations were.

Call descriptions

Ke-ee-ee-ah: Sixty-four recordings from nine identified birds and 15 recordings from unidentified birds were obtained.

Figure 3. *Ke-ee-ee-ah* spectrogram

Description: The *ke-ee-ee-ah* call (Fig. 3) is a high frequency (peak frequency 1.22 - 2.84 kHz (median 2.5 kHz)) oscillatory vocalisation. This call has 2 - 8 harmonics (median 6). The dominant harmonic ranges from first to fourth (median 2), shifting to the third at the end of the oscillatory period. This call starts with the same characteristic increase then decrease in frequency of the *keeah* vocalisation, followed by a series of 1 - 23 oscillations (median 5), 11 - 79 ms (median 44 ms) in length. These oscillations are unique to this vocalisation. The final phase of this call has a constant frequency with a terminal frequency drop. This call lasts for 0.55 - 1.14 seconds (median 0.76 sec.).

Variation: There is a high level of variation within this vocalisation in the number of oscillations (1 - 23 median 5), oscillation duration, period between oscillations (onset to first oscillation 0 - 39 ms, median 23 ms, last oscillation to the last non-oscillatory section 0 - 24 ms, median 13 ms) and peak/valley ratios. There may also be an increase in duration of oscillations accompanied by a decrease in period between oscillations. The non-oscillatory onset and end of the call also vary in duration (onset 0 - 195 ms, median 110 ms, end 0 - 426 ms, median 222 ms). There is a low level of variation in the number of peaks present at the onset of the vocalisation (0 - 2, median 2). The ratio of oscillatory to non-modulated portions is highly variable, with the non-modulated portion comprising 14% to 84.9% of the vocalisation (median 40%).

Growl: Nine recordings from four birds were obtained.

Figure 4a. *Growl* spectrogram showing the *kee-ah* start

Figure 4b. *Growl* with sudden onset

Description: The *growl* call (Fig. 4a & b) is a high intensity, medium frequency (peak frequency 0.78 - 2.67 kHz, median 2.22 kHz) oscillatory vocalisation. It has 2 - 8 harmonics (median 5.5), the second being most often dominant. There is no shift in the dominant harmonic in this call. The *growl* call is long and abrasive sounding. It has a series of rapid increases and decreases in frequency of 0.87 - 1.19 kHz (median 1.06 kHz), with a duration between 29 and 34 ms (median 31 ms). This vocalisation has a sudden onset and end, with no initial expansion or terminal compression in the harmonics. Duration is 0.75 - 1.65 seconds (median 0.92 sec.).

Variation: There is minimal variation in this vocalization, with the largest variation being in the onset of the call. This vocalisation may either begin as *ke-ee-ee-ah* then, where the oscillated portion of the call would otherwise begin, there is a shift to the *growl* vocalization. Or it may have a sudden onset, immediately beginning the *growl* pattern.

Ah-ah-ah: Fifty-two vocalisations from eight identified birds and two recordings from unidentified birds were obtained.

Figure 5a. *Ah-ah-ah* spectrogram

Figure 5b. *Ah-ah-ah* spectrogram showing the two parts of the call

Description: The *ah-ah-ah* vocalisation (Fig. 5 a and b) is a medium frequency (peak frequency 1.61 - 2.56 kHz, median 1.83 kHz) regularly modulated vocalisation. It has 2 - 7 harmonics (median 5). The dominant harmonic is most often the second, shifting to the third during the last

three peaks. This vocalisation has sharp high frequency peaks with longer intervening depressions in the frequency, giving a 'u' shape to each phrase. These are joined and continuous. There is a sudden onset and ending, with no initial expansion or terminal compression of the harmonics. The duration of this call is 0.40 - 1.1 seconds (median 0.79 sec.).

Variation: This vocalisation is highly variable. There is a large amount of variation in the length of the vocalisation. Short vocalisations sound quieter and less abrasive than the longer vocalisations. There are also variations in the structure of this call. In seven recordings, this call was given as a two-part vocalisation with the initial period being as described above followed by a 0.32 - 0.79 sec. (median 0.5 sec.) period. This secondary vocalisation sounds softer, having a lower peak frequency (1.39 - 2.35 kHz, median 1.91 kHz).

Kee-ah: Thirty-eight recordings from nine identified birds and five recordings from unidentified birds were obtained.

Figure 6. *Kee-ah* spectrogram

Description: The *kee-ah* vocalisation (Fig. 6) is a medium frequency (peak frequency 0.66 - 3.06 kHz (median 2.09 kHz)) smoothly modulated vocalisation. It has 2 - 12 harmonics (median 4), the second being most often dominant. There may be shifts of the dominant frequency throughout the vocalisation, with the most common shift being from the second to third harmonic as the frequency of each harmonic decreases. There is a rapid increase in frequency, which then rapidly declines within 11 - 108 ms (median 46 ms) of the on-set of the vocalisation. This change in frequency distinguishes it from the *ahh* vocalisation. The vocalisation then becomes structurally similar to the *ahh* vocalisation, with the harmonics either maintaining a constant frequency or slowly declining over the duration of the call. There is a terminal drop at the end of the call, which lasts for 0.50 - 0.86 seconds (median 0.65 sec.).

Variation: There may be up to three sharp increase-decrease phases at the start of the vocalization, this increase and decrease not always present in all harmonics. The structure of this peak also varies from sharp peaks to soft rounded peaks. Bond and Diamond (submitted) separated this vocalisation into four sub-categories based on these variations. This call may have a 20-30 ms ‘flick’ at the onset or end.

Ahh-ahh: Thirty-one recordings from seven identified birds and one recording from an unidentified bird were obtained.

Figure 7a. *Ahh-ahh* spectrogram

Figure 7b. *Ahh-ahh* with expansion after compression.

Description: The *ahh-ahh* vocalisation (Fig. 7 a and b) is a low frequency (peak frequency 1.13 - 2.35 kHz (median 1.91 kHz)) regularly modulated vocalisation. It has 1 - 8 harmonics (median 4), the second being most often dominant. Terminal compression, with a decrease in the frequency of the dominant harmonic, is present. There is no shift in the dominant harmonic in this call, but intensity in frequencies other than the dominant harmonic may increase during the final expansion period. There is a repeated, gradual, increase then decrease in frequency, which results in broadly rounded peaks as opposed to the sharp peaks of the *growl* vocalisation. The upward peaks are held for a longer duration than the depressions. This vocalisation has a duration of 0.40 - 1.07 seconds (median 0.78 sec.).

Variation: This highly variable vocalisation can be divided into two sub-categories; (a) vocalisations with an expansion lasting 46 - 196 ms (median 68 ms) after the compression, and (b) vocalisations with no extra expansion after the terminal compression. There is also variation in the number of peaks (2 - 4 excluding the extra syllable) and the duration and rate of frequency

increase during each rise. The duration and frequency of each peak is not always uniform within a vocalisation.

Ahh: Two hundred and six recordings from twelve identified birds and nine from unidentified birds were obtained.

Figure 8. *Ahh* spectrogram

Description: The *ahh* call (Fig. 8) is a low frequency (peak frequency 0.56 - 2.72 kHz (median 1.97 kHz)) un-modulated vocalisation. It has 3 - 12 (median 8) harmonics, the third being most often dominant (1 - 4, median 3). This vocalisation may rapidly shift in dominant frequency several times within a call. This shift may also occur during a gradual decline in harmonic frequency. It has a gradual on-set with no sudden increases or decreases in frequency. There is no terminal drop. The duration ranges from 0.41 - 0.82 seconds (median 0.63 sec.).

Variation: Rather than having a constant number of harmonics, each of which maintain a constant frequency from start to finish, there may be points in this vocalisation where harmonics appear or end in higher frequencies. These increases often begin and end suddenly. Frequency also varies with some of the vocalisations sounding quite harsh and others sounding like a soft sigh. This call may have a 30 ms 'flick' (presence of an isolated harmonic, see Fig. 1c) at the onset or end.

Squeal: Two recordings from one individual were obtained.

Figure 9. *Squeal* spectrogram

Description: The *squeal* vocalisation (Fig. 9) is a medium frequency (peak frequency 2.06 - 2.41 kHz; median 2.23 kHz) irregularly modulated vocalisation. This vocalisation has five harmonics

that drop off to two or three during the vocalisation and do not re-appear. The second harmonic is dominant. There is no shift of the dominant harmonic in this vocalisation. The *squeal* is comprised of a series of wide, irregular peaks (5 - 7). There is a high level of variation within the duration and frequency of peaks within a single vocalisation. The *squeal* has a sudden onset and ends with a gradual decline in the number of harmonics. There is no terminal drop. The duration of this vocalisation is 1.10 - 1.51 seconds (median 1.3 sec.).

Variation: This vocalisation is highly variable. The number of peaks, peak duration, call duration, time between peaks all vary considerably within and between vocalisations.

Aww: Only ten vocalisations from a single individual were obtained.

Figure 10. *Aww* spectrogram

Description: The *aww* vocalisation (Fig. 10) is a low frequency (peak frequency 1.28 - 1.68 kHz; median 1.47 kHz) smoothly modulated vocalisation. It has two harmonics with the second harmonic being dominant. There is no shift in the dominant harmonic in this vocalisation. The *aww* vocalisation starts with a deep drop in frequency, which then increases. This increase is followed by short plateau in the frequency, then a rapid decrease. This decrease slows after 20-52 ms (median 37 ms) when there is also a surge in intensity (peak time 112 - 316 ms, median 168 ms). This vocalisation has a rapid onset and no terminal drop. This call lasts for 0.22 - 0.35 sec. (median 0.27 sec.).

Variation: What little variation there was occurred in the frequency range. However, this was most probably due to the large distance of the bird from the microphone causing the high frequencies to drop out. There was slight variation in the length of the plateau period before the harmonic frequency drops.

Ehhh: Only four recordings from a single individual were obtained.

Figure 11. *Ehh* spectrogram

Description: This appears to be a blend of the *ahh* and *growl* vocalisations. (Fig. 11). It is a high frequency (peak frequency 2.28 - 2.44 kHz (median 2.41 kHz) oscillatory vocalisation. There are 5 - 6 harmonics (median 6), the second harmonic being dominant, but there is no shift in dominant harmonic in this vocalisation. It has a sudden onset with harmonics retaining a constant frequency, followed by a series of short, rapid and indistinct peaks. There may or may not be a terminal drop. The duration is 0.63 - 1.59 seconds (median 0.87 sec.).

Variation: The largest variation occurred in the length of the vocalisation. There is also a large amount of variation in the extent and time of harmonic loss and the time of onset of the peaks. The vocalisations may end abruptly with a terminal drop or gradually with the harmonics individually dropping off.

Ke-eh-eh: Only one recording from a single individual was obtained.

Figure 12. Spectrogram of the *ke-eh-eh* vocalisation.

Description. This appears to be a blend of the *kee-ah*, *ahh-ahh* and *growl* vocalisations (Fig. 12). It is a high frequency (peak frequency 2.6 kHz) oscillatory vocalisation. The *ke-eh-eh* had seven harmonics, the second harmonic being dominant. There is a shift in dominant harmonic to the third harmonic in the final 100 ms in this vocalisation. It has a sudden onset with the increase and decrease in frequency that is characteristic of the *kee-ah* vocalisation. This increase/decrease phase is followed by a series of short, rapid peaks reminiscent of the *growl* vocalisation,

separated by smoothly modulated portions. There is a slight terminal drop, but no terminal compression. This vocalisation lasted for 0.9 seconds.

Discussion

The first conclusion that stands out from the findings of this study and the study of Bond and Diamond (submitted) is that kea have an especially large vocal repertoire. There are however, considerable differences between my findings and the findings of Bond and Diamond.

Bond and Diamond identified 13 distinct vocalisation types. Of these, only six were represented in the Mount Cook population. Three of these I have classified under one vocalisation (the smoothly modulated calls *kee-ah*, *meow* and *warble* from Bond and Diamond's (submitted) study, I have grouped as one vocalisation under *kee-ah*). The other calls found in both studies were the *squeal*, the *whinny* and the *growl*. I have grouped the *whinny* and *growl* as one vocalisation type under the term *growl*. I have categorised the calls in broader groups than Bond and Diamond did in their paper because I did not want to over separate the vocalisation types to the level where they could not be examined for intra-individual variation (Chapter 7). The *aww* vocalisation may be the same as the juvenile *kee-ah* described by Bond and Diamond. However, as this vocalisation has an initial decrease in frequency, instead of an initial increase, I have classified them separately. The frequency of use of each call type also varied significantly between the two studies. Bond and Diamond found one of the most common vocalisations amongst juvenile birds to be the *squeal*. I only obtained two recordings of this vocalisation, both from the same individual within 10 seconds of each other. My most commonly recorded vocalisation was the *ahh* vocalisation. The *ahh* vocalisation made up 215 of the 448 recordings I obtained, yet this call was not described by Bond and Diamond.

Causes of variation

Several non-mutually exclusive factors may account the high level of variation observed between these two studies. The first, and most likely, possibility may be due to the differences in the kea population dynamics in the two studies. In my study, 94% of the recordings were from

fledglings, juveniles or sub-adults. In Bond and Diamond's study, these three age classes accounted for about 50% of the studied population. Our findings were probably different primarily because of this difference in the age classes sampled.

Young kea are known to have extensive play behaviour that changes in character as kea mature to sub-adults and adults (Diamond and Bond 1999). Perhaps vocalisations associated with play in juvenile kea were underrepresented in the Bond and Diamond's study and any behaviours associated with the sub-adult and adult play behaviours may have been less likely to be present in my study. My study also notably lacks calls between mated pairs or parents and offspring that may be present in Bond and Diamond's study.

In a review of repertoire identification techniques, Garamszegi *et al* (2002) reported that some song elements may be sung less often than others and such components can be missed in species with large repertoires. Both my study and Bond and Diamond's show that kea do have a large repertoire for a parrot species (at least 17 call types) and that both studies lacked vocalisations from the total repertoire of the kea (i.e. vocalisations associated with nesting behaviour).

Geographic variation in vocalisations has been observed in at least 75 bird species (Tracy and Baker 1999), suggesting that geographic variation may account for some of the variation between the two kea studies. Parrots are known to be able to learn vocalisations throughout their life, with learned vocalisations playing a significant role in the formation and maintenance of social bonds (Farabaugh & Dooling 1996). This ability to learn new vocalisations, coupled with my study site being a geographically isolated area (see map, Chapter 2), may have resulted in kea vocal repertoire in the Mount Cook region varying from that of other kea populations. Bond and Diamond (submitted) did examine geographical variation in kea vocalisations, but did not find entirely different calls in each population. This suggests that, although present, geographic variation is unlikely to be the major cause of variation between the two studies.

Temporal differences between the two studies may explain some of the observed variation. Bond

and Diamond (submitted) collected their recordings from 1988 - 2003, whereas mine were collected from 2003 - 2004. The vocal repertoire of the kea may have undergone slight changes between the time of Bond and Diamond's initial recording period and the time of my recordings. However, because the kea are a long lived, k-selected species, changes in vocal repertoire over a 14 year period would probably not be dramatic enough to account for the differences observed in the two studies.

As a result of intensive study (Huber 2003 pers. comm.), the Mount Cook kea population are almost surely more accustomed to human interaction than kea populations in other areas sampled by Diamond and Bond. Non-habituated kea may have behaviour, including vocalisations, that are considerably different from that of habituated kea.

A final reason for differences in vocalisations between studies may be the differing behavioural context in which the calls were recorded. A large proportion of Bond and Diamond's recordings were obtained from foraging areas. Most of my recordings were obtained at juvenile congregation areas where foraging was not the main activity. The activities of kea in these areas as well as their interactions, could possibly be very different, with varying accompanying vocalisations.

Chapter 4

Vocalisation response sequences - kea in 'conversation'

Introduction

There has been a long tradition of looking for examples of communication that overlap with human capabilities among the higher primates, chimpanzees and bonobos being the best known (King 1996). This appears to have stemmed from hypotheses such as the 'continuation theory' which contends that human language evolved from and elaborated on language like precursors in the communication system of non-human primates (Ujihelyi 1996). However, more recently there has been increasing interest in the communication behaviour of birds. Unlike non-human mammals, bird brains are highly lateralised with one side dedicated to complex song or language in a similar manner to humans (Leiber 1999). Add to this the recent discoveries about the language ability of Alex, an African grey parrot (*Psittacus erithacus*), and the notion that birds might have the rudiments of language ability begins to seem credible. Alex has been trained to speak and reply to short English words and sentences. For example, Alex will reply to questions about 'how many of so and so kind' in English when viewing arrays containing several kinds of objects, with disturbing accuracy (Pepperberg 1990, 1994, 2002, Pepperberg *et al* 2000).

In this chapter I considered the communication of another parrot species, the kea. My study was based entirely in the field and did not entail lab based work like the experimental work for which Alex is famous. Although kea do not appear to be suitable for the kind of laboratory-based research that was carried out with Alex, the complexity of kea vocal repertoire, illustrated in Chapter 3, suggests that more in depth studies of this remarkable parrot's means of communication will be rewarding.

There has been a large amount of work published on the responses of passerines to the vocalisations of conspecifics (Naguib and Todt 1997, Nielson and Vehrencamp 1995, Rogers 2004, Naguib *et al* 2002, Langemann *et al* 2000), but very little on the responses of parrots or other social bird species.

Although bird song might be directed to all conspecifics within hearing range, the interactions between the two individuals in the roles of sender and receiver play an important and complex role in communication. For example two birds may alternate their songs to avoid interference, or in some species such as the nightingale, singers are known to specifically adjust their timing of song onset in order to overlap the vocalisations (Naguib and Todt 1997). An example of this was given by Langemann *et al* (2000), who used playback experiments on male great tits (*Parus major*) to simulate territorial invasion. They found that rates of overlap in vocalisations were greater for playback vocalisations in which the strophe length was not related to that sung by the subject, than when the relative strophe length was increased and overlapped the strophe length of the subject. They argued that this indicates that great tits are capable of extracting information about a willingness to escalate conflict from an opponent's vocalisations and adjust their response accordingly.

Male passerines have also been shown to have consistently different ways of replying when they hear different song categories (Naguib *et al* 2002). Naguib *et al* (2002) argues that this indicates the birds are able to first distinguish between song categories, and second that different categories have different functions in communication. For example, Beecher *et al* (2000) found that the responses in song sparrows (*Melospiza melodia*) were dependent on the season. In the early breeding season (14-28 April), song sparrows more frequently matched their vocalisation with the initial sender (73%). Later in the season (29 May-8 June) they only rarely type matched (18%). In seasons other than the early breeding season, song sparrows typically replied to a neighbour's vocalisation with another shared vocalisation (repertoire matching) rather than type-matching. Beecher *et al* (2000) suggested that this indicates that type matching in songbirds is an aggressive response.

Previous studies on vocalisation responses in the kea

Higgins (1990) stated that *kee-ahs* often gained a response of the same vocalisation. This was supported by Bond and Diamond (submitted) in a series of playback experiments. Bond and Diamond (submitted) also found *whinnies* incited a response of the same vocalisation but may also be responded to by *bleating* and playback of *squeals* elicited a response of *squeals* from other birds. *Break* calls are a vocalisation used by a mated pair, possibly to negotiate movements. These were found to be reliably replied to with the same vocalisation. *Whines* were found to elicit *whinnies* or *kee-ahs* as responses.

Introduction to my study

Bond and Diamond (submitted) stated that there are two ways to determine functional significance of vocalisation in terms of the information content of the signal. The first is to examine the context in which the call is produced and the second is to examine the responses of the call recipients, particularly whether they vocalise in reply and whether they give the same or a different call type. Behavioural context will be discussed further in Chapter 5. In this Chapter I have compared the rates at which each vocalisation received each of the other vocalisations as a response to fledgling, juvenile and sub-adult kea vocalisations. It is not possible to know for certain whether a vocalisation was an intended response to the vocalisation of another individual or if two vocalisations given in quick succession are entirely independent. Therefore, identification of what I have termed as ‘a possible response vocalisation’ is necessary. I have considered a possible response to be any vocalisation given within one second of a vocalisation from another individual in the absence of any other obvious stimulus that may have incited the vocalisation. Eight of the ten vocalisation categories recorded in this study were used as part of an apparent exchange as either an initial vocalisation or a possible response (see Chapter 3). Comparisons of initial vocalisation with response were only conducted for five of the ten call types recorded in this study (*kee-ah*, *ahh-ahh*, *ahh*, *ah-ah-ah* and *ke-ee-ee-ah*). This is because only recordings of vocalisations with responses clear enough to produce a reliable spectrogram were used.

Langemann *et al* (2000) suggested that overlapping of the initial vocalisation with a vocalisation

from another bird is important in assessing the vocalisation's message. This is because experimental evidence suggests that the overlapping of vocalisations in passerine species can be viewed as a form of aggressive behaviour. I have compared the presence of overlap in kea vocalisations with the behavioural context of the call to determine if overlap of kea vocalisations may be an indication of aggressive intent.

Results

Response results: The vocal response to a vocalisation of a conspecific in kea is not always the same as the initial vocalisation (Fig. 1, Tables 1-5). Kea appear to receive the same vocalisation as a response in 50% of vocal interactions with the other 50% being comprised of four vocalisations, *ahh*, *kee-ah*, *ke-ee-ee-ah* and *ah-ah-ah*. The *kee-ah* vocalisation (Table 1) gained the same vocalisation as an apparent response in 42.9% of vocal interactions. The *ke-ee-ee-ah* appeared to be given as the responses in 50% of interactions and *ahh* in 7%. The *ahh-ahh* vocalisation (Table 2) gained the same vocalisation as an apparent response in 83.3% of vocal interactions with the *ahh* appearing to be given in response in 16.7% of the vocalisations. The *ahh* vocalisation (Table 3) gained the same vocalisation in what appeared to be a response in only 10% of vocal interactions, while gaining the *kee-ah* in 60% and the *ke-ee-ee-ah* in 30% of apparent vocal interactions. The *ah-ah-ah* vocalisation (Table 4) only gained the same vocalisation as a possible response (100%). The *ke-ee-ee-ah* vocalisation (Table 5) gained the same vocalisation as an apparent response in 55.3% of vocal interactions with the *kee-ah* being given in 42% and the *ah-ah-ah* in 2.6% of apparent responses.

Figure 1. Proportion of time in which each vocalisation was followed by a specific vocalisation.

Table 1. The proportion of time each vocalisation was an apparent response to the *kee-ah* vocalisation.

Table 2. The proportion of time each vocalisation was an apparent response to the *ahh-ahh* vocalisation.

1)

2)

Table 3. The proportion of time each vocalisation was an apparent response to the *ahh* vocalisation.

Table 4. The proportion of time each vocalisation was an apparent response to the *ah-ah-ah* vocalisation.

3)

4)

Table 5. The proportion of time each vocalisation was an apparent response to the *ke-ee-ee-ah* vocalisation.

5)

As well as different vocalisations being given in response to another vocalisation, a single kea may use several different vocalisations within a single bout of exchange. Figure 2 shows a vocal exchange between two kea, white green and red lime. The initial vocalisation was a *kee-ah* vocalisation given by white green, this appeared to incite a response of the *ahh* vocalisation from red lime, which in return appeared to incite a *ke-ee-ee-ah* response from white green. Although these vocalisations change, they tend to stay within the same basic morphological categories (see Fig. 1, Chapter 3). Fig. 3 shows two *ah-ah-ah* vocalisations given in an apparent exchange. The initial vocalisation was from the kea green yellow, the apparent response was from the kea green lime.

Figure 2. Three different vocalisations used in an apparent exchange between two kea.

Figure 3. *Ah-ah-ah* vocalisation from ‘green yellow’ and *ah-ah-ah* response from ‘green lime’

Overlap results: There were only three vocalisation types used by kea to overlap vocalisations of other individuals. These were *ke-ee-ee-ah* (50%) (Fig. 4), *Kee-ah* (42.5%) and *ah-ah-ah* (7.5%) (Table 1). Overlap occurred in a variety of behavioural contexts in the kea. The highest level of overlap, representing 44.8% of all occurrences, was when the initial sender was engaged in perching behaviours. Overlap while the initial sender was perching provided the majority of this, with 34.5 % of all occurrences. Exchanges associated with the arrival of other birds at the study site had the second highest incidence of overlap (17.2%), followed by vocalisations while the initial caller was scanning (13.8%) and when the initial caller was standing below the perch (10.3%). Vocalisations which were associated with arrival at the study site, after displacement and walking departure from the study site each accounted for 6.9% of observed overlap with vocalisations occurring before walking departure from the study site accounting for 3.4% of the total occurrences of overlap.

Figure 4. The initial *ke-ee-ee-ah* vocalisation with the overlap from the *ke-ee-ee-ah* response vocalisation.

Table 6. Proportion of time each vocalisation was used to overlap another vocalisation.

Table 7. Proportion of time overlap occurred during each behaviour of the initial sender.

Discussion

In this chapter I investigated how the kea responded to the vocalisations of other kea. Although there was no reason to suspect that there was not an equal probability of receiving any of the ten identified vocalisations (see Chapter 3) as a response, repeating the initial vocalisation was usually favoured. When a different vocalisation was used in the response, it tended to be a vocalisation that was, according to a hierarchical cluster analysis (see Chapter 3), closely morphologically related. The only exception to this was the vocalisation *ahh*. A kea was recorded possibly responding to this vocalisation with the vocalisation *ahh-ahh*, which is not closely morphologically related (see Chapter 3). However, this exchange only occurred once so it is not possible to determine the frequency of this call/response combination, or even if the vocalisations are used in exchange together and not two independent vocalisations ‘accidentally’ produced together. The *ke-ee-ee-ah* vocalisation appears to have gained an *ah-ah-ah* response. Although these vocalisations are not closely related, *ah-ah-ah* is the third nearest neighbour to *ke-ee-ee-ah* (according to the hierarchical cluster analysis, see Chapter 3). It is possible that vocalisations given in what appeared to be responses serve the specific function of response vocalisations, but this is unlikely. If the specific function of a vocalisation was to serve as a response, it would be expected that there would be low levels of use outside the context of vocal exchange. This was not the case. The highest level of responses (from vocalisations with a sample size greater than two) was demonstrated in the *ke-ee-ee-ah* vocalisation. Although this was used in apparent exchange in 67.5% of recordings, only 43.3% of these were possible responses. The similarity in response call types may support Naguib *et al*’s (2002) hypothesis that birds can discriminate between song types.

The vocalisation type given by the initial caller and the vocalisation type given in an apparent response, appear to be interchangeable at least within three vocalisations, *ahh*, *ke-ee-ee-ah* and *kee-ah*. This suggests that as well as being morphologically similar, these three vocalisations may

have similar functions or type of messages at varying levels (for example identification, location or behavioural intentions) (see Chapter 5). The only situation in which all three of these vocalisations were not used in apparent exchanges together was the *ahh* not being given to the *ke-ee-ee-ah* as a response. This suggests that if the vocalisations do have similar message types the *ke-ee-ee-ah* may carry a more complex message than the *ahh*. The possibility of these three vocalisations carrying varying levels of a similar message is supported by the staggered responses. The *ahh* vocalisation gained the highest proportion of *kee-ahs* as a response, and the *kee-ah* gained the highest proportion of *ke-ee-ee-ahs* as a response with the *ke-ee-ee-ah* vocalisation most commonly gaining another *ke-ee-ee-ah*.

In passerines, overlap in vocalisations often corresponds with the bird being aggressive (Naguib and Todt 1997). In this study, only 6.9 % of the observed overlap was associated with aggressive interactions. 34.5 % of overlapping occurrences were while the kea giving the initial vocalisation was perching. The next highest proportion occurred with vocalisations given at the arrival of other individuals to the study area. Vocalisations associated with either of these behaviours may have aggressive messages. Perching was defined as a separate behaviour to scanning in this study because of the high level of aggression surrounding possession of the perch (see Chapter 5). Vocalisations given to or from new arrivals may also signal aggressive intent, yet there were no aggressive interactions or postures associated with the vocalisations. Overlap only occurred when there were groups of 3-6 birds present at the study site. This may have increased the level of excitement or aggression at the study site, or due to the vocal nature of kea, may have caused accidental overlap because of the high numbers of individuals present. It appears most likely that overlap in kea is a result of an increased level of excitement. This excitement may be caused by several reasons. It is possible that excitement is caused by the desire to assert status to other individuals. However, considering the highly social nature of young kea, it may also be due to excitement over more individuals being present at the study area providing potential playmates.

Chapter 5

Association between vocalisations and other behaviours

Introduction

The vocal behaviour of a species is influenced by evolutionary constraints and selective pressures imposed by the species environment and social system (McShane *et al* 1995).

Environmental factors, such as the terrain a vocalisation must pass through before reaching the receiver, have a large effect on the structure of a vocalisation. For example, travelling through water, long grasses or, as in the case of the kea, forest habitat. However, vocal behaviour is not only subject to pressures from the environment, social organisation and the context in which communication is used also are important in shaping a species repertoire (McShane *et al* 1995)

Many parrot species are known to display a broad array of behaviours (e.g. St. Lucia parrots, *Amazona versicolor*; Copesey 1995). There are over 40 distinct behaviours described for the kea (Potts 1976, 1977, Bond and Diamond 1991, 1999, Jackson 1963), including extensive play behaviours well beyond the level of other bird species. Vocalisations have been linked with behavioural context in several parrot species (Saunders 1983, Martella and Butcher 1990). Linking behaviour with vocal signals is a useful tool that may allow us to interpret the function or meaning of a vocal signal.

There are strong links between the sociality of parrots and their vocal communication. For example, Farabaugh and Dooling (1996) found that changes in the social environments of parrots are often associated with adult vocal plasticity. Farabaugh and Dooling (1996) also argue that solitary parrot species have very simple repertoires compared to their social counterparts (for example the kakapo, *Strigops habroptilus*; Powesland 1992). Although previous studies have contributed to our understanding of parrot vocalisations, there is still little known about their structural variability or possible roles in social organisation, particularly in wild populations (Fernandez and Martella 2000). Furthermore, the majority of these studies have provided a large amount of qualitative information, but very few have conducted any quantitative analysis.

In a study of short-billed white-tailed black cockatoos, Saunders (1983) found that most vocalisations were related to group maintenance and co-ordination. Saunders (1983) described the vocalisations and the context in which they were given, but did not give functions or any quantitative information. Fernandez-Juricic *et al* (1998) conducted a study on the vocalisations of the blue-fronted amazon. They identified nine vocalisations, three of which had specific functions and six that were non-specific. These functions were determined through qualitative analysis, listing situations in which the vocalisations occurred, but they did not conduct any quantitative analysis. In a more recent study Fernandez-Juricic and Martella (2000) further analysed the vocalisations of the blue-fronted amazon, focusing on the context of the guttural call. They conducted principal component analysis (PCA) on the vocalisations, but provided no quantitative analysis of the behavioural associations.

Roberts (1996) argued that classifying calls of the Puerto Rican parrot by function was not possible because the parrot produces the same calls in multiple contexts. Numerous other authors have also demonstrated difficulty determining possible functions to parrot calls. Fernandez-Juricic and Martella (2000) found that most types of gutturals were given in all contexts although some were more frequently recorded in specific circumstances. They also noted that gutturals were combined with other vocalisations in a specific order and structure, concluding that categories could not be exclusively ascribed to specific contexts (Fernandez-Juricic and Martella 2000). This difficulty in determining the function of vocalisations is not restricted to parrots. Barklow (1979) found that all three call types of the 'tremolo' vocalisation in the common loon (*Gavia immer*) could be given in any behavioural situation.

Because of the difficulty of ascribing the specific functions to parrot vocalisations, I will instead provide a quantitative analysis of the behavioural situations in which the vocalisations occurred, with the frequency of use in exchange. I will also offer a possible interpretation of the vocalisations as opposed to defining a specific function.

In Bond and Diamond's (submitted) recent study of kea vocalisations they provided possible functions for six of the vocalisations I recorded. They found the *kee-ah* was the primary general-purpose contact call, used to establish communication between widely separated individuals. *Meows* had a similar function to *kee-ah* but at closer quarters. *Squeals* were found to be juvenile contact calls, produced only by young birds. They observed that *growls* were associated with agonistic interaction over resources and appeared to be associated with aggressive motivation. *Warbles* were found to be produced at the moment of take off. They suggested that *whinnies* indicated excitement or arousal and were commonly associated with group decision making. Although Bond and Diamond (submitted) have provided qualitative interpretations of the function of vocalisations and conducted playback experiments with kea, there have been no quantitative studies done.

Introduction to my work

Vehrencamp (2000) defined signals as actions or structures that have been selected to provide information to receivers about sender attributes or environmental contexts. Vehrencamp (2000) states that senders encode the information from signals by linking distinctive signals or signal variants to specific contexts. In this chapter I have attempted to provide an interpretation of the possible context of each recorded vocal signal based on behavioural associations through quantitative analysis. The primary focus of this chapter will be the behavioural associations with vocalisations, with consideration given to the terrain the vocalisations travel through. The behaviour is the primary consideration over the habitat because the habitat of the kea is highly variable, including both densely forested areas and open tussock fields.

I initially describe the behaviours of the kea that were associated with the recorded vocalisations. Because of the broad array of behaviours demonstrated by the kea, I have only described behaviours observed immediately before, during or after a vocalisation. I have also included any behaviours that may strongly influence any following behaviours or vocalisations (for example high level aggression behaviours such as attacks). I have then used quantitative analysis to explore the association between the vocalisations and behaviours in an attempt to extrapolate the

functions of kea vocalisations. To determine if the vocalisations used in apparent exchanges between birds are dependant on behaviour, I have conducted quantitative measurements of the proportion of times each vocalisation is given as a response to or gains a vocal response from other kea.

Kea behaviours

The categorisations of the behaviours observed in this study are shown in Table 1. Behaviours such as object manipulation and facing towards Glencoe Bush, which have not been categorised into larger groups or do not have any sub-categories, were omitted from this table and are defined below. Note that the use of the terms ‘aggressive’ and ‘aggression’ were to group any behaviours that were perceived to result in an individual either being physically harmed (for example bitten), chased (for example run-rush) or any behaviour that resulted in another individual ‘running away’ (for example turn towards).

Table 1. Shows the broad behavioural categories with the specific behaviours discussed in this thesis.

Definitions of behaviours discussed in this thesis

Comfort movements

Body shake: This consists of a fluffing of the entire plumage, followed by a sharp side to side twisting of the body (Potts 1976) (Fig. 1). *Both-wings stretch:* Both wings, slightly bent at the carpal joints, are raised over the back so the bows and tips come close together, are held for a few seconds, then folded to rest (Potts 1976) (Fig. 2).

Figure 1. Comfort movements: *Body shake*
stretch

Figure 2. Comfort movements: *Both-wings*

Leg and wing stretch: One wing and the leg on the same side are extended downwards and backwards from the body while the tail is fanned to the same side. The wing and the leg are not

always returned to rest simultaneously. The leg is sometimes returned to the substrate while the wing remains stretched for a few seconds longer. This is often performed after long periods of inactivity and lasts for approximately five seconds (Potts 1976) (Fig. 3).

Figure 3. Comfort movements: *Leg and wing stretch*

Autopreening

Preening: This may occur as an isolated event, as when a bird preens its breast feathers during a break in feeding, or it may occur for extended periods, usually following feeding or bathing. It is sometimes preceded by a slight ruffling of the plumage to facilitate the grasping and preening of individual feathers (Potts 1976) (Fig. 4). *Bill-wipe:* The bill is rubbed against a solid surface, first on one side and then the other (Fig. 5).

Figure 4. Autopreening: *preening*

Figure 5. Autopreening: *bill wipe* (Half-bill)

Foot-and-leg-nibble: A bird may stand on one leg and bring the other up to the bill so that the foot or leg can be nibbled or it may instead lower the bill to the foot or leg. Kea may also compromise by raising the leg and lowering the bill so that they meet each other halfway (Fig. 6) (Potts 1976).

Figure 6. Autopreening: *foot-and-leg-nibble*

Altruistic behaviours

Allopreening: Preening of one bird by another (Potts 1977) (Fig. 7). *Allofeeding:* One bird regurgitates food into the bill of another bird (Fig. 8).

Figure 7. Altruistic behaviour: *allopeening*

Figure 8. Altruistic behaviour: *allofeeding*

Bill-head touching: One kea touching the head of another kea with its bill (Fig. 9). *Bill*

touching: When a kea uses the bill to touch the bill of another kea (Fig. 10).

Figure 9. Altruistic behaviour: *head-bill touch*

Figure 10. Altruistic behaviour: *bill touch*

Play

Roll over: The kea rolls over and lies on its back while gently moving its feet, accompanied by a squealing vocalisation (Diamond and Bond 1999) (Fig. 11). *Jumping on:* One kea repeatedly

jumps on the back or stomach of another kea, then they switch roles (Fig. 12).

Figure 11. Play behaviour: *roll over*

Figure 12. Play behaviour:

jumping on

Aggressive behaviours

Displacement: Any action of a kea that leads to another kea moving from its place (Fig. 13). *Bill-*

gaping: This action involves holding the bill open for a few seconds while turning towards another bird. It is often performed in association with lunging and run-rushing or in response to these actions (Potts 1977). *Bite:* Grasps opponent with bill, particularly by the legs and feet (Bond and Diamond).

Figure 13. Aggressive behaviour: *displacing by biting feathers*

Chasing: Chasing does not have to include lowering of the head or specific body positions as in the run-rush. It is usually performed when an opponent is fleeing and may be accompanied by lunging and bill-gaping (Potts 1977). *Run-rushing:* This consists of a fast walk toward another bird while the head is lowered and the body held almost parallel to the substrate; bill gaping often accompanies it. A high intensity of aggression is indicated when the carpals are held slightly away or straight out from the body (Potts 1977).

Figure 14. Aggressive behaviours: *Run-rush*

Clawing: Clawing frequently occurs when birds are perched close together. An aggressor may sidle toward an opponent, turn partially toward it, raise a claw and strike out sideways in a pushing motion. The clawed bird may respond by walking or sidling away, usually slowly. Clawing in this context probably functions to maintain individual distance. More intensive clawing is used in fighting. It often precedes, follows, or is used together with pecking or bill-gaping (Potts 1977). *Hunching:* The rump feathers are fluffed and the tail is fanned out. The humeri are held slightly out and upwards from the body and the forewings are dropped. While the bird is immobile the head is directed downwards and the body is crouched, but on walking the head may be raised slightly and the body made more erect (Potts 1977).

Figure 15. Aggressive behaviour: *hunching*
(lateral view)

Figure 16. Aggressive behaviour: *hunching*
(posterior view)

Object manipulation

Exploration of an object, usually using the bill but occasionally with the claw or both. This behaviour can involve touching, biting, pulling or prodding with bill and gripping or touching with claws (Figs. 17 and 18).

Figure 17. Object manipulation: using bill

Figure 18. Object manipulation: using bill and claws

Foraging behaviour

Red tray: Foraging from a red tray containing stones smeared with butter. This tray was part of another study being conducted on kea in the study area (Werdenich 2003 pers. comm.).

Behaviours associated with the tray were often more aggressive than those in *ground foraging*, this was possibly caused by the tray being a more valuable and guarded food resource than the usual substrate (Fig. 19). *Ground foraging:* Foraging on the substrate. This includes foraging for natural food sources and food placed on the substrate by the Vienna University Kea Research group as part of their study (Fig. 20).

Figure 19. Foraging behaviour: *red tray*

Figure 20. Foraging behaviour: *on ground*

Scanning

The head is raised and moved from side to side (Fig. 21). Scanning may also involve standing stretched out with the head raised high.

Figure 21. Scanning

Perch behaviour

On perch: When a kea is sitting or standing on a perch above the study area (Figs. 22 and 23).

The perches three fence posts along the edge of the stopbank (see map, Chapter 2). Perching was classified as a separate behaviour to scanning because of the high level of aggressive interaction involved in the acquisition of a perch. *Facing perch:* This behaviour is defined as a kea standing on the ground directly beneath a perch, looking up towards another individual on the perch.

Figure 22. Perching behaviour: *on perch, scanning*
vocalising

Figure 23. Perching behaviour: *on perch,*

Leaning on fence

When a kea leans or stands against the mesh fence running the length of the stop bank (see map, Chapter 2) with very little or no movement (Fig. 24).

Figure 24. Leaning on fence: *standing against fence*

Facing bush

When a kea stands motionless, facing towards Glencoe Bush (see map, Chapter 2). There is no other behaviour or action occurring at the time.

Facing across stream

When a kea stands still at the edge of the stop bank facing across the stream towards Governor's Bush (see map, Chapter 2) (Fig. 25).

Figure 25. Facing across stream.

Arrival

Walking: The kea walks up to the study area from the base of the stop-bank (see map, Chapter 2). *Flight:* Birds arrive at the study sites after flying in, often from the rubbish corner (see map, Chapter 2), or the roof of the Hermitage Hotel (see map, Chapter 2) (Figs. 26 and 27).

Figure 25. Arrival: *flight*, Sealy Tarns

Figure 26. Arrival: *flight*, kea landing

Departure

Walking: The kea walk up the stop bank from the study area towards the water tanks at the top of the ridge (see map, Chapter 2) before taking flight. *Flight:* Departing the study area by immediately taking flight (Fig. 28).

Figure 28. Departure: *flight*

Results

Ahh: One hundred and thirty-five recordings from eleven individuals were studied.

Associated behaviours: This call is used by kea in 14 behavioural categories and 30 distinct behaviours (Table 2). The primary behaviours associated with this vocalisations were scanning (25.9%), during departure (17.2%), during aggressive interaction (14.98%) and perch behaviour (12.52%). It was also used in smaller proportions in comfort (2.2%), autopreening (5.2%), foraging (7.5), altruism (2.8%), arrival (2.9%), object manipulation (1.4%), facing across the stream (0.7%), leaning against fence (1.5%), approach of another kea (5.9%) and at the flight departure of another bird (2.2%).

Responses: The *ahh* vocalisation was used in apparent exchanges in 25.2% of the vocalisations occurrences (Table 3). The highest level of exchange occurred while the kea giving the initial vocalisation was foraging. Vocalisations given during this behaviour seemed to elicit a response in 40% of occurrences. There was an apparent responses gained on one of the two occasions the *ahh* vocalisation was used by kea leaning against the fence. The *ahh* call was only given by kea as an apparent response in association with two behavioural categories, aggressive behaviour (15%) and scanning (22.9%). *Ahh* appeared to gain a response in a larger range of behaviours, aggression (10%), foraging (40%), allopreening (25%), scanning (11.4%), departure (12.5%), object manipulation (50%), against fence (50%) and in approaching (16.7%). The *ahh* vocalisation was given as a response and gained a response when the kea giving the initial vocalisation was scanning (5.7%), departing the study site (4.2%), and engaged in object manipulation behaviours (50%).

Table 2. Percentage of times the *ahh* vocalisation was given for each behavioural category

Table 3. Percentage of times the *ahh* vocalisation was given in or gained a response for each behavioural category

Kee-ah: Forty-two vocalisations from nine individuals were studied

Associated behaviours: The *kee-ah* vocalisation was most frequently given by kea that were scanning (28.6%) and during aggressive interactions (23.9%) (Table 4). It was also used at the red tray (2.4 %), which as a food resource often incites aggressive behaviours, possibly adding this to the aggressive category. Kea also gave the *kee-ah* vocalisation when departing the study site (9.6%), during comfort movements (4.8%), during arrival to the study site (7.1%), during object manipulation (2.4%), in association with perch behaviour (7.2%), when leaning on the leaning mesh fence (7.1%) and when facing the across the stream (7.1%).

Responses: The *kee-ah* vocalisation appeared to have a high level of use in exchange (64.3% of vocalisations) (Table 5). It appeared to gain a response more frequently than it appeared to be given in response. The *kee-ah* vocalisation seemed to incite responses when the kea giving the initial vocalisation was engaged in an aggressive interaction (20%), foraging (100%), scanning (33.3%), departing the study site (25%), perch behaviour (66.9), facing across stream (33.3%) and leaning on the mesh fence (100%). This vocalisation seemed to be given in response to other

vocalisations when the focus kea was engaged in an aggressive interaction (20%), scanning (25%), departing the study site (50%), object manipulation behaviours (100%) and facing across stream (33.3%). Kea both gave *kee-ah* as a response and gained a response to the same *kee-ah* vocalisation during aggressive interactions (10%) and while scanning (8.3%).

Table 4. Proportion of time the *kee-ah* vocalisation seemed to be used in exchange for each behavioural category

Table 5. Percentage of times the *kee-ah* vocalisation was given in or gained a response for each behavioural category

Ke-ee-ee-ah: Forty vocalisations from eight individuals were studied.

Associated behaviours: Kea primarily used the *ke-ee-ee-ah* vocalisation during scanning (27.5% of *ke-ee-ee-ah* vocalisations), departure (25%) and aggression (20%) (Table 6). 12.5% of the departure vocalisations occurred after walking departure from the flock when the kea were at the top of the stop bank near the water towers (see map, Chapter 2). The *ke-ee-ee-ah* vocalisation was also used after arrival (2.5%), during object manipulation (2.5%) perching (12.5%), facing bush (2.5%) and leaning (7.5%).

Responses: This vocalisation was used in apparent exchanges in 67.5% of the vocalisations (Table 7). This was the highest proportion of a vocalisation being used in exchange. The call had reasonably even proportions between gaining a response, being given in response and both being and inciting response. Scanning had the highest level of use in exchanges (for a behaviour with a sample size greater than one) with 91% of vocalisations given during scanning being used in an apparent exchange. This was followed by aggression (66.4%), leaning on fence (66.3%), perch behaviour (60%) and departure (40%). Both the object manipulation and facing bush behaviours were associated with exchange 100% of the time, but only had sample sizes of one, so were not conclusive.

Table 6. Proportion of time the *ke-ee-ee-ah* vocalisation seemed to be used in exchange for each behavioural category.

Table 7. Percentage of times the *ke-ee-ee-ah* vocalisation was given in or gained a response for each behavioural category

Growl: Nine recordings from four individuals were studied.

Associated behaviours: Kea tended to *growl* primarily during aggressive interactions (77.8% of *growl* vocalisations) (Table 8) (after being clawed (11.1%), during hunching (11.1%), before displacing (11.1), after displacing (11.1%), after being displaced (22.2%) and during a fight (11.1%). The vocalisation was given by both the aggressor and the recipient of aggression during aggressive interactions. When the *growl* vocalisation was used by a kea after being attacked, the vocalisation seemed to incite a second attack from the same attacker. This vocalisation also occurred during two non-aggressive actions, while scanning (11.1%) and while leaning on the fence (11.1%).

Responses: In 66.7% of the times recorded the *growl* was given during an apparent vocal exchange (Table 9). The *growl* vocalisation was used during apparent vocal exchange in 71.4 % of recorded vocalisations associated with aggressive behaviours (51.7% elicited a response and 14.3% were given as a response, Table 3). The small sample of *growl* vocalisations recorded during non-aggressive behaviour (n=2) limited the ability to determine the extent to which the *growl* is used in exchange in this behavioural context. This vocalisation was only used in exchange in one non-aggressive interaction, as a response to a vocalisation from Governor's Bush (see map, Chapter 2) while the kea was leaning on the fence.

Table 8. Percentage of times the *growl* vocalisation occurred within each behavioural context.

Table 9. Percentage of times the *growl* vocalisation was given in or gained a response for each behavioural category.

Ehh: Four recordings from one individual were studied.

Associated behaviours: This vocalisation was given four times in two behavioural contexts. Three of the *ehh* vocalisations were given while the kea was leaning against the fence (75%) and one was given when the kea was facing across the dam to Governor's Bush (25%). The *ehh* vocalisations were given by one kea on the same morning and were alternated with the *squeal* vocalisation in an apparent exchange.

Responses: The *ehh* vocalisation appeared to gain a response, or was given by the kea in an apparent response, on three occasions (75% of times used) (Table 10). When the *ehh* vocalisations was given while the kea was facing across the dam to Governor's Bush, it appeared to both be given as a response and to incite a response from a kea in Governor's Bush (see map, Chapter 2). *Ehh* was given in an apparent response to a vocalisation from Governor's Bush once while leaning on the fence (33.3%) and was both given as an apparent response and appeared to receive a response once (33.3%).

Table 10. Percentage of times the *ehh* vocalisation was given in or gained a response for each behavioural category

Ke-eh-eh: One recording from one individual was analysed.

Associated behaviours: This vocalisation was only recorded once, after an unspecified aggressive interaction during a fight.

Responses: The *ke-eh-eh* vocalisation was not used as part of a vocal exchange.

Squeal: Two recordings from one individual were studied.

Associated behaviours: Kea *squealed* during two behavioural contexts, once when the vocalising kea was scanning and once after object manipulation (poking bill through mesh in a fence). It appeared that the *squeal* vocalisation was being used in long distance vocal exchange with a kea in Governor's Bush.

Responses: This vocalisation was only recorded twice, both apparently being given in response to a distant vocalisation and one also appearing to receive a reply (Table 11). These exchanges were with a kea out of visual contact, vocalising from Governor's Bush.

Table 11. Percentage of times the *squeal* vocalisation was given in or gained a response for each behavioural category.

Aww: Ten recordings from one individual were studied.

Associated behaviours: This vocalisations was recorded ten times. The *aww* was given by an

unidentified kea in flight near a nesting site above Sealy Tarns (see map, Chapter 2). The kea in flight flew down in a swooping motion above our heads twice before flying behind a ridge. This vocalisation was recorded after a kea was vocalising then took flight from a nest site disturbed by a Department of Conservation ranger investigating for signs of nesting activity. This vocalisation is possibly from the kea recorded vocalising from the nest site prior to the *aww* vocalisation. A comparison of the vocalisations to determine if they were the same was not possible because sound degradation caused by the distance between the microphone and the caller resulted in inadequate recordings to produce a reliable spectrogram of the vocalisations given from the nest.

Responses: Although there were repeated vocalisations from a kea at a nearby nest site prior to the *aww* vocalisations being given, there were no vocalisations immediately preceding the *aww* vocalisations to suggest they were a response. There were no vocalisations given after this vocalisation in response.

Ah-ah-ah: Eleven vocalisations from five individuals were studied.

Associated behaviours: The *ah-ah-ah* vocalisation is most commonly used by young kea in flocks of 3-8. It was only given by males and is possibly a male specific vocalisation.

Interactions with high levels of aggression accounted for 36.4% of the behaviours associated with the vocalisation (Table 12) (18.2% during chasing, 9.1% after chasing, 9.1% during displacement). 27.3% of the times kea used the *ah-ah-ah* vocalisation it was given during or after departing a congregation area (18.2% while walking, 9.1% after walking). A further 27.2% of the times the *ah-ah-ah* vocalisation was given occurred while kea were scanning. This vocalisation was produced once before play (9.1%). It is possible the vocalisation incited the play, but it is most probable that the vocalising bird was scanning when another kea incited the play by jumping on the back of the vocalising kea.

Responses: This vocalisation appeared to be used as an exchange in 45.5% of my recordings (Table 13). Responses appeared to be gained by 25% of the vocalisations given during

aggressive interactions, 66.7% of vocalisations given while scanning and one vocalisation given when departing the study area by flight (33.3%). 33.3% of scanning vocalisations appeared to both be given in response and to receive a response.

Table 12. Percentage of times the *ah-ah-ah* vocalisation was given for each behavioural category

Table 13. Percentage of times the *ah-ah-ah* vocalisation was given in or gained a response for each behavioural category

Ahh-ahh: Twenty-seven vocalisations from five individuals were studied

Associated behaviours: This vocalisation was only recorded from male kea. It is primarily associated with perch behaviours (perched 59.3%, below perch 3.7%) (Table 14). It was also used by a kea during solitary ‘*roll over*’ play behaviour (22.2% of vocalisations), scanning (3.7%), after arrival by flight (3.7%), before flight departure (3.7%) and after walking departure (7.4%).

Responses: 44.4% of the vocalisations appeared to be used in an exchange (Table 15). All of the apparent exchanges were with kea in either Glencoe Bush or Governor's Bush (see map, Chapter 2). This call seemed to have a high level of responses in departure (66.7%) and perch behaviour (62.6%), but was not used in exchanges during play behaviour, scanning or after arrival at the study area.

Table 14. Percentage of times the *ahh-ahh* vocalisation was given in each behavioural category.

Table 15. Percentage of times the *ahh-ahh* vocalisation was given in or gained a response for each behavioural category.

Discussion

Inferred function

Ahh: This was the most general vocalisation recorded, with one of the lowest levels of use in exchange (25.2%) (Table 3). Kea used *ahh* across the widest range of behaviours of all the vocalisations (14 behavioural categories and 30 distinct behaviours), which suggests that the behaviour at the time of the vocalisation was unimportant. Although this vocalisation has a high level of variation in intensity, it is most frequently a low intensity vocalisation. The lack of responses and the broad range of associated behaviours suggest that this vocalisation is a non-targeted proclamation of identity and/or location most probably used in short-range communication.

Kee-ah: The *kee-ah* vocalisation was used more frequently in apparent exchanges than the *ahh* vocalisation. It was used in a broad range of behavioural contexts (although not as broad as *ahh*), with kea giving *kee-ah* vocalisations in association with 10 behavioural categories and 17 behaviours. This vocalisation is used in both solitary and social behaviours. This broad range of associated behaviours suggests that the vocalisation may be giving information unrelated to the current behaviour. Bond and Diamond (submitted) suggested this call is the primary general-purpose contact call of the species, used to establish communication between widely separated individuals. Based on the wide contextual use of the *kee-ah* vocalisation, it is most probably a proclamation vocalisation, as with the *ahh*, but due to the increase in call complexity it most probably carries a more complex message. The high level of use in aggression as well as long distance communication suggests this call could be giving information on caller identification, status or condition as opposed to location.

Ke-ee-ee-ah: This vocalisation had the highest proportion of vocalisations being used in possible exchanges, with one of the lowest amounts of associated behaviours (8 behavioural categories and 13 behaviours). The *ke-ee-ee-ah* vocalisation had the highest number of occurrences in behaviours involved with social interaction and no occurrences of solitary behaviours with the

exception of scanning. However, 91% of the *ke-ee-ee-ah* vocalisations associated with scanning were used in apparent exchanges, so this was most probably not a solitary behaviour. It has a more complex structure than the *ahh* or *kee-ah* vocalisations and is used in the highest level of possible exchanges of any of the vocalisations. This suggests that the *ke-ee-ee-ah* vocalisation may indicate greater levels of excitement or carry a more emphatic message than the *ahh* or *kee-ah* vocalisations.

Growl: The findings of this study support those from Bond and Diamond's (submitted) study, that the *growl* vocalisation appears to signal aggressive intent. Bond and Diamond (submitted) found that kea *growled* primarily during aggressive interactions over resources. They argued that this indicated the *growl* vocalisation was associated with aggressive motivation. When produced by the recipient of an attack the *growl* appeared to incite an aggressive response from a more aggressive, or dominant, individual. This suggests that the kea producing the vocalisation may not just be signalling aggressive intent, but could be challenging another individual.

Ehh: This vocalisation was used in conjunction with the *squeal* vocalisation in an extended long distance exchange. Although not given in association with aggressive behaviours, it is possibly a long distance aggressive vocalisation. The *ehh* vocalisation consists of unmodulated frequencies that switch to an oscillatory pattern with oscillations the same frequency and duration as found in the *growl* vocalisation. The similarity of the *ehh* to the *growl* may be caused by the motor pattern control mechanisms controlling the production of the two vocalisations being the same, which may be expected if they are affected by the 'emotional state' of the kea. This would suggest that the vocalisations may have the same or similar motivation.

Ke-eh-eh: With only one recording it is not possible to accurately determine the function of this vocalisation. However, this vocalisation was recorded after an aggressive interaction and the oscillatory portions throughout the call are similar to the *growl* and *ehh* vocalisations. This suggests that, on the basis of possible similarities in the motor pattern control mechanisms producing the vocalisations, it is possible this vocalisation may also be an aggressive signal.

Squeal: Ability to determine the function of this vocalisation was limited as only two recordings were obtained. However, in this study it appears to be used in extended communication with an individual out of visual contact. The *squeal* was not used in association with any aggressive behaviours, but it may have been used to signal aggressive motivation. Bond and Diamond (submitted) stated that fledglings often alternate *squeals* with *growls* during aggressive interactions. My study found that the *squeal* was also alternated with the *ehh* vocalisation in exchanges with birds at a distance. Bond and Diamond (submitted) described the function of the *squeal* as ‘serving to draw individuals together’ and ‘to aid in negotiating group decisions’. They stated that the *squeal* is only used by young birds, but in a wide variety of context primarily when preparing to depart from a foraging ground and during social play. This indicates that the *squeal* may be an indication of arousal or excitement in immature kea, which can be used in association with other vocalisations to determine the motivation of the excited state.

Aww: This vocalisation was recorded from an unidentified kea in flight after nest disturbance. This suggests that the vocalisation may serve the function of an alarm or nest defence call. Bond and Diamond (submitted) described this vocalisation as the juvenile *kee-ah*. They suggested that it is used by kea as a general purpose, close quarters, low motivation contact call, which serves as little more than an acknowledgement to other individuals when given as a response. None of the recordings I obtained elicited a vocal or behavioural response from other kea. However, there were no other kea identified in the area at the time of these vocalisations. It is possible that this vocalisation may serve as a contact or flight call, but as there were no other kea observed in the area, it is not possible to determine this as the function.

Ah-ah-ah: Although this vocalisation was only used in a moderate level of exchanges, it appears to serve the function of both close range and long distance communication for young kea. The aggressive behaviours associated with this vocalisation were high intensity aggression involving a kea chasing other individuals. The high levels of excitement and the size of groups this vocalisation is associated with suggest that this vocalisation may serve to co-ordinate the group

activities of young kea.

Ahh-ahh: The *ahh-ahh* vocalisation did not gain any responses during the bout of play, but was used in exchange in 62.6% of cases whilst perched (all from the same kea during the same recording session) and 66.7% with departure. This suggests that the vocalisations produced during play and perch behaviour may serve two distinctive functions. The kea were usually solitary or present in low numbers when this vocalisation was produced. This vocalisation appears to be used as both a 'personal' vocalisation by solitary kea and a long distance communication vocalisation by solitary or small groups of kea.

Lefevre *et al*'s (2001) claim that vocalisations of non-passerine birds tend to be given in specific contexts or behaviour patterns was not supported by this study. The results of this study indicate that most kea vocal signals are given in a wide range of behavioural contexts, rendering categorisation by behaviour unviable.

Cameron (1968) noted that the most commonly uttered signals in the red-rumped parrot (*Psephotus haematonotus*) lacked specific context. There were similar results found in this study. The most commonly recorded kea vocalisation, the *ahh*, was recorded being given during the widest range of behaviours. In 135 recordings of the *ahh* vocalisation, I recorded 30 distinct behaviours within 14 behavioural categories. The next most frequent vocalisation, the *kee-ah* for which 42 recordings were obtained was recorded in association with ten behavioural categories and 17 distinct behaviours. The *ke-ee-ee-ah* vocalisation was recorded 40 times in association with eight behavioural categories and 12 distinct behaviours. Twenty-seven recordings of the *ahh-ahh* were obtained from five behavioural categories and seven behaviours. The *ah-ah-ah* was recorded 11 times and was associated with four behavioural categories and five behaviours. The *aww* vocalisation was recorded ten times, with all of these recordings being obtained from a kea in flight. Nine recordings of the *growl* were obtained. These vocalisations were associated with three behavioural categories and seven distinct behaviours. The *ehh* vocalisation was only recorded four times and was associated with two behaviours. The *squeal* was recorded only

twice, both times in association with a different behaviour. The *ke-eh-eh* was recorded once, being used in an aggressive interaction.

Of all these vocalisations, the only vocalisation with strong enough evidence to suggest that the behavioural context is directly related to the vocalisation was the *growl*. The *growl* was found to be used in association with aggressive interaction in 77.8% of recordings. The 11% of the vocalisations not used in aggressive interactions were given in the same recording session by birds that had been involved in aggressive interaction earlier that morning.

Cameron (1968) noted that the most commonly uttered signals lack specificity of context and suggested that they fulfil several functions. It is possible that the most commonly uttered call, the *ahh* vocalisation in this study, is unrelated to the behaviour of the sender, and is perhaps an identification signal or is used in different contexts for several different functions. The less frequently used vocalisations had a narrower range of associated behaviour than the more frequently used vocalisations. This may be due to an increased specificity of a vocalisation leading to less frequent use, or that with a smaller number of recordings, the full range of behavioural associations for a call were not observed. It is most likely that both these factors contributed to the results, as the *keeah* and *ke-ee-ee-ah* vocalisations were both recorded similar amounts of times (*kee-ah* 42 and *ke-ee-ee-ah* 40), yet the *ke-ee-ee-ah* was observed in association with less behavioural categories and less call types than the *kee-ah*. This suggests that this vocalisation has a more specific function than the *kee-ah* vocalisation.

Several other studies on psittacine vocal signals also found classification of vocal signals by behaviour unviable (Saunders; 1983, Roberts; 1996, Cameron; 1968 and Fernandez-Juricic *et al*; 1997). For example, Saunders (1983) found that the most common call given in the short-billed white-tailed Black Cockatoo was produced in a wide variety of situations with the highest variation between individuals, sexes and geography. Farabaugh and Dooling (1996) suggest this difficulty in classification of parrot repertoires may be because some functionally distinctive parrot calls may have an array of structural variants. Whereas Fernandez-Juricic and Martella

(2000) offered the possibility that the high contextual variability found in blue fronted amazon vocalisations may be partly accounted for by two possibilities 1) an incompletely specialised vocal repertoire (with high degrees of redundancy) or 2) a vocal repertoire in which combinations of calls convey different messages. Shettleworth (2001) states that species may have unspecialised or redundant vocalisations in their repertoire because a receiver may act more quickly or reliably to two stimuli together than alone. This may also account for the high number of kea behaviours that are associated with several vocalisations.

Barklow (1979) and Roberts (1996) both proposed that identified lacks in specific vocalisation contexts were due to grading of the vocalisations. Grading is slight differences in the vocalisation, giving the signal a different meaning. For example, the addition of a harmonic to the duck call of the European blackbird indicates an increased probability of flight (Barklow 1979).

The extensive use of signal grading is unusual in animals. This may in part be accounted for by the difficulties inherent in maintaining signal clarity while introducing graded variations (Barklow 1979). Mistakes would be likely to occur in cases where a number of morphologically similar signals code qualitatively different (discrete) messages. However, in vocal communication, this problem may be overcome by grading the amplitude, or varying the interval between the signals. Such simple forms of grading, which leave the structural characteristics of the sound unaltered, have been reported in a number of bird species, including parrots (see Roberts 1996, Fernandez-Juricic and Martella 2000) (Barklow 1979).

The *ahh*, *kee-ah* and *ke-ee-ee-ah* vocalisations appear to be the major identification and communication vocalisations. As the complexity of the vocalisation increases the number of situations it occurs in decreases and the number of times it is used as an exchange increases. This suggests that the more complex *ke-ee-ee-ah* may have a more specific message than the *ahh* vocalisation. It is possible that these vocalisations could be graded variations of the same vocalisation. They all have the same basic unmodulated base of which the *ahh* vocalisation is constructed. The *kee-ah* and the *ke-ee-ee-ah* then increase in complexity with the addition of a

rapid increase then decrease with a terminal compression. The *ke-ee-ee-ah* then also has a modulated section between the increase/decrease period and the terminal compression. However, this would be an extreme form of grading. It is more plausible that each of these vocalisations contains various levels of gradation. This will be discussed further in Chapter 7.

It is also possible, and more plausible, that these vocalisations are used together in order for their various functions to send a more complex message. Lefevure (2001) argues that vocalisations over short distances mainly serve to attract receiver's attention and identify the signaller so further communication with more subtle cues can begin. If more complex signals carry messages of increased complexity then this may be what is occurring in the kea. The *ahh* is the simplest of the vocalisations with the least intensity, this would suggest it is a short range signal with a small amount of information and the function of this vocalisation may be to initiate contact and identify the caller. The *kee-ah* and *ke-ee-ee-ah* vocalisations, which are most commonly given in response then follow, providing respectively increasingly complex information. As each of these vocalisations becomes more complex the amount of time it is responded to by a less complex vocalisation reduces. However, this study has only explored the possible responses gained from other individuals (see Fig. 2, Chapter 4), to confirm this, comparisons of vocalisations given in extended exchange by the same sender would have to be conducted.

Bond and Diamond (submitted) found that kea occasionally use the *squeal* vocalisation with the *growl* during aggressive interactions and suggested that this may signal aggressive intent. In this study I found that the *ehh* and *squeal* vocalisation were alternated by an individual engaged in an exchange with a distant kea. I propose that based on the presence of the short, sharp peaks present in both the *ke-eh-eh* and the *ehh* vocalisations which are also present in the same duration and frequency range in the *growl*, these vocalisations may indicate varying levels of aggression. Bond and Diamond (Submitted) suggest that the *squeal* may be a juvenile identification call. It is possible that the use of the *squeal* with another vocalisation may give a more complex message concerning the motivation of the vocalising individual.

A specie's vocal behaviour is influenced by evolutionary constraints and selective pressures imposed by their environment and social system (McShane *et al* 1995). Typically songs given in an open habitat are characterised by relatively high frequency and a wide frequency range consisting of complex notes, produced with short inter-note intervals, often in the form of trills. By contrast, songs in dense forests are characterised by relatively low frequency and narrow frequency range, consisting of long and simple notes (Slabberkoorn *et al* 2002). The habitat of the kea varies and includes both densely forested areas and open tussock areas above the tree line. This suggests that they may either have vocalisations specific to each habitat type or generalist vocalisations that may be used in both. The *ke-ee-ee-ah* and *ke-eh-eh* vocalisations appear most likely to, by this definition, be used for communication in open areas. They both demonstrate high peak frequencies (*ke-ee-ee-ah* 2.5 kHz, *ke-eh-eh* 2.6 kHz), complex structures and wide frequency ranges. The *ahh* and *ahh-ahh* vocalisations appear to best fit the criteria for vocalisations used in dense forest habitats. Both of these vocalisations have a relatively simple structure, with the *ahh* being unmodulated and the *ahh-ahh* being smoothly modulated, low peak frequencies (*ahh* 2 kHz, *ahh-ahh* 1.9 kHz), but the frequency ranges in both vocalisations are highly variable (see Chapter 3). However, even though there are vocalisations that fit into the two categories, this seems unlikely to be the main factor affecting kea vocalisations. When the behavioural context of the *ahh-ahh* vocalisation is included in the comparison it shows that when used in long distance exchange across open areas the *ahh-ahh* vocalisation had a simpler call structure than when used by an individual in solitary play (see Chapter 7). The *ahh* vocalisation was also used in long distance exchanges over open areas on numerous occasions. Naguib (2000) claims that non-modulated vocal signals may lead to more difficulty for receivers to estimate the distance of the sender. This is caused by the lack of frequency modulation leading to a low potential for distance cues related to frequency-dependant attenuation (Naguib 2000).

Slabberkoorn *et al* (2002) offers the explanation that simplification of a call used in over long distance communication (such as observed in the *ahh-ahh* vocalisation) may be beneficial. Proposing that transmission properties of dense vegetation can lead to degradation of animal vocalisations. Slabberkoorn *et al* (2002) argues that this is not always detrimental, but may

enhance signal effectiveness. By avoiding frequency modulation a longer, louder signal can be produced for the same amount of energy. Decreasing the frequency bandwidth may lead to an increase in amplitude and consequently an increase in transmission distance (Slabberkoorn *et al* 2002). The *ahh-ahh* vocalisation still had modulations present when used in long distant communication, but they were simple in comparison with the modulations in the same vocalisation not used in long distance communication. By this theory the *ahh* vocalisation may also have adapted for use in long distance communication. If this adaptation has occurred then there would be expected to be louder *ahh* vocalisations with reduced bandwidths that are used in long-range communication. The *ahh* vocalisation was used in long distance communication accompanied with observed variations in amplitude (see Chapter 7).

McShane *et al* (1995) argues that vocal signals are not necessarily selected for transmission over maximal distances but rather optimal ones. Other considerations, such as the potential for transmission of complex information, may be more important to some vocalisations than the ability to be heard over long distances. McShane *et al* (1995) provides the example of sea otter mothers and offspring, but this may be transferred to animals such as the kea, which engage in close range social interaction with other individuals.

Another way of determining the function for parrots may be to follow parameters describing ideal signals for specific functions set by other authors. The first of these would be to distinguish between a vocalisation intended for intra-specific identification and inter-specific identification. Although kea are the worlds only alpine parrot, in areas such as Fordland National Park, the Hurinui and Nelson Lakes National Park the lower altitudinal limits of kea habitat cross with the habitat of the kaka (*Nestor meridionalis*). The kaka is the closest living relative of the kea (Higgins 1990). In these areas species identification signals may be necessary. Previous workers have suggested that signal characteristics with little intra-specific variation may be potentially useful in species recognition (Sparling *et al* 1983). Lefevre *et al* (2001) suggest the ideal signal for species recognition to be highly stereotyped amongst individuals, where as the ideal signal for intra-specific (or inter-individual) variation would be highly stereotyped within an individual,

but vary noticeably among individuals. Accordingly vocalisations ideal for expressing differences in motivation (intra-individual variation) would vary noticeably within an individual. This will be explored further in Chapter 7 (intra-individual variation).

Comparison of the size and complexity of the vocal repertoire among species of parrots is difficult because most have not been described. Whilst any or several of the previously mentioned possibilities may be responsible for the lack of obvious behavioural distinction, it is also possible I selected context classifications that are not relevant to the kea. What may seem the most obvious behavioural context to a human observer is not necessarily the most important context to the kea. It is most probable that most or all of the factors discussed in this Chapter have an impact on the structure and complexity of kea vocalisations and the nature of the vocal system.

Chapter 6

Gender specific vocalisations

Introduction

Gender specific vocalisations are common among passerines with males having a variety of well-documented territorial defence and mate attraction calls (Beecher *et al* 2000a, Beecher *et al* 2000b, Naguib *et al* 2002). Sexually dimorphic and gender specific vocalisations are also common in non-passerine species. Many Australian parrot species have been shown to have gender specific vocalisations (Higgins 1990). Yet, despite studies giving detailed descriptions of parrot vocalisations, including behavioural contexts, age groups and inter-individual variations (see Pidgeon 1981, Fernandez-Juricic *et al* 1998, Baker 2000), there has been little focus on gender specific vocalisations. Two studies on parrot vocal systems that included gender specificity were Roberts (1996) and Saunders (1983). In a study of vocal communication in the Puerto Rican parrot, Roberts (1996) identified two call types exclusive to females and none that were exclusive to males. In a study of the vocal repertoire of the short-billed white-tailed black cockatoo, Saunders (1983) identified at least four vocalisations specific to males and four specific to females.

Previous studies on the kea

The lack of information on gender specificity in vocalisations may be due to the difficulties involved with accurately identifying the gender of most parrot species. The gender of the kea is easily determined by the shape and size of the bill (12-15% longer and more curved in the male than the female) (Figs. 1 and 2), and body size (males are 5% heavier than females; Bond *et al* 1991). For this study these observational identifications of gender were supported with DNA sexing based on blood samples taken by the Vienna University Kea Research Group (Werdenich 2003 pers. comm.). The blood samples were analysed using DNA fingerprinting by Bruce Robertson at the University of Canterbury (2003).

There have been three gender specific vocalisations previously described in the kea. Jackson (1969) described a soft cooing call given by the male from outside a nest to chicks inside and Bond and Diamond (submitted) identified one possible female specific vocalisation, the *step*

call, and one possible male specific vocalisation, the *buggle*. None of these vocalisations were recorded in this study.

Introduction to my study

I have also examined the possibility of gender specific vocalisations in the repertoire of the kea. This is because of the vast differences observed in the vocal repertoire of the kea in this study compared with Bond and Diamond's (submitted) study (see Chapter 3). It was necessary to determine whether the vocalisations recorded in this study that were not described by Bond and Diamond (submitted) were gender specific. I was not able to determine whether the *aww* vocalisation was gender specific in this study because the vocalisation was only given by one kea and this individual was unidentified.



Figure 1. Adult male kea



Figure 2. Fledgling female kea.

Results

There were five vocalisations recorded only from males; *ahh-ahh* ($x^2=32$, $p=1.54^{-8}$), *ah-ah-ah* ($x^2=51$, $p=9.24^{-13}$), *squeal*, *ke-eh-eh* and *ehh* (Table 1, Fig. 3). There were no vocalisations recorded that were only given by females. Table 1 shows the percentage of each vocalisation type recorded from males and the percentage of each vocalisation type recorded from females with the total number of each call type recorded. This information is displayed in Fig. 3.

Table 1. Proportion of time each vocalisation was recorded from males and females

	keeah	ke-ee-e	ahh	ah-ah-a	eh-eh-e	ahh-ahh	squeal	ke-eh-e	ehh
Males	80	83	65	100	78	100	100	100	100
Females	20	17	35	0	22	0	0	0	0
Counts	6	6	10	5	9	3	2	1	4

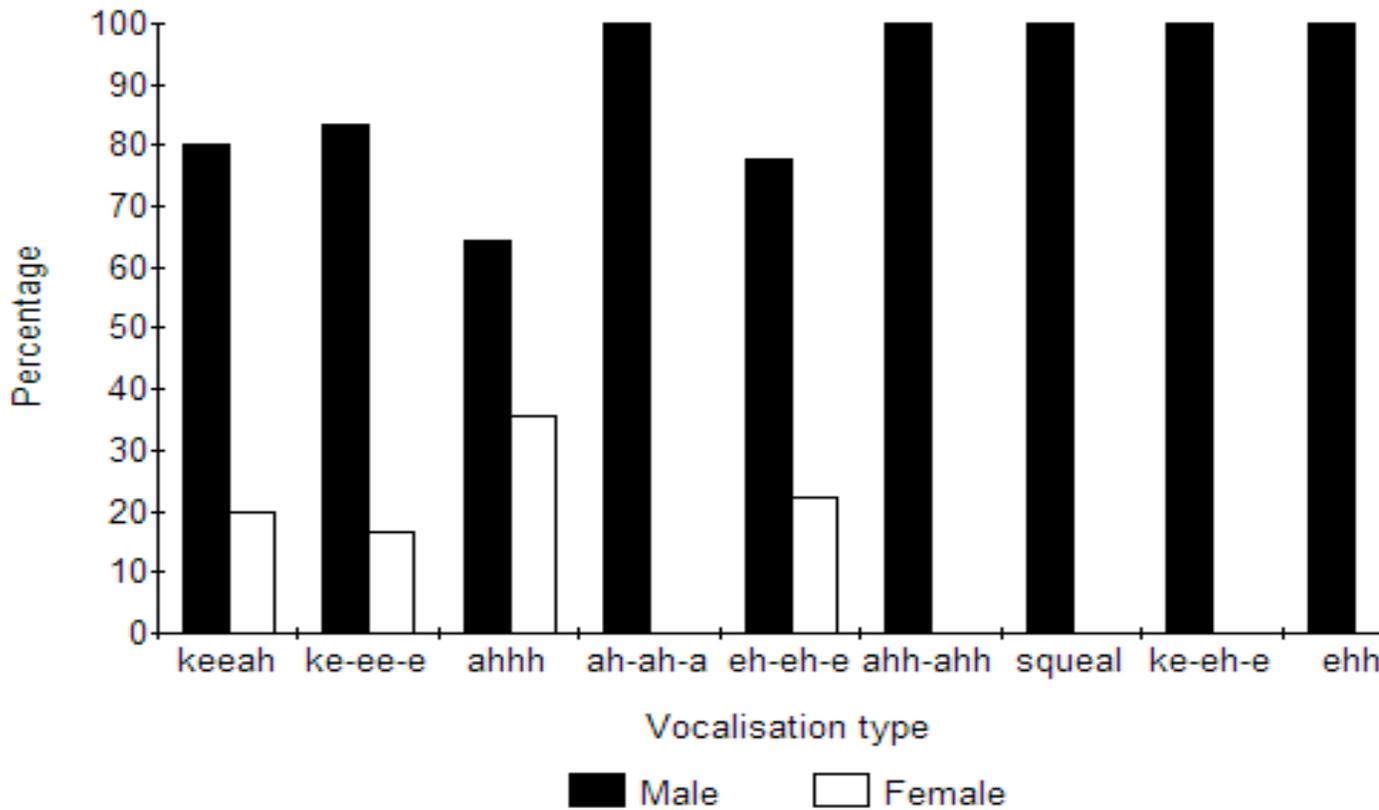


Figure 3. Proportions of each vocalisation recorded from males and females.

Discussion

Of the nine vocalisations studied in this section, there were no vocalisations given only by females but five vocalisation types that were recorded only from males. The lack of recorded female specific vocalisations may be because young female kea do not have gender specific vocalisations, although this is unlikely. The lack of identified female specific vocalisations was most probably caused by the lack of recordings due to females being noticeably less vocal than

males and there being significantly fewer females present at the study site.

There were five possible male specific vocalisations identified in this study, *ke-eh-eh*, *ehh*, *ahh-ahh*, *ah-ah-ah* and the *squeal*. Of these five vocalisations, *ahh-ahh* and *ah-ah-ah* were highly significant (*ahh-ahh* $p=1.54^{-8}$, *ah-ah-ah* $p=9.24^{-13}$), and therefore likely to be male specific. Despite the high significance of the *ahh-ahh* and *ah-ah-ah* vocalisations, it is still possible that females do make these vocalisations. The low number of females frequenting the study site and their low rate of vocal activity compared to males resulted in a lower sample size of vocalisations recorded from females than from males (there were 98 recordings of female vocalisations and 331 recordings of male vocalisations obtained in this study). This may have resulted in missing aspects of the vocal repertoire of the female kea.

It is possible that females were not recorded giving these vocalisations because these vocalisations are infrequently used. The *ahh-ahh* ($n=32$) and the *ah-ah-ah* ($n=51$) were the only two of the five vocalisations with large enough sample sizes to suggest that infrequent use of the vocalisations was not the cause of the apparent gender variation.

Each of these vocalisations were recorded from seven different kea. This suggests that they are not vocalisations used in high frequency by a small number of individuals (such as a dominant bird displaying territoriality), which may restrict their use by females. It is possible that these vocalisations are indications of status produced by aggressive or dominant birds, and due to the more dominant role of males in the social system these are rarely produced by females. This is also unlikely because although these vocalisations were most frequently used by more aggressive or dominant kea, they were also used by non-aggressive birds.

None of the kea vocalisations identified by previous authors to be gender specific were recorded in this study. This is most probably due to differences in ages of the kea recorded in each of the studies. However, one of the vocalisations recorded only from males in this study, the *squeal*, was described in Bond and Diamond's study (submitted). They obtained recordings of the *squeal* vocalisation from both male and female juvenile keas showing that this vocalisation is not gender specific.

Chapter 7

Intra-individual variation

Introduction

Acoustic signals that facilitate inter-individual recognition have been identified in a wide range of species. These include primates (Cheney and Seyfarth 1990), birds (for example, thick-billed murre (*Uria lomvia*; Lefevre *et al* 2001), black-capped chickadees (*Poecile atricapilla*; Phillmore *et al* 2002), king penguins (*Aptenodytes catanonicus*; Jouventin *et al* 1999), adelic penguins (*Pygoscelis adeliae*; Jouventin and Aubin 2002), odontocete cetaceans (for example, bottlenose dolphins (*Tursiops truncatus*; Sayigh *et al* 1998), pinnipeds (for example, northern fur seal (*Callorhinus ursinus*; Insley 2000) and numerous other marine and terrestrial mammals (for example, sea otters (McShane *et al* 1995), Amazonian manatees (*Trichechus manatus*; Sousa-Lima *et al* 2002), African elephants (*Loxodonta Africana*; McComb *et al* 2000). Signals used for inter-individual recognition can be complex (Higgins 1990). This complexity facilitates vocal inter-individual recognition of conspecifics, allowing receivers to discriminate between similar sounds of different individuals in the absence of other identifying cues (Falls 1982).

The occurrences of inter-individual variation of calls within species is well documented (Lessells *et al* 1995, Huxley and Wilkinson 1979, Monk 1997, Lefevre *et al* 2001, Martin *et al* 1995, Rebbeck *et al* 2001, Deregnacourt and Guyomarc'h 2003, Gentner and Hulse 1988, Weary and Krebs 1992, Phillmore *et al* 2002, Jouventin *et al* 1999, Jouventin and Aubin 2002, McComb *et al* 2000, Insley 2000). However, despite the large interest in inter-individual recognition, few studies have gone beyond this to examine intra-individual variation. In those studies that have considered intra-individual variation it is most often only a brief foray within inter-individual variation studies. This lack of study on intra-individual variation is surprising considering that vocal differences in numerous species are known to be sufficient for recognition not only of individual and species identity but of variables such as age, sex, genetic relatedness and condition (Barklow 1979).

Intra-individual variation in vocalisations would be expected to occur in similar species and in similar situations to inter-individual variation. Acoustic communication is not as limited by factors affecting visual or olfactory communication (McShane *et al* 1995). Thus, intra-individual variation would be expected to occur in species living in densely populated colonies and species in habitats such as the ocean or dense forests. This is because these habitats restrict other communication methods more than they restrict acoustic signals. Falls (1982) defines an ideal signal for inter-individual recognition as highly stereotyped within an individual, but highly variable amongst individuals. Whereas an ideal signal for expressing motivation or intentions was defined as being highly variable within an individual (Falls 1982).

Introduction to this study

Saunders (1983) claims that within each group there is certain to be a range of variations of each call within one individual bird's repertoire and that each variation may convey a different meaning depending on mood and situation. In this chapter I have explored this theory by examining the level of intra-individual variation in the spectrogram morphology of kea vocalisations. I have compared spectrograms of each vocalisation given during non-aggressive behaviours with spectrograms of the vocalisation given during aggressive behaviours (see Chapter 5). Where possible I compared vocalisations given during the behaviour that I termed 'scanning' (see Chapter 5) with vocalisations given during behaviours with high levels of aggression, such as run-rushing, chasing or aerial attacks (see Chapter 5). I selected these behaviours for comparison because they appeared to be the least similar of the observed behaviours. Aggressive behaviours are usually high intensity interactions between kea, whereas scanning behaviour does not usually involve any interaction with other birds. These behaviour types were also selected because I had obtained high numbers of recordings of the same vocalisation from the same individual during both behaviours. The vocalisations selected for comparison were limited to those that I had obtained recordings of the same individual giving the same vocalisation during the two different behavioural contexts. There was an exception to this, with the *ahh-ahh* vocalisation. Two different birds were compared for this vocalisation because I did not obtain sufficient recordings to compare vocalisations from different behavioural contexts from one kea. In all the vocalisations sample size was limited by recording quality. Only those that produced a clear spectrogram were compared.

Roberts (1996) found that in some parrot species spectrograms were not accurate enough to identify inter-individual variation. It would be expected that intra-individual variation would be as equally difficult to detect as inter-individual variation. Therefore, I conducted further analysis by applying human speech analysis, using SpeechStation software (see methods, Chapter 2), to the *ahh*, *kee-ah* and *ke-ee-ee-ah* vocalisations. This analysis was selected as a potential means of exploring the level of intra-individual variation in kea because of the similarities in parrot vocalisations to human speech. Unlike passerine species, which communicate by means of notes arranged in the forms of song, parrot repertoires consists of calls and call sequences which may be likened in structure to words in human speech (Roberts 1996). This is because psittiforme vocal tracts resemble those found in humans by having a single syrinx, trachea and tract (Fig. 1) (Kahrs and Avanzini 2001). This analysis, which examines variations in the fundamental frequency, acoustic energy concentrations and vowel analysis on the first and second formants (see methods Chapter 2), may provide a powerful tool in identifying subtle variations not identified by spectrogram analysis alone. This analysis has not been applied to the vocalisations of a parrot species in any other studies.

Physiology of parrot vocal systems

The fundamental frequency is produced from air passing through the syrinx of a bird (Fig. 1). The frequency of this is determined by the size of the syrinx and can be altered by tension in the syringeal muscles reducing or increasing airflow. From the syrinx the sound travels through the trachea to the mouthparts and bill. These areas act as chambers that can be altered in size and form by the bird. These changes alter the resonating harmonics (formants), affecting the overall structure of the sound. Resonating harmonics are low in large chambers and high in small chambers.

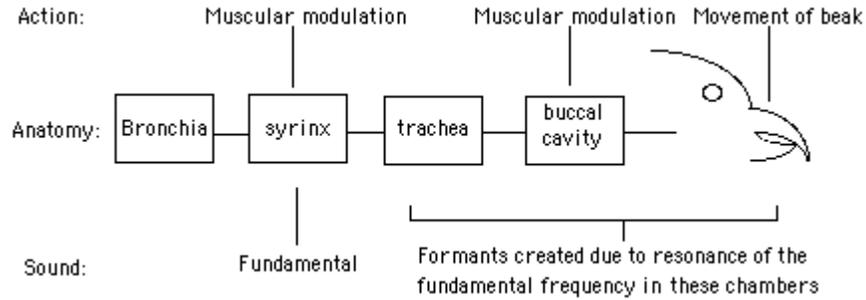


Figure 1. Psittacine vocal tract model

Physiological analysis

Fundamental frequencies: This analysis was used to examine the level of variation in the fundamental frequencies between vocalisations given during different behavioural contexts. The fundamental frequency analysis shows the fundamental frequency (f_0) enlarged 10x (Fig. 2). This enlargement illustrates subtle changes in frequency that are not otherwise visible. Differences present in the fundamental frequency between behavioural contexts would indicate that keas are altering the muscle tension in the syrinx during different behaviours. Increased muscle tension in the syrinx would increase the frequency of f_0 . Relaxing the syrinx muscles would result in a lower f_0 . This change in tension of the syrinx could be either a voluntary or involuntary reaction.

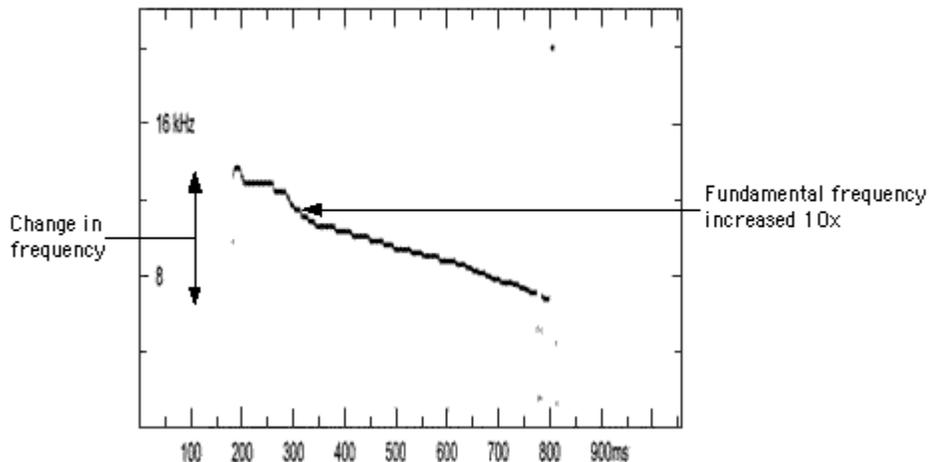


Figure 2. Fundamental frequency increased by 10x, without harmonics.

Distribution of acoustic energy: Waterfall plots were used to map the changes in the levels of acoustic energy through the duration of a vocalisation. These can then be compared between vocalisations given during different behavioural context. Waterfall plots show acoustic energy levels by the height and shade of the peaks (Fig. 3). High white peaks show high levels of acoustic energy, whereas black valleys show areas of little or no acoustic energy. The z-axis of the waterfall plot represents intensity of acoustic energy; however, the software used for this analysis does not provide measurements for this axis, so it is unlabeled on the figures.

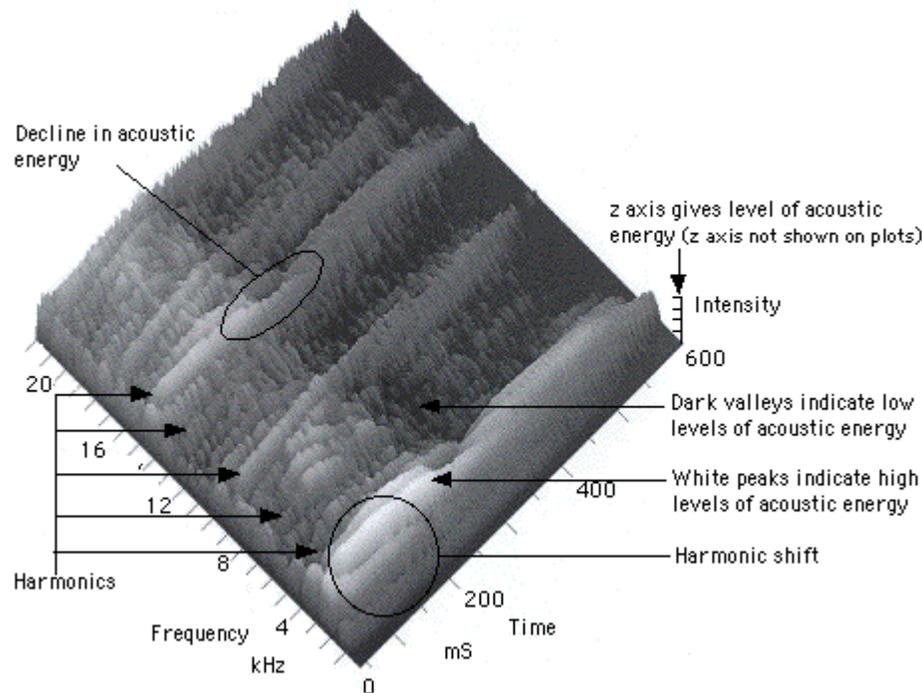


Figure 3. Waterfall plot illustrating the high acoustic energy areas (white peaks), low acoustic energy areas (dark valleys), harmonic shift (white peak declining in one harmonic whilst increasing in another), declines in acoustic energy and harmonics.

Formant positioning: Vowel space plots (VSP) were used to determine if the positioning of the first and second formants alters in vocalisations given during different behavioural contexts. Change in the positioning of the formants would indicate that the kea altered the size of the resonating chambers through which the fundamental was being driven. This is done by altering the volume of the cavities in the throat, mouth and bill (but not the trachea, which cannot be altered), by tensing or relaxing the throat muscles and altering the position of the tongue. VSP analysis illustrates how formants are affected by change in the vocal tract resonating

compartment. This is shown by mapping the changes in the first formant (f_1) against the changes in the second formant (f_2) (Fig. 4). Resonating frequencies, or formants, are lower in large chambers and higher in small chambers. Changes in the vowel space plots would indicate that the kea is changing the size of these chambers, which affects the final sound. Vowel space plots could not be produced for the *ke-ee-ee-ah* vocalisations because the period between oscillations interfered with the plotting of the graph.

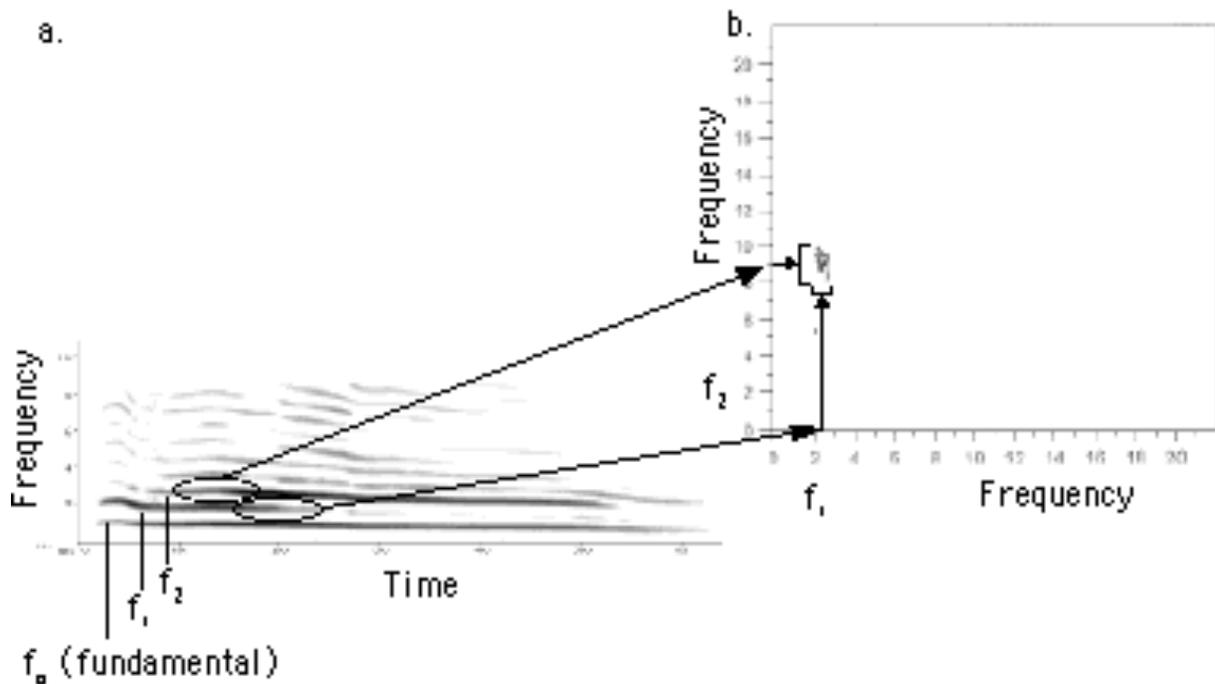


Figure 4. Changes in f_1 are plotted on the x-axis, changes in f_2 are plotted on the y-axis. Note the low level of drift in the x-axis. This indicates that f_1 is relatively stable. Comparatively, f_2 has high levels of variation, illustrated by the larger level of drift in the y-axis. The high levels of drift in f_2 were a result of the kea varying the volume of the resonating chamber supporting this formant.

Grading

Graded signals are signals that vary over a continuum rather than forming discrete units (McShane *et al* 1995). Extensive grading is uncommon in animals, Barklow (1979) suggests this is possibly due to difficulties inherent in maintaining signal clarity while introducing graded variations. However, lower levels of signal gradation have been identified in a number of bird and animal species, including the common loon (*Gavia immer*; Barklow 1979), sea otters (McShane *et al* 1995) and the Puerto Rican parrot (*Amazona vittata*; Roberts 1996). Roberts (1996) found that the identification of vocalisation function in the Puerto Rican parrot

(*A. vittata*) was not possible by examining the behavioural context because most vocalisations occurred in numerous contexts. Roberts (1996) proposed instead that the vocalisations of the Puerto Rican parrot were graded and suggested that identification of the type of gradation used in signals may lead to a better understanding of the call functions. The same high contextual use of vocalisations that was identified in the Puerto Rican parrot is found in kea vocalisations (see Chapter 5). This suggests that kea vocalisations may also have graded signals. In this chapter I have explored possible evidence that graded signals are present in kea vocalisations (see methods, Chapter 2), and have attempted to identify the gradation in vocalisations across the different behavioural contexts.

Playback experiment

Most of what we know about the acoustic basis of individual, group and species recognition has come from field playback studies. Unfortunately few such studies have been performed on parrots (Farabaugh and Dooling 1996). Of those that have been done the focus has been inter-individual recognition with few studies considering intra-individual variation.

Falls (1982) argues that variation alone does not facilitate inter-individual recognition; the receiver must be able to discriminate between the vocalisations and alter their behaviour accordingly. This would be expected to apply to intra-individual variation in vocal signals if the variations are messages as opposed to ‘accidental’ physiological responses. To determine if the variations observed in vocalisations were perceived by receivers I conducted a playback experiment using two *kee-ah* vocalisations recorded during different behavioural contexts. Both vocalisations were recorded from the kea with the band combination right metal, left plastic white green. Vocalisation one was given after white green had been displaced from a perch by being bitten by a kea she had previously been allopreening. Vocalisation two was given after an altruistic behaviour (head-bill touch), while white green was scanning (see methods, Chapter 2).

Bond and Diamond (submitted) conducted two playback experiments on kea. The first tested responses from kea to different vocalisation types. The second examined responses from kea to vocalisations of kea from different geographic regions. However, responses to the same

vocalisation from different behavioural contexts were not explored. In this chapter I conducted playback experiments to determine if receivers respond differently to any intra-individual variation in the vocalisations (see methods, Chapter 2).

Results

The results of the analysis conducted on the spectrogram morphology of each vocalisation are presented first. The term ‘morphology’ is used in this thesis to describe the two dimensional changes in spectrograms of kea vocalisations. This is followed by the physiological analysis (vowel space, acoustic energy levels and fundamental frequency analysis) for each vocalisation.

In an attempt to distinguish the intra-individual variations from the inter-individual variations, and for the sake of brevity, for each of the comparisons I have only listed variations which were consistent across all the kea that were compared for each call type. This has resulted in more variations being visible in the figures between the two behavioural contexts of each vocalisation than what I have listed.

Morphology of spectrograms

Ahh-ahh: The *ahh-ahh* vocalisation was most commonly given during apparent exchanges while perching (59.4%, see Chapter 5) and during solitary play (22.2%, see Chapter 5). The vocalisations given during these two behaviours showed the highest levels of morphological variation in the spectrograms with the vocalization given during perching having more harmonics (4 – 8 med 4, mean 6.9) than the vocalization given during play (3 – 4 harmonics, med 3, mean 3.8). The peaks within each *ahh-ahh* vocalisation given while perching were each a similar frequency and length, where the peaks in the play vocalizations were more variable (Figure 5). However, because of an inadequate sample size it was not possible to compare vocalisations given from the same bird in these two behavioural contexts. The perching behaviour appears to be associated with other aggressive behaviours (see Chapter 5). Therefore, of the contexts this vocalisation was given during, the vocalisations given while perching were the only ones that may have been associated with aggression. Therefore, the play and perching behaviour vocalisations were selected and compared between two different kea.

The harmonic modulations in the vocalisations recorded during solitary play were less regular than those of vocalisations recorded during perching (Fig. 5 a and b). An extra expansion after the terminal compression occurred in the vocalisations recorded from kea preening, scanning and perching, but not from the vocalisation given during solitary play.

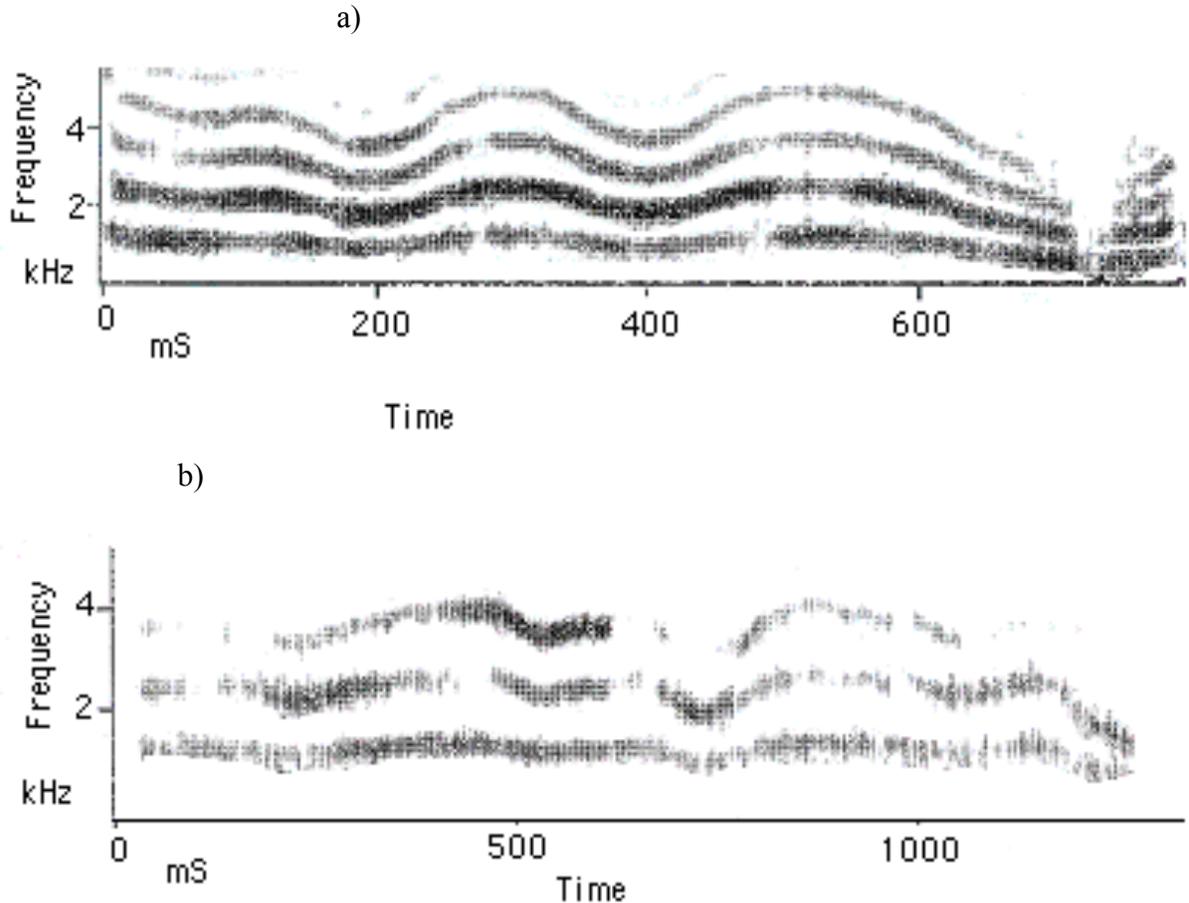
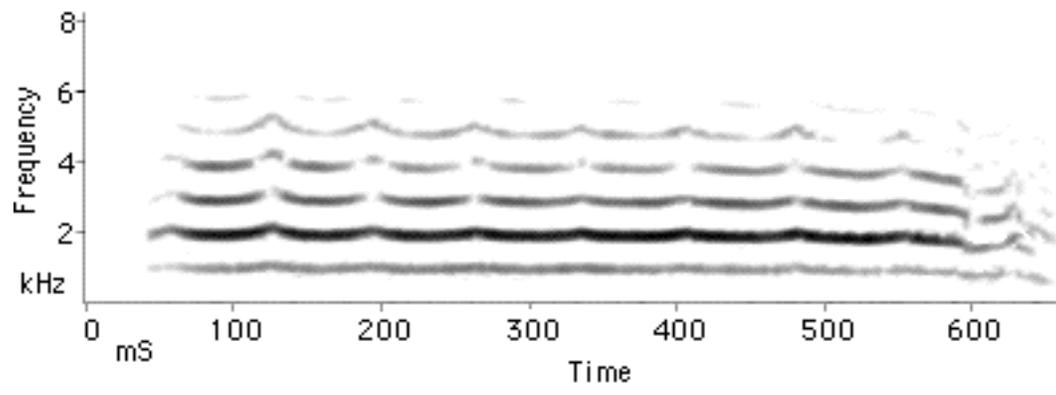


Figure 5. *Ahh-ahh* vocalisation. a) vocalisation given during perching, b) vocalisation given during solitary play.

Ah-ah-ah: The *ah-ah-ah* vocalisations that were given by a kea during aggressive interactions had a higher number of oscillations (10-13, mean 11.25), with deeper peak/valley ratios (1.83-2.26, mean 2.06 aggressive behaviours) than the *ah-ah-ah* vocalisation given by kea while scanning (1.7 – 1.78, mean 1.74 scanning) (Fig. 6 a and b).

a)



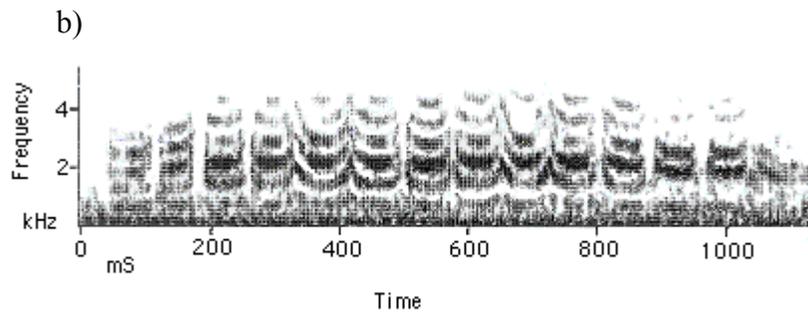
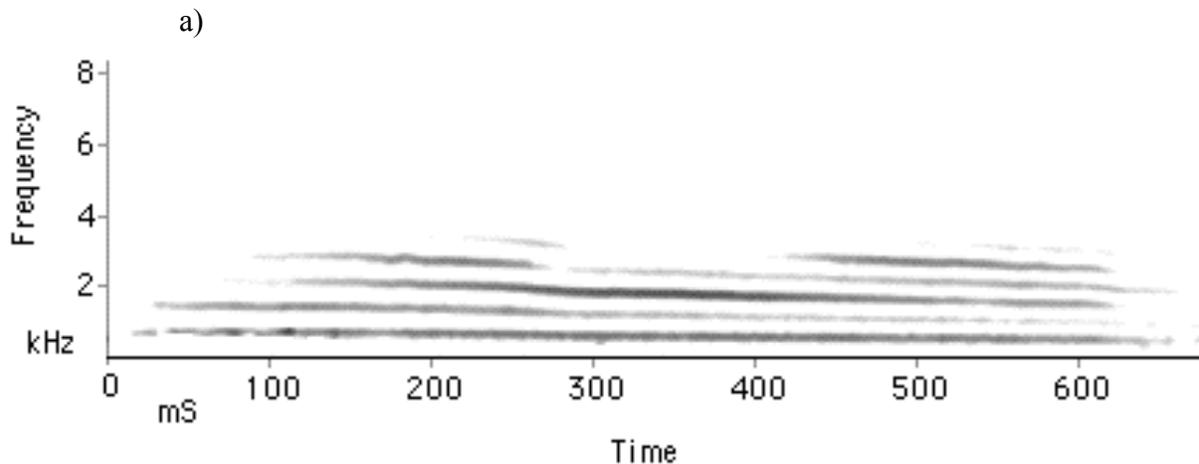


Figure 6. *Ah-ah-ah* vocalisation. a) vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Ahh: The *ahh* vocalisations given by kea during aggressive interactions were longer (600 ms-850 ms, median 650 ms) than those given by kea while scanning (400-600 ms, median 500 ms) (Fig. 7 a and b). There were more harmonics present in vocalisations given during aggressive interactions (12 harmonics) than vocalisations given while scanning (4 - 7 harmonics). The vocalisation given by the kea during a high intensity aggressive interaction was recorded at 5 m from the microphone and the non-aggressive vocalisations were within 3 m of the microphone. Therefore, the observed difference in the number of harmonics in vocalisations given during different behavioural contexts was not a result of the microphone distance to the kea. The upper harmonics are stronger in the vocalisations given during aggression than in the vocalisations given during scanning.



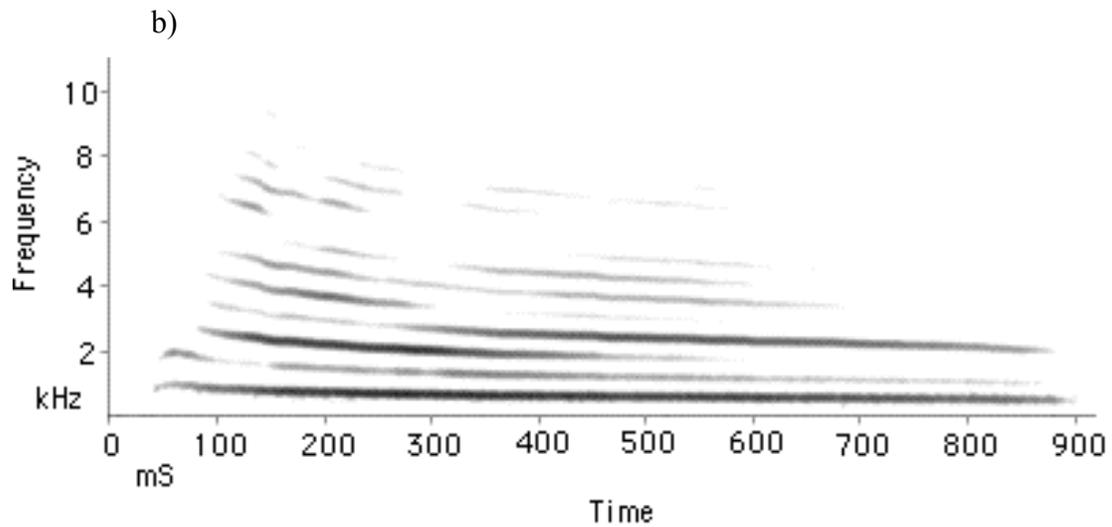
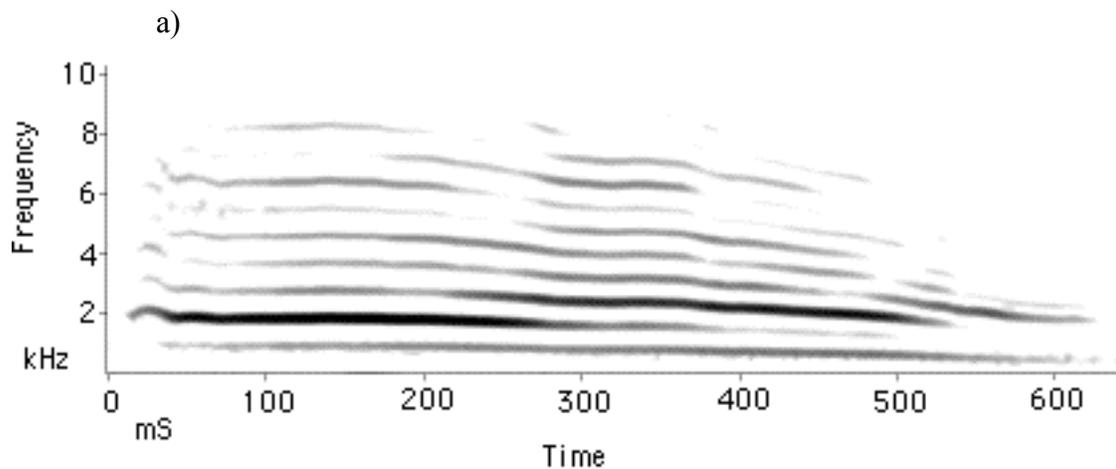


Figure 7. *Ahh* vocalisation. a) vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Kee-ah: There were only low levels of variation in this vocalisation between the behavioural contexts in which it was given. The onset peak had a longer duration in vocalisations given during aggressive interactions (116-408 ms, mean 219.6 ms) than vocalisations given while scanning (12 ms - 228 ms, mean 105.5 ms) (Fig. 8 a and b).



b)

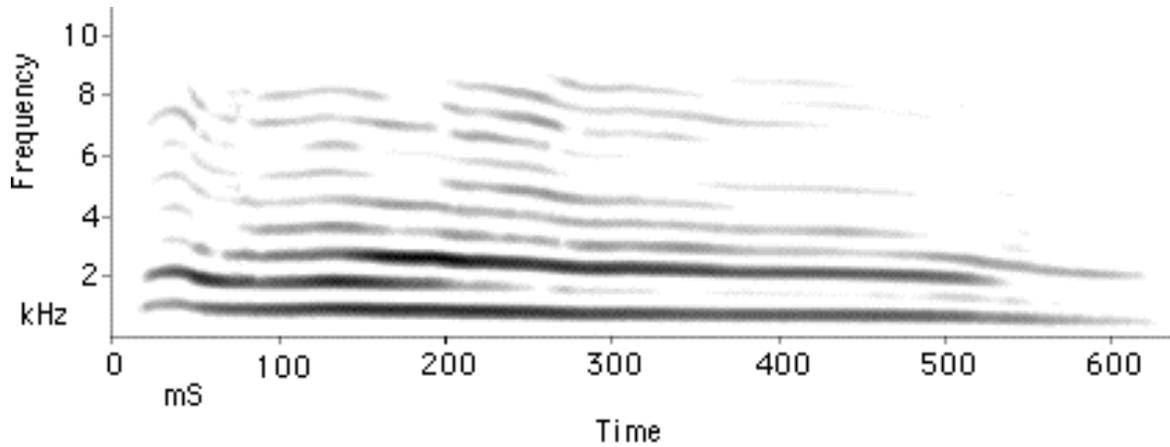
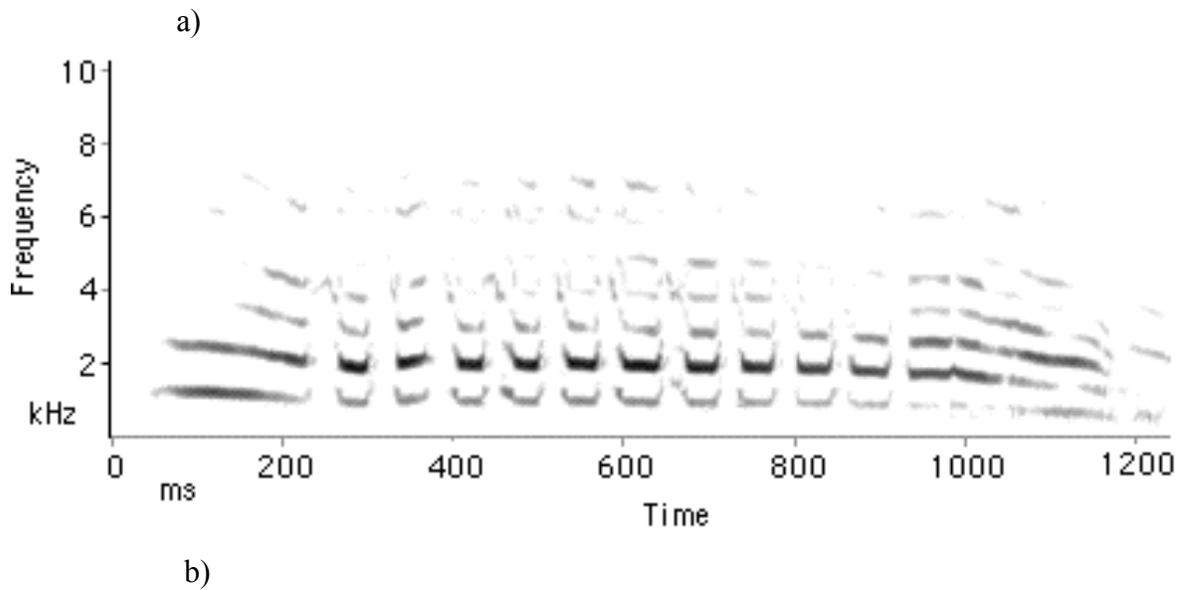


Figure 8. *Kee-ah* vocalisation. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Ke-ee-ee-ah: The vocalisations given during aggressive behaviours had fewer oscillations (3-6) and higher, longer onset peaks than the vocalisations given while scanning (5-11) (Fig. 9 a and b).



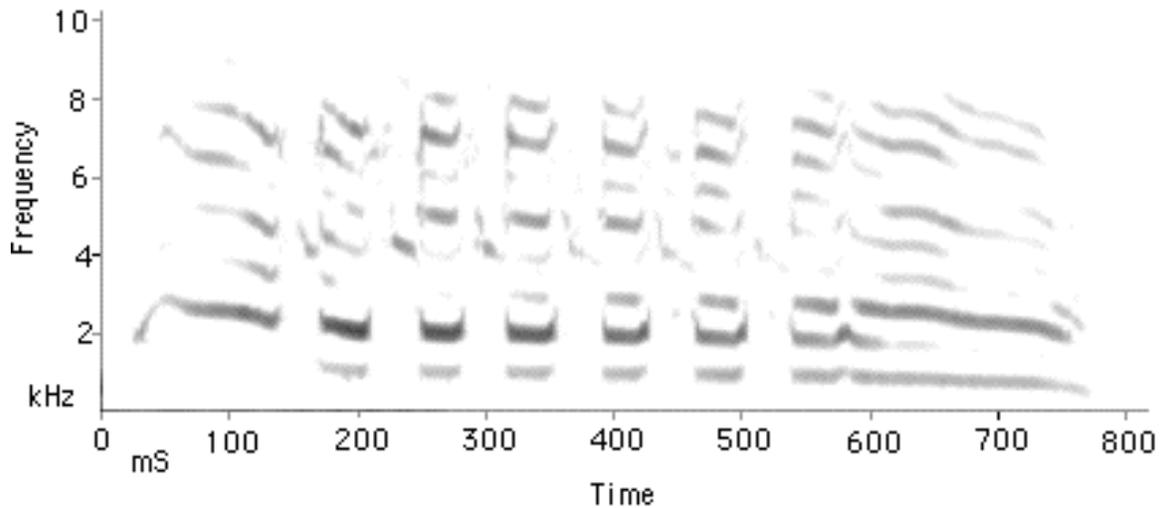


Figure 9. *Ke-ee-ee-ah* vocalisation. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

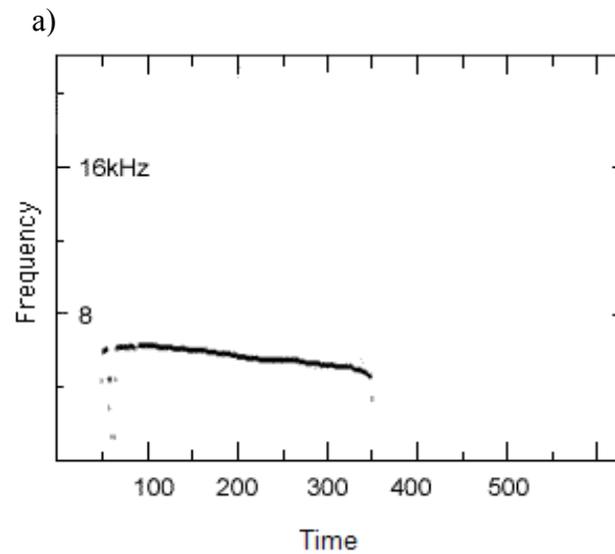
The variation in the morphology of the spectrograms of vocalisations during different behaviours indicates that there may be physiological responses to the different behavioural contexts. In the next section I attempted to determine if there were any variations in the physiological response associated with each vocalisation and behavioural type, to what extent these occurred and to determine what these responses may have been.

Physiological analysis

Ahh vocalisation

Fundamental frequency analysis: Plots of the fundamental frequency of *ahh* vocalisations for four birds were constructed. There were consistent differences in the fundamental frequency between the vocalisations given during aggressive interactions and vocalisations given during scanning for each kea (Fig. 10a and b). Across the four birds the fundamental frequency was always higher in vocalisations given during aggressive interactions (9-12 kHz for hunching and run rushing) than vocalisations given while scanning (6-8 kHz). The vocalisations given during aggressive behaviours also show a slight peak in the fundamental at the on-set of the vocalisation. This peak is similar to the one present in the *kee-ah* vocalisation, but has only a 50 - 120 Hz change in frequency as opposed to peaks of the *kee-ah*, which have a change in frequency of .3 -2 kHz. The onset peaks which are present in the enlarged fundamental

frequency of the *ahh* vocalisation, are not visible as peaks on a spectrogram, but occasionally show as slight rises in frequency. Although the *ahh* vocalisation appears to be almost monotone in spectrograms, analysis of the fundamental frequency revealed slight variations in frequency. In vocalisations given during aggressive interactions, the fundamental shows a comparatively larger decrease in frequency than the fundamental in vocalisations given by kea when scanning. Gradation of the vocalisations was present with increased frequency height and increased change in frequency for more aggressive vocalisations.



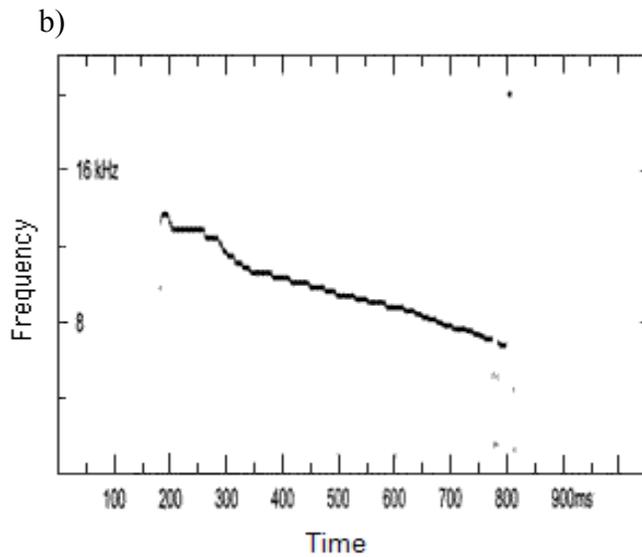
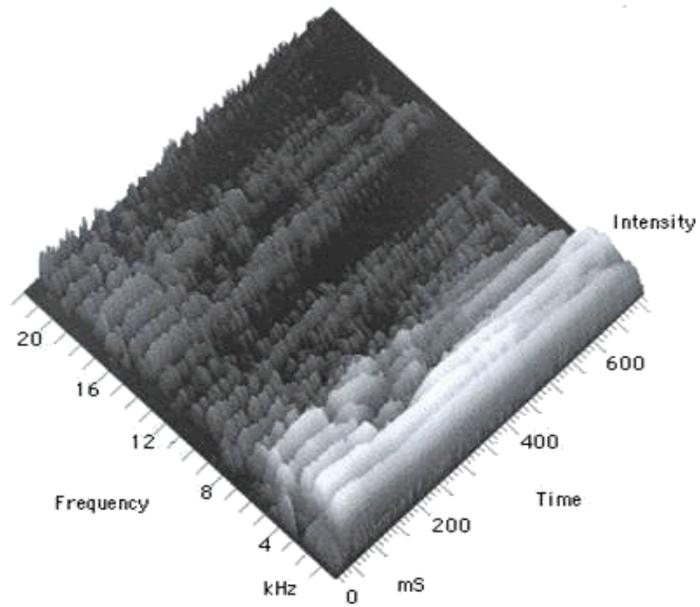


Figure 10. *Ahh* fundamental frequency. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Waterfall plots: Plotting the levels of acoustic energy over frequency and time in *ahh* vocalisations showed that *ahh* vocalisations given by a kea during highly aggressive interactions shifts harmonics more than *ahh* vocalisations given by kea that are scanning. This is illustrated (Fig. 11b) in the harmonics between 2-3 kHz at 500 ms where the peak tapers down, declining in height and becoming darker indicating a drop in acoustic energy, while the peaks at a frequency of 3-4 kHz become higher and lighter, indicating the level of acoustic energy is increasing. This pattern occurs in the vocalisation given during scanning (Fig. 11a), but to a lesser degree. This shows that in aggressive interactions kea fluctuate the level of acoustic energy within a harmonic more than in non-aggressive interactions. These fluctuations of acoustic energy across the harmonics appear to be graded, with the level of the intensity fluctuations increasing with increased aggressive intensity.

a)



b)

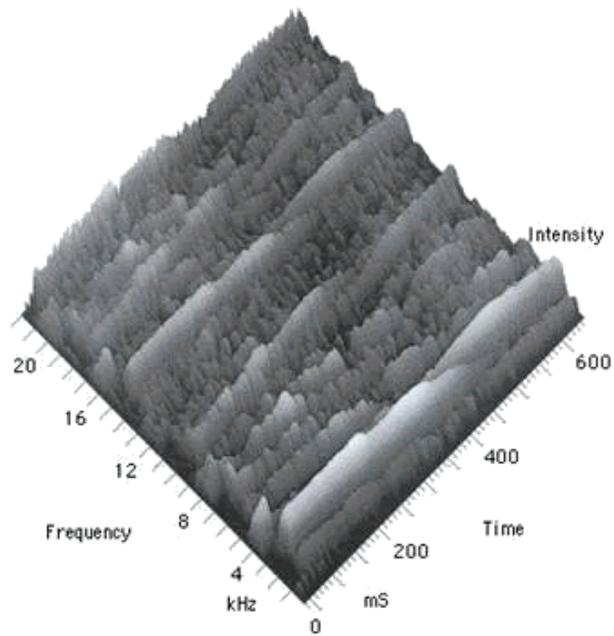
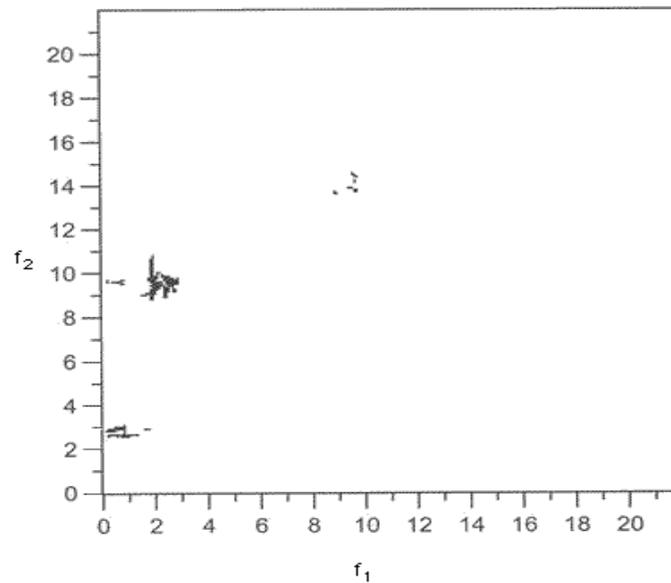


Figure 11. *Ahh* waterfall plot showing distribution of acoustic energy. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Vowel space analysis: Vocalisations given during aggressive interactions also had a higher

level of frequency variation in f_2 (illustrated by less spread in the energy plots in f_2) than non-aggressive vocalisations. Although there was no clear grading or distinction as levels of aggression increased, variations between behavioural contexts were identified. Note that the plots at the 10 kHz range are most probably sound artefacts and the frequency of the actual formant is in the 2 - 3 kHz range.

a)



b)

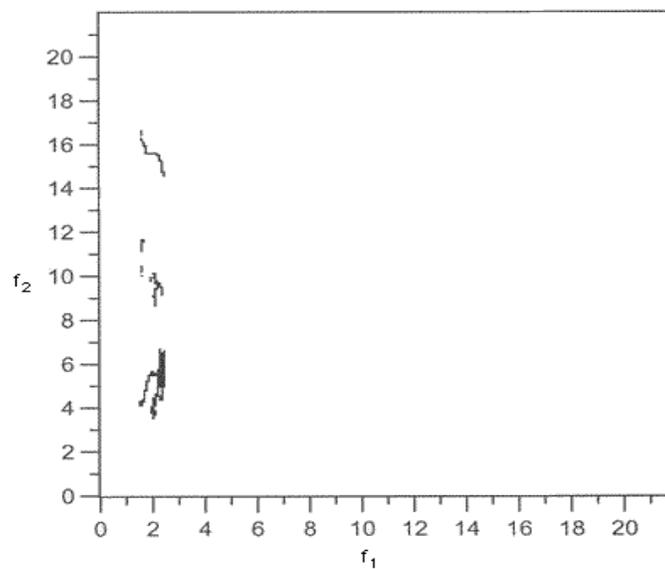
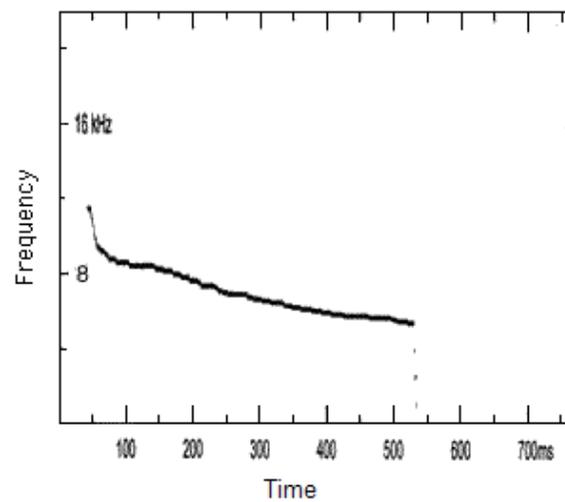


Figure 12. *Ahh* vowel space plots showing frequency of the first and second formants. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Kee-ah vocalisation

Fundamental frequency: The onset peak in the fundamental frequency of vocalisations given after aggressive interactions were almost twice the duration of the onset peak in vocalisations given during scanning (Fig. 13 a and b). The fundamental frequency in vocalisations given during aggressive interactions was higher and had increased levels of frequency variation compared to vocalisations given while scanning.

a)



b)

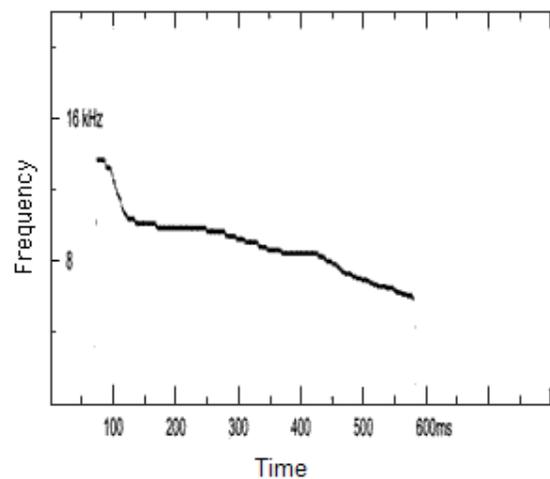
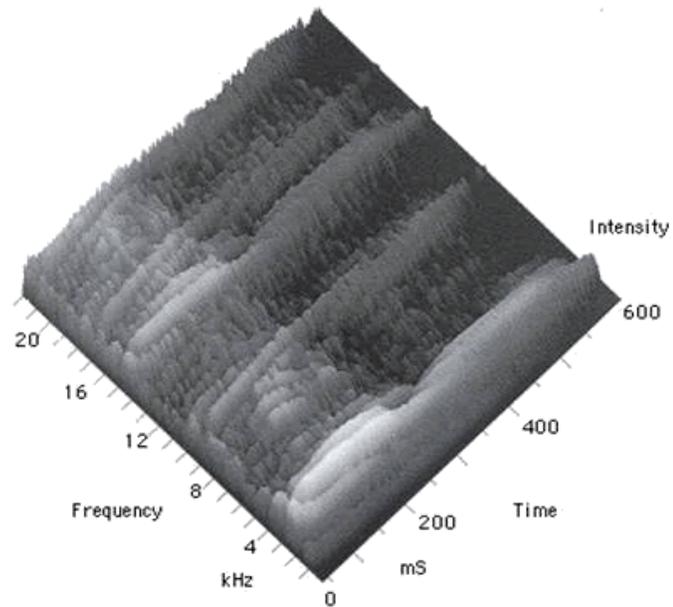


Figure 13. *Kee-ah* fundamental frequency. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Waterfall plots: Vocalisations given during aggressive behaviours showed greater levels of acoustic energy fluctuation in the high intensity harmonics than in vocalisations given during scanning (Fig. 14 a and b). Although the harmonics in vocalisations given during scanning showed lower levels of energy fluctuation, the levels of acoustic energy did decrease over time.

a)



b)

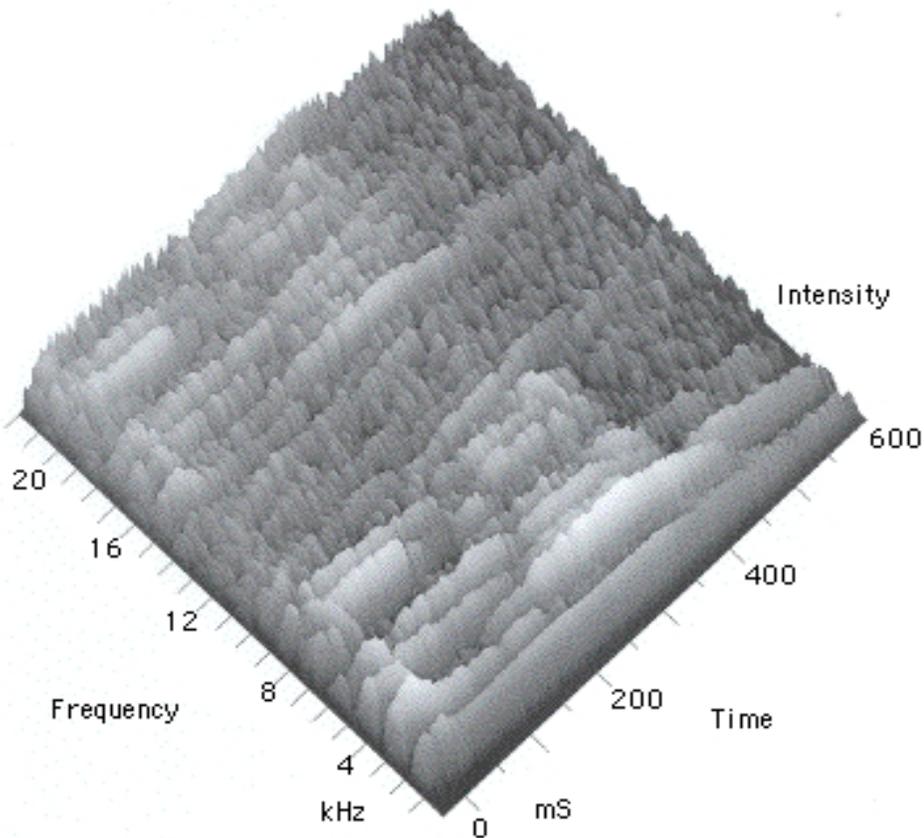
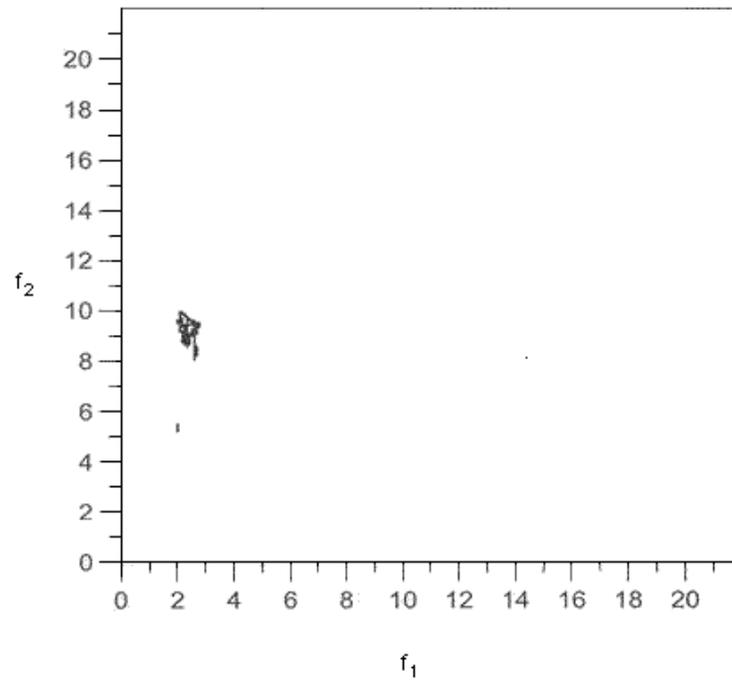


Figure 14. *Kee-ah* waterfall plot showing distribution of acoustic energy. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Vowel space plots: There was minimal variation in the vowel space plots of the *kee-ah* vocalisation between the two behavioural contexts. The vocalisation given during aggressive interactions had a larger change in frequency in f_2 than the vocalisations given during scanning (Fig. 15 a and b). This variation is illustrated by the f_2 plots for the vocalisation given during aggression (Fig. 15b) ranging from 3-9 kHz, whereas the f_2 plots for the vocalisation given during scanning only range from 8-10 kHz (Fig. 15a). However, in all the VSPs produced for this vocalisation there were high frequency f_2 plots (8-10 kHz) present in both behavioural contexts. These unlikely to be the actual f_2 , and are possibly caused by sound artefacts.

a)



b)

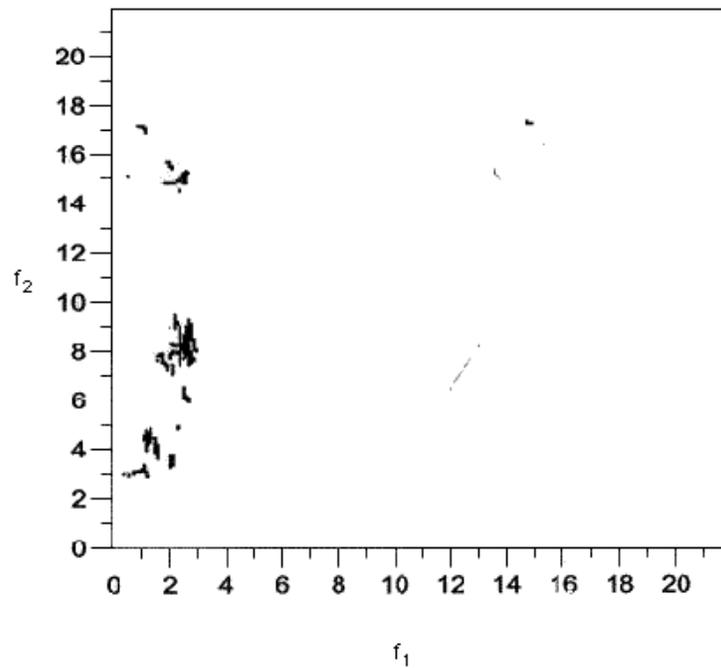
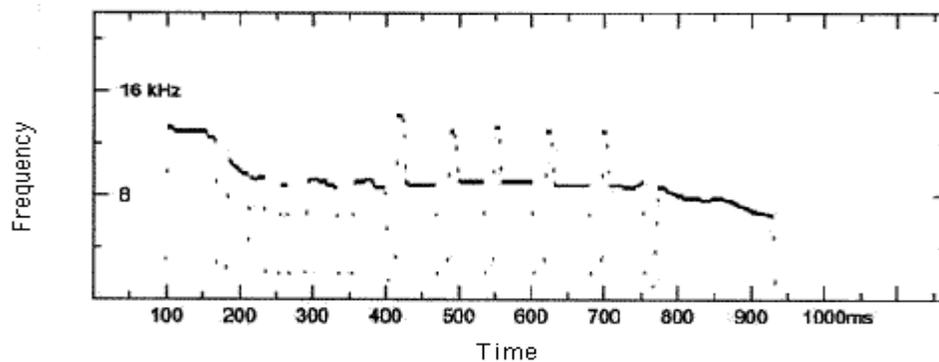


Figure 15. *Kee-ah* vowel space plots showing frequency of the first and second formants. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Ke-ee-ee-ah vocalisation

Fundamental frequency: There were low levels of variation in the fundamental frequency between vocalisations given in the two different behavioural contexts. The onset peak in the fundamental frequency in vocalisations given during aggressive behaviours was shorter than in vocalisations given during scanning.

a)



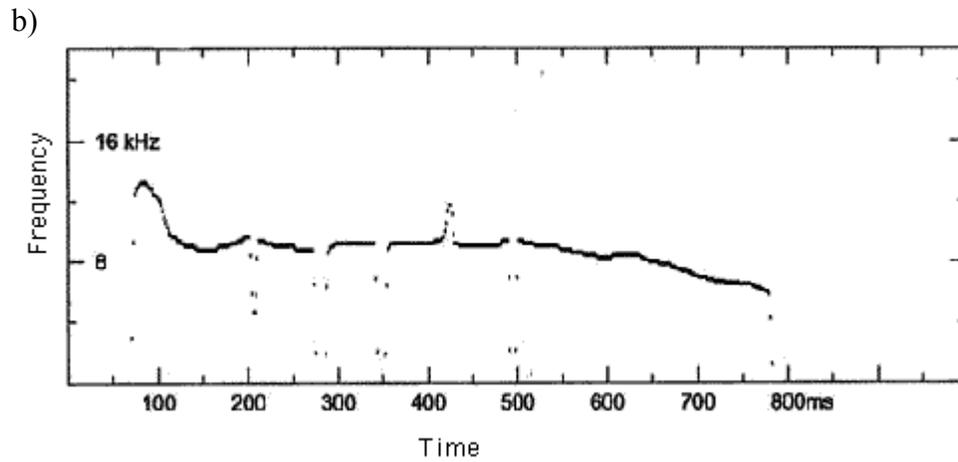
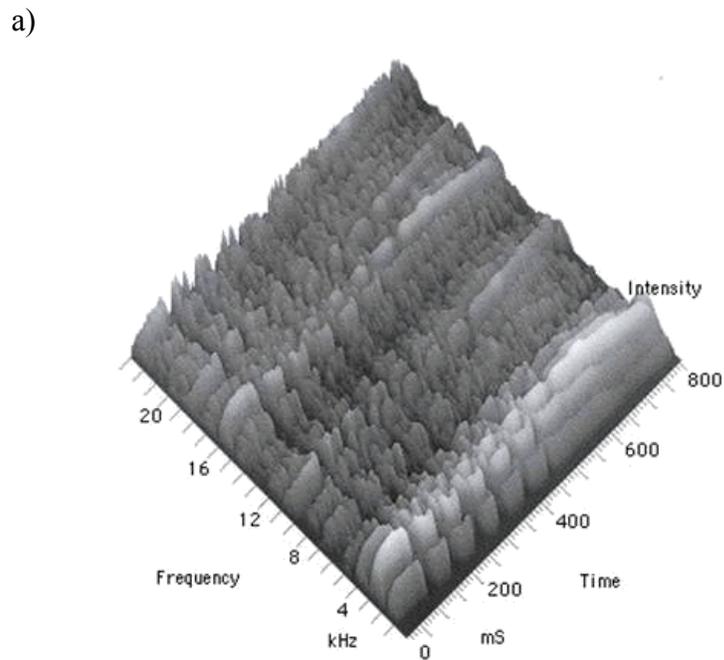


Figure 16. *Ke-ee-ee-ah* fundamental frequency. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Waterfall plots: There were no strong differences in the distribution of acoustic energy between vocalisations given in the two behavioural contexts that were consistent across all of the kea.



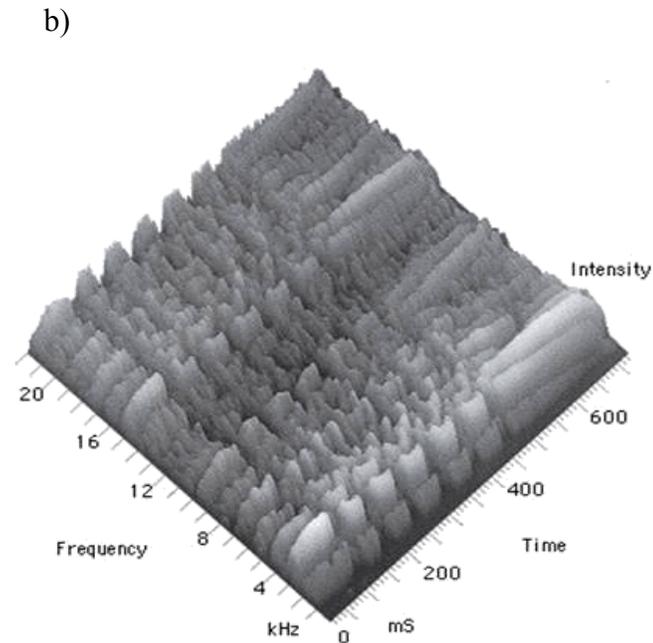


Figure 17. *Ke-ee-ee-ah* waterfall plot showing distribution of acoustic energy. a) Vocalisation given while scanning, b) vocalisation given during an aggressive interaction.

Playback experiments

For the playback experiment a total of five stimulus vocalisations were played (see methods, Chapter 2). The vocalisation recorded from white green during a non-aggressive interaction was played twice and the vocalisation that was recorded from white green during an aggressive interaction was played three times, before the experiment was terminated by the kea departing the study area. There were no kea present at the study site at the time the first vocalisation was played. However, there were a large number of kea around the Hermitage Hotel and in the nearby Glencoe Bush and Governor's Bush (see map, Chapter 2) that could be seen in flight and heard vocalising.

The first stimulus played was the vocalisation recorded from white green during an aggressive interaction (aggressive vocalisation). This did not appear to gain a response from any other kea (Table 1). The second stimulus played was the vocalisation recorded from white green during a non-aggressive interaction (non-aggressive vocalisation). After this playback stimulus six kea took flight from the lawn on the other side of the Hermitage Hotel, vocalising and immediately

flying to the stop bank where the vocalisations were being played. The third stimulus played was a repeat of the aggressive vocalisation. There was no apparent response to this playback stimulus. The fourth stimulus played was a repeat of the non-aggressive vocalisation which appeared to immediately gain a vocal response of ‘*kee-ah*’ and the behavioural response of a head turn from a kea perched at the study site. In the time between the fourth and fifth playback the group of kea departed from the study site and flew to Glencoe Bush. The fifth vocalisation played was another repeat of the aggressive vocalisation. This vocalisation was overlapped by a vocalisation from a kea in flight above Glencoe Bush. This overlapping vocalisation was most probably independent of the playback stimulus. This is because most of the recorded overlaps in this study occurred near the end of the initial signaller's vocalisation (see chapter 4) whereas the vocalisation from the kea in flight appeared to be at the same time as the playback stimulus. Therefore, although this may have been a response, it is unlikely. There were other vocalisations given in response from Glencoe Bush, but it is unclear as to whether these were in response to the playback stimulus or the kea in flight.

Table 1. Apparent responses gained to the playback stimulus for the recordings obtained in each of the two selected behavioural categories.

		<i>Aggressive</i>	
<i>Non-aggressive</i>		<i>Aggressive</i>	
<i>Vocalisation</i>	<i>Behavioural response</i>	<i>Vocalisation</i>	<i>Behavioural response</i>
<i>Vocalisation</i>	<i>Behavioural response</i>	<i>Vocalisation</i>	<i>Behavioural response</i>
<i>Vocalisation</i>	<i>Vocalisation</i>	<i>Vocalisation</i>	<i>Behavioural response</i>
<i>Vocalisation</i>	<i>Vocalisation</i>	<i>Vocalisation</i>	<i>Behavioural response</i>
<i>Vocalisation</i>	<i>Vocalisation</i>		

Discussion

Ahh-ahh vocalisation

Morphology: The *ahh-ahh* vocalisation shows the greatest level of variation in call morphology of the five vocalisations examined. The most significant difference was in the modulation of the harmonics. The vocalisations given by a bird during a bout of solitary play behaviour had a large amount of variation in the modulation of the harmonics and duration of the modulations. Whereas the modulations in the vocalisation recorded from a kea perching and engaged in a vocal exchange were more consistent in frequency and duration. The vocalisations with simpler, smoothly modulated frequencies were primarily used in the context

of an apparent vocal exchange, whereas the vocalisation with irregularly modulated frequencies was not used in vocal exchange (see Chapter 4).

There was also an extra harmonic expansion after the terminal compression in the *ahh-ahh* vocalisation given during perching/exchange that is not present in the vocalisation given during solitary play. This harmonic expansion was also present in the *ahh-ahh* vocalisations that were given in association with preening and scanning. The added expansion and the regulation of the modulations were used in association with non-interactive behaviours, but not when the kea was alone. Terminal compression is often used in human speech to indicate the end of a signal. It is possible the compression serves a similar function in kea. The added harmonic expansion was only present in vocalisations that appeared to be used in exchange. This expansion could possibly serve the function of inducing or encouraging a response after the end of the message. The observed variation in the complexity of frequency modulation of the signal between behavioural contexts supports Slabberkoorn *et al's* (2002) conclusion that simplification of a signal used over long distance communication may be beneficial. They propose that because transmission properties of dense vegetation can lead to degradation of signals, decreasing modulation and frequency bandwidth would allow for production of a louder signal with the same energy expenditure, increasing transmission distance.

It is possible that due to the inability to compare the *ahh-ahh* vocalisation in two differing behavioural contexts within one bird, these differences may be caused by inter-individual variation. This is unlikely to be the major cause of the variation because the kea recorded giving this vocalisation during solitary play was also recorded using the vocalisation during scanning. The spectrogram of the scanning vocalisation showed the same regularly modulated frequencies as the perching/exchange *ahh-ahh* vocalisation. This shows that the regularity of modulations within a vocalisation are not dependent on the individual giving the vocalisation.

Ah-ah-ah

Morphology: This vocalisation was used in both long and short distance communication. This suggests that the observed variations may also be adaptations to the distance the sender intends the vocalisation to travel. It is possible that a vocalisation given in association with an

aggressive interaction may be an indication of aggressive motivation or a response to aggression. If the vocalisation is carrying a message about intentions or is a vocal response to aggressive behaviour, then the signal may be directed to other kea in close range. For this hypothesis to be correct, in accordance with Slabberkoorn *et al's* (2002) suggestion that long distance signals are simpler than short range signals, the vocalisation given during scanning would be expected to be less complex. Whereas the vocalisation given during an aggressive interaction would possibly be highly complex. This variation in complexity level between the vocalisations given in aggressive and non-aggressive behavioural contexts was identified in this vocalisation. *Ah-ah-ah* vocalisations that were given by kea during aggressive behaviours had an increased number of oscillations and deeper peak/valley ratios than vocalisations given during scanning. There was also an increase in the number of harmonics early in the vocalisation given during aggressive interactions, which dropped off towards the end giving the vocalisation a more abrasive sound.

Vocalisations from the kea with the band combination left plastic green yellow were longer during aggressive interactions, with a higher dominant harmonic than in vocalisations given during non-aggressive behaviours. These variations were not represented across different kea. This may have been due to the presence of other birds in the non-aggressive vocalisations of the other kea, whereas green yellow was solitary when the *ah-ah-ah* vocalisation given during non-aggressive behaviour. This suggests that the function of this vocalisation was either long distance communication or a personal vocalisation.

Ahh:

Morphology: The *ahh* vocalisation demonstrated three subtle variations in spectrogram morphology between vocalisations given in the two behavioural contexts. There are two possible explanations for this variation. The length of the *ahh* vocalisations given during scanning may be reduced to better facilitate long distance travel of the signal. Fernandez-Juricic and Martell (2000) found that levels of inter-individual variation in the guttural vocalisations of the blue fronted amazon (*amazona aestiva*) decreased when the birds were alone compared to when they were in flocks. This suggests that parrots may have gradings of vocal signals that serve as personal vocalisations. Therefore, the vocalisations given while

scanning may be personal vocalisations not intended for other individuals.

Although there were no recordings of the *ahh* vocalisation given during aggressive and scanning behaviours by the same kea at the same distance to compare, there were still more harmonics in an aggressive vocalisation at a distance of 5 m from the microphone, than the non-aggressive behaviours at 3 m. The upper harmonics are stronger in the vocalisations associated with aggression than in the vocalisations given while scanning. This indicates a reduction in the resonating chambers of the vocal tract during the aggressive vocalisation. The extra harmonics in the vocalisations associated with aggression give a higher, more shrill sound to the vocalisation.

Fundamental frequency: The variation observed in the fundamental frequency between the two behavioural contexts does not confirm to the motivation-structural rules proposed by Moreton (1982). Moreton (1982) argued that call structure is correlated with the emotional state and status of the caller (McShane *et al* 1995). In this model calls with harsh and lower frequencies tend to indicate an aggressive stance. Conversely, high-frequency or tonal calls indicate fear (McShane *et al* 1995). If applied to the vocalisations of the kea, this change is not so straightforward. The vocalisations given by the recipient of an aggressive interaction had a consistently higher fundamental frequency, than vocalisations given during scanning, as would be expected based on this rule. However, vocalisations given by individuals engaging in high level aggression behaviours such as run-rushing at an opponent also had a higher fundamental frequency than vocalisations given while scanning. The fundamental frequency of vocalisations given during run-rushing was 9-12 kHz, whereas in vocalisations given during scanning the fundamental frequency was 6-8 kHz. Based on Moreton's (1982) hypothesis, this suggests that kea may have been indicating fear in the vocalisation whilst attacking another individual. This seems to be unlikely due to the nature of the run-rush behaviour. The most plausible explanation is that this rule is not applicable for the function and motivation of kea vocalisations.

McShane *et al* (1995) found that this rule did not fit with changes in vocalisation structure in the sea otter, and suggested that the increased fundamental frequency indicated an increased

level of excitement, but not in any clear or distinctive manner. Due to the broad range of aggressive behaviours that displayed the increased fundamental, this suggestion appears to be the most plausible explanation for the variation in kea *ahh* vocalisation.

The presence of a slight peak in the fundamental frequency at the on-set of the vocalisations given during aggressive interactions may be due to heightened levels of excitement. This may be evidence of graded signals within the *ahh* vocalisation. It is possible that as the behavioural situation increases in intensity, for example due to a change in activity, arrival or departure of other individuals or the onset of an aggressive action, the vocalisation may be required to convey more information. This would account for the presence of the slight modulation at the onset of the vocalisation.

Although the *ahh* vocalisation appears to be almost monotone in spectrograms, analysis of the fundamental frequency revealed that in vocalisations associated with aggressive interactions the fundamental shows a comparatively larger decrease in frequency than the fundamental in vocalisations made by scanning individuals. This is another possible indication of increased complexity in a vocal signal accompanying increased levels of excitement. These variations were consistent across all of the kea studied and may represent gradation in the signals.

Distribution of acoustic energy: Kea fluctuated the level of acoustic energy within a frequency more in vocalisations given during aggressive interactions than in vocalisations given during scanning. This variation in levels of fluctuation within a vocalisation may be due to the distance the vocalisation is intended to carry. The decreased level of energy fluctuation in the vocalisation given during scanning supports both hypotheses. The lower levels of energy fluctuation simplify the vocalisation. Based on Slabberkoorn *et al's* (2002) hypothesis that simpler vocalisations are more efficient for communicating over long distances, the *ahh* vocalisation given during scanning is ideal for long distance communication.

It is possible that since this fluctuation occurs at a higher level in vocalisations given during aggressive interactions than in vocalisations given during scanning this variation may be a graded signal. This probably serves to increase the level of information used in a vocalisation.

Formant positioning: Vocalisations given during aggressive interactions had lower level of variation in frequency in f_2 and a higher level of variation in frequency in f_1 than vocalisations given while scanning than non-aggressive vocalisations. This shows that the first formant is more variable in frequency than the second formant. This indicates that the kea is altering the size of the vocal chambers less when vocalising during scanning behaviours than during aggressive behaviours. It also indicates that the kea is varying the size of the part of the vocal tract that supports f_1 more than the part that supports f_2 . This allows the larger frequency range of f_1 , while simultaneously restricting the frequency range of f_2 . Although there were variations between these two behavioural categories, none were sufficiently consistent across the varying behavioural contexts to suggest the formant positioning may be graded.

Kee-ah vocalisation

Morphology: There was only a small number of differences in the *kee-ah* vocalisation across the two behavioural contexts that were consistent amongst all the studied kea. The duration of onset peak was slightly longer in the vocalisations associated with aggressive behaviours. Although this variation is of approximately 50 ms it is possible this is large enough to be detected by a kea. Rook and Knight (1977) noted that although birds and humans have comparable abilities to detect change in frequency, avian discrimination of time is 10 to 100 times better than that of humans. They suggest that the latter figure is most likely and proposed that birds can discriminate to 0.5 ms. This suggests that the variation in peak duration is well within the discrimination capabilities of most birds. Even if this figure is incorrect by up to two orders of magnitude, it is possible that kea may be able to discriminate between the vocalisations. Although not visible in these spectrograms, harmonic doubling was present in some *kee-ah* vocalisations given during high levels of aggression. Harmonic doubling is often found in human infants when highly distressed, and may also signal a distressed state in kea.

Fundamental frequency: The variations in the frequency and change in frequency between vocalisations the fundamental frequency in *kee-ah* vocalisations recorded in the two behavioural contexts are consistent with the variations identified in the *ahh* vocalisation. These results support the possibility that as the kea becomes more excited the fundamental both

increases in frequency and the level of variation. The duration of the onset peak in the fundamental frequency after an aggressive interaction was almost twice that of the non-aggressive. The change in frequency over time of the fundamental frequency was larger for vocalisations given during aggressive interactions than those given during scanning. This variation is caused by larger extremes in the tightening and relaxing of the syrinx through the duration of the vocalisation. The higher onset frequency may indicate a higher level of excitement that decreases over the duration of the vocalisation. However, as these vocalisations are less than a second it seems unlikely the level of excitement would decrease that rapidly. Vocalisations given during aggressive interactions also had a higher fundamental frequency than vocalisations given during scanning. This variation was also found in the *ahh* vocalisation, indicating that both vocalisation types demonstrate the opposite to what would be expected in the fundamental frequency of vocalisations from an aggressive individual (McShane *et al* 1995). This unexpected variation further supports McShane *et al's* (1995) hypothesis that an increase in signal frequency indicated an increased level of excitement, but does not differentiate between behaviours.

Distribution of acoustic energy: The levels of fluctuation of acoustic energy between the two behavioural contexts varies, possibly showing graded signals. This variation could be either an intentional or an unintentional physiological response to increased levels of excitement. The harmonic with the highest intensity in the vocalisation given during scanning shows low levels of energy fluctuation. These harmonics have no sudden shifts or declines but gradually decline over the duration of the vocalisation. In comparison, the energy levels in vocalisations given during aggressive behaviours had several fluctuations and shifts in the peak frequencies. Each of these variations were consistent with the *ahh* vocalisation, suggesting that the gradation of the signals may be the same in both vocalisation types.

Formant positioning: There was minimal variation in the vowel space plots between the two behavioural categories. There was a slight increase in the level of variation in frequency in f_2 during vocalisations associated with aggression. This variation could possibly represent the shifts in acoustic energy, this would suggest that opposed to the energy concentrations shifting between formants, the f_2 is shifting and the energy concentration may be shifting with it,

causing the shifts illustrated by the waterfall plots.

Ke-ee-ee-ah vocalisation

Morphology: The observed variation between the two behavioural contexts for this vocalisation may be a result of the distance of the sender to the intended receiver. Although Slabberkoorn *et al* (2002) argue that simpler signals are the most efficient for communication over long distances, McShane *et al* (1995) point out that not all signals are necessarily designed for maximum distances, but rather optimal ones. Naguib (2000) suggests that increased modulation may give receivers more information, and allow for easier estimates of direction and distance by utilising the sound degradation. Kea may use more the complicated forms of the *ke-ee-ee-ah* vocalisation for long distance communication, utilizing the sound degradation in the environment to send messages. This vocalisation was shorter when given by a kea during an aggressive interaction. The difference in length comes from a change in oscillation number with vocalisations associated with aggressive behaviour having 3-6 oscillations, and vocalisations used in non-aggressive behaviours, such as scanning, ranged from 5-11 oscillations. Based on the lower numbers of oscillations in vocalisations associated with aggression, Naguib's (2000) hypothesis supports my earlier suggestion that vocalisations associated with aggressive interactions are signals intended for close neighbours as opposed to distant communication.

Fundamental frequency: There were no consistent differences in the fundamental frequency across the behavioural contexts.

Distribution of acoustic energy There are no strong differences in the distribution of acoustic energy between the two moods that are consistent across each kea.

The *kee-ah* and *ahh* vocalisations show the same variations between behavioural contexts. Both vocalisations demonstrate a higher fundamental frequency with increased duration of the onset peak and a larger frequency range in vocalisations associated with aggressive behaviours than vocalisations associated with non-aggressive behaviours. They both also demonstrate higher levels of energy fluctuations and shifting in the vocalisations given during aggressive

behaviours and increased frequency variation in the second formant.

Although the *ke-ee-ee-ah* vocalisation is possibly the most variable vocalisation in the repertoire of the kea, these variations could not be categorised by behavioural contexts. This implies that the vocalisation is unrelated to the behavioural situation at the time of the vocalisation. The variations in the *ke-ee-ee-ah* vocalisation that was observed between behavioural contexts is considerably different to the variations present in the *ahh* and *kee-ah* vocalisations. This suggests that although the structure of the *ahh*, *kee-ah* and *ke-ee-ee-ah* vocalisations are similar, and the *ke-ee-ee-ah* vocalisation appears to be frequently used in vocal exchanges with the *ahh* and *kee-ah* vocalisations (see Chapter 4), the *ke-ee-ee-ah* vocalisation probably contains a different message or has a different function to the other two vocalisations.

Each of the vocal signals given by the kea have components that conform to various and conflicting theories that suggest they are used for various distances of communication with messages of varying complexity. However they do not conform to any single hypothesis. Ujhelyi (1996) states that signals essentially express the emotional states of animals. If this is occurring in the kea the vocalisations may vary due to an internal stimulus that is even more difficult to identify than the behavioural context. As emotional states of animals can not reliably be defined and identified and can only be inferred by behavioural contexts, the validity of Ujhelyi's (1996) statement is difficult to confirm. The results of this study do however show that keas have a complex repertoire that does not conform to any single theory of signal evolution based on optimal call travel distance or the habitat a vocalisation must pass through. This suggests that alternative hypotheses may need to be explored in order to accurately determine the function of kea vocal signals.

Playback

Saunders (1983) hypothesised that within each group there is certain to be a range of variations in each call within one individual bird's repertoire and each variation may convey a different meaning depending on mood and situation. The presence of intra-individual variation in kea vocalisations based on behavioural context was confirmed by this study. However, Falls (1982)

argues that presence of variation in vocalisations is not enough to confirm recognition by other individuals. Discrimination of the vocalisations by individuals must be demonstrated via playback experiments.

Of the two different *kee-ah* recordings played to wild kea one was from a non-aggressive interaction and one was from an aggressive interaction. The playback stimulus recorded from a kea during a non-aggressive interaction appeared to receive both behavioural and vocal responses during both of the playback experiments. None of the three times the vocalisation recorded from a kea during aggressive behaviours was played gained any obvious responses during this experiment. The playbacks of the vocalisation given during scanning both gained vocal responses of the same vocalisation. The initial playback of the non-aggressive vocalisation seemed to attract a group of six young kea to the study site. This is significant because this study site had not been used for almost two months and the kea had stopped congregating independently. This apparent behavioural response was accompanied by several *kee-ah* vocalisations from the birds in flight and landing. The second non-aggressive *kee-ah* vocalisation played appeared to gain a slight behavioural response and a *kee-ah* from a kea perched at the study site. Of the three playbacks of the aggressive vocalisation, only two were able to be used for comparison with the responses from the non-aggressive vocalisations. This is because at the time of playing the third aggressive vocalisation a bird in flight above Glencoe Bush also vocalised. It is possible this was a response to the playback stimulus, but as the vocalisation was almost simultaneous to the playback as opposed to overlapping at the end, it is unlikely. It is most probable that this vocalisation was independent of the playback stimulus. Of the two vocalisations given in association with aggression, neither gained a vocal or behavioural response. These results suggest that not only is there variation between the two behavioural context of the same vocalisation, but kea may discriminate between these variations. However, due to limitations from low playback repetition size, these observations need to be confirmed with further playback experiments.

The results of this study indicate that kea do show variation in the same vocal signal when it is given in varying context. They also suggest that kea may be able to discriminate between these variations. Although it is not possible to know if these variations are intentional made by the

kea or if they are a physiological response, they are present.

This study has also identified the use of human speech analysis techniques as an effective way of identifying subtle differences in the vocalisations of parrot species. The technique allowed identification of variations in call structure to a much finer level than is possible with spectrograms alone. As well as this more detailed analysis, it provided the possibility to identify the physiological mechanisms that may be causing the specific variations. The knowledge of both the variation and the possible physiological mechanisms controlling the variation may provide greater incite to the highly complex vocal systems of parrot species.

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