Vocal repertoire of the New Zealand kea parrot *Nestor notabilis*

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Abstract   The unique alpine-living kea parrot *Nestor notabilis* has been the focus of numerous cognitive studies, but its communication system has so far been largely neglected. We examined 2,884 calls recorded in New Zealand's Southern Alps. Based on audio and visual spectrographic differences, these calls were categorised into seven distinct call types: the non-oscillating 'screech' contact call and 'mew'; and the oscillating 'trill', 'chatter', 'warble' and 'whistle'; and a hybrid 'screech-trill'. Most of these calls contained aspects that were individually unique, in addition to potentially encoding for an individual's sex and age. Additionally, for each recording, the sender's previous and next calls were noted, as well as any response given by conspecifics. We found that the previous and next calls made by the sender were most often of the same type, and that the next most likely preceding and/or following call type was the screech call, a contact call which sounds like the 'kee-ah' from which the bird's name derives. As a social bird capable of covering large distances over visually obstructive terrain, long distance contact calls may be of considerable importance for social cohesion. Contact calls allow kea to locate conspecifics and congregate in temporary groups for social activities. The most likely response to any given call was a screech, usually followed by the same type of call as the initial call made by the sender, although responses differed depending on the age of the caller. The exception was the warble, the kea's play call, to which the most likely response was another warble. Being the most common call type, as well as the default response to another call, it appears that the 'contagious' screech contact call plays a central role in kea vocal communication and social cohesion [*Current Zoology* 58 (5): 727–740, 2012].

Keywords   Acoustic signals, Communication, Kea, Psittacidae, Social behaviour, Habitat

Precedence for expecting a strong link between communication systems and cognitive ability (Rowe and Skelhorn, 2004) originates from studies showing that vervet monkeys *Cercopithecus aethiops* elicit predator-specific defences from conspecific group members by broadcasting predator-specific alarm calls (Seyfarth et al., 1980). A considerable body of work also suggests that there are parallels in cognitive ability between primates and birds, particularly crows, jays (Emery and Clayton, 2004; Taylor et al., 2007, 2009), and parrots (Funk, 2002; Pepperberg, 2004).

The kea *Nestor notabilis* is an endangered psittaciform endemic to New Zealand and is the world's only alpine parrot. These large, long-lived birds can fly long distances (ca. 20−30 km) within and between different mountain ranges (Elliott and Kemp, 2004). Belonging to the oldest lineage of parrots to branch off from the Psittacidae (Grant-Mackie et al., 2003), the Nestoridae (superfamily Strigopoidae) (Joseph et al., 2012), the kea's behaviour is still largely unstudied. While research on kea has increased markedly in recent years, these studies are primarily focused on cognition, typically in a laboratory setting, and results suggest that the kea has cognitive abilities rivalling that of primates (Gajdon et al., 2004; Gajdon et al., 2006; Huber and Gajdon, 2006; Auersperg et al., 2009; Miyata et al., 2010). In fact, there is very little recent information (within 40 years) regarding natural kea behaviour (but see Young et al., 2012) and there has been surprisingly little research (but see Bond and Diamond, 2005) on the vocal behaviour of this parrot.

Vocal communication in non-human animals can exhibit high levels of complexity. In particular, the vocal repertoire of many species, especially among mammals (Seyfarth and Cheney, 1986; Mateo, 1996; Randall et al., 2005; Hollén et al., 2008) and birds (Miller and Gottlieb, 1981; Earle, 1986; Lefevre et al., 2001; Cardoso and Mota, 2007; Benedict and Bowie, 2012) can be very large. For example, vervet monkeys may have at least nine different calls (Seyfarth and Cheney, 1986), Gun-

nison's prairie dogs *Cynomys gunnisoni* four (Slobod-chikoff and Placer, 2006), and the barred owl *Strix varia* thirteen (Odom and Mennill, 2010).

As some of the earliest published work on the diversity of animal communication and the ontogeny of vocal communication comes from birds (Scott, 1902), it may seem odd that parrots have only recently surfaced as subjects for vocalisation studies (Power, 1966; Rowley, 1980). Since then many Psittaciformes have been shown to have large vocal repertoires. For example, the blue-fronted amazon *Amazona aestiva* and the monk parakeet *Myiopsitta monachus* were found to have at least nine call types (Martella and Bucher, 1990; Fernández-Juricic et al., 1998), the ground parrot *Pezoporus wallicus wallicus* at least ten (Chan and Mudie, 2004), and both the kaka *Nestor meridionalis septentrionalis* and the yellow-faced parrot *Alipiopsitta xanthops* at least seven call types (van Horik et al., 2007; de Araújo et al., 2011).

The literature suggests that the cognitive skills of parrots, coupled with high levels of sociality, facilitate the evolution and use of complex communication systems (Marler, 1996; Wanker et al., 1998; Pepperberg, 1999; Bradbury et al., 2001; Wanker and Fischer, 2001; Byrne and Bates, 2007; van Horik et al., 2007). In addition to their cognitive abilities, kea life-history traits are also suggestive of complex communication, as they regularly congregate in flocks comprised of both sexes and all ages, with a non-linear hierarchy defining relationships within groups (Diamond and Bond, 1991, 1999; Gajdon et al., 2006).

The ontogeny of vocalisations is also an important facet of the link between cognition and communication and, as such, we might expect longer-lived animals to develop and refine their communication and signalling skills over a long period of time, in accordance with their stage of development. While most studies have focused on the ontogenetic differences in call structure (e.g., Rice and Thompson, 1968; Slater and Ince, 1982; Baker, 2003; Randall et al., 2005; Guilette et al., 2011; Lipkind and Tchernichovski, 2011), some researchers have recently investigated the differences in behaviour based on age (e.g., Hollén and Radford, 2009). For example, vervet monkeys use many of the same calls as the adults, but learn through experience the appropriate context in which to use them (Seyfarth and Cheney, 1986). Unlike songbirds, parrots make extensive use of the tongue to articulate calls, as well as subtly altering beak gape to modulate frequency (Ohms et al., 2012), and it is possible that, as in humans, this skill takes time

to refine in order to modulate sounds appropriately.

Previous work on parrot vocalisations has typically focused on 'contact calls' (Wanker and Fischer, 2001; Wright and Wilkinson, 2001; Bond and Diamond, 2005; Guerra et al., 2008; Wright et al., 2008), which are used to convey information on the location of group members, and may contain information that facilitates individual recognition (Rowley, 1980; Wanker and Fischer, 2001; Wanker et al., 2005; Cortopassi and Bradbury, 2006; Balsby and Adams, 2011; Berg et al., 2011). However, it is becoming increasingly clear that parrots produce a wide variety of types of calls (Fernández-Juricic et al., 1998; Venuto et al., 2000; Chan and Mudie, 2004; van Horik et al., 2007).

With the ultimate purpose of understanding the functional significance and variation in the call types of kea, here our aim was to describe the vocal repertoire of wild kea. We classified the calls based on audible and structural differences, as reliable automated categorisation is still in its infancy and is outperformed by humans (Giret et al., 2011). We then looked at the characteristics and use of different call types across different age groups and sexes, as well as kea vocal responses to nearby calls. Similarly to the prediction made for mammals by Lea and Blumstein (2011), we expected to find that, as a slowly maturing species (Diamond and Bond, 1999), kea would show ontogenetic differences in use across the call types.

1 Materials and Methods

1.1 Subjects and study sites

Kea are large (45−50 cm in length) alpine parrots that live in complex, stratified social systems involving individuals of all ages (Diamond and Bond, 1999). They typically live between 700 and 2,000 m in altitude in the Southern Alps of New Zealand. Kea are sexually dimorphic, with males being larger (mean weight: 780 and 960 g for females and males, respectively) and having a longer, more sharply curved beak (Bond and Diamond, 1991; Higgins, 1999). In addition to being sexually dimorphic, kea undergo clearly discernable ontogenetic changes with age, involving changes in colour of the plumage and beak (Diamond and Bond, 1999; Higgins, 1999). Fledglings (≤ 1 year) have completely yellow ceres and eye-rings, partial yellow colouration of the base of the beak and yellow-tinted crown feathers. The crown feathers of juveniles (2−4 years) has turned green and their eye-rings, ceres and the base of their beak has begun to fade to grey. Sub-adults (4−6 years) retain only blotches of yellow on their eye-rings and cere, and the

beak is uniformly dark-grey. The eye-rings and cere of adults (≥ 6 years) are uniformly grey. The ages mentioned for the age groups overlap somewhat because they represent the natural range observed of colouration for banded birds with known ages.

Kea vocalisations were recorded in Arthur's Pass (42°57′S 171°34'E) and Aoraki/Mount Cook (43°44′S 170°6′E) National Parks, New Zealand, from October 2009 to May 2011, excluding the winter months of June-September. Kea tend to form larger groups and forage above the treeline during the summer period before dispersing into smaller groups and retreating to lower altitudes during winter (Jackson, 1960). Kea are most active a few hours after sunrise and before sunset, which is when most of the recordings were made. The number of kea present at any one time ranged from 1 to 20 birds, and included all four age groups, although rarely in equal numbers as there is typically a preponderance of younger birds at high altitude in the summer (see Young et al., 2012). Many kea were banded as part of conservation initiatives, and were accurately identifiable for age and sex. The age and sex of unbanded birds was only recorded and included in the analysis when the observer was confident in their visual assessment.

1.2 Audio recording and call type analysis

All recordings were made with a directional Sennheiser ME66 microphone (frequency response 40–20,000 Hz ± 2.5 dB) with a K6 powering module (bass roll-off filter; frequency response 30–20,000 Hz ± 1 dB). Sound files were generated and stored as uncompressed PCM audio .WAV files on a Sound Devices 722 portable high definition digital audio recorder with an internal hard drive (24-bit sampling rate, 48 kHz sampling frequency, 10–40,000 Hz +0.1 dB/-0.5 dB frequency response).

Spectrograms of recordings were examined in Raven Pro 1.4 interactive sound analysis tool (Cornell Lab of Ornithology; Hann window, overlap 50%, hopsize 2.67 ms, grid spacing 188 Hz, discrete Fourier transformation 256-points). Calls were chosen for analysis in Raven when they had low background noise, and no overlap with other calls. Chosen calls were isolated into individual .WAV sound files. In total 2,884 calls, selected from over 20 h of recordings, were isolated and chosen for analysis. An estimate of the number of birds that we assessed, based only on banded birds is $n > 47$. Additionally, we obtained recordings from an unknown number of individual unbanded birds of different age groups.

Using the spectrograms generated in Raven we classified the vocalisations visually into different call types based on structural differences, choosing several quantitative measures to describe the calls. In many vocalisation studies, quantitative measures such as the minimum and maximum frequency, the frequency range and power of the fundamental harmonic, and power of the whole call (e.g., Seyfarth and Cheney, 1980, 1986; Fernández-Juricic et al., 1998; Lefevre et al., 2001; Guillette et al., 2011), are included in the analysis. We decided against their inclusion primarily because our recordings were obtained in alpine habitats where wind noise distorts the lowest frequency range (Foss, 1979). Because of the unpredictable nature of kea, loud and soft calls were often recorded within a few minutes, which necessitated changes in gain (sensitivity of the digital recorder) to obtain good quality recordings from the upper and lower ranges of amplitude; this resulted in unreliable information on the dB levels found in many recordings. Consequently, the ratio of power between the second harmonic and the whole call was included (Fig. 1), as both values would have been equally affected by the change in gain. Finally, most kea call harmonics extend beyond the upper accurate range of the microphone (ca. 20 kHz) and were thus not available for analysis. Instead, we compared calls based on: call duration; frequency range of the second harmonic (Δ frequency 2nd); ratio of power of the second harmonic to power of the whole call (power ratio 2nd H); frequency range of a repeated frequency modulation (Δ frequency RFM); duration of a frequency modulation (length RFM); the number of repeated frequency modulations, and the difference in frequency between two harmonics, or harmonic density (Δ frequency H-H). Once calls had been classified we then re-examined the recordings and, if the original caller vocalized more than once, we noted the type of call used by the same bird within the 10 s before and after the analysed call (henceforth, the 'call of interest') in order to determine any sequence patterns to the vocalisations.

1.3 Use of vocalisations by kea of different sexes and ages

In addition to analyzing individual variation within calls for each of the above measured parameters (excluding the 'power ratio 2nd H'), for a subset of the classified calls, age and sex information were available (noted when recordings were made). We conducted Kruskal-Wallis and Mann-Whitney tests to analyse individual variation and whether sex affected the propensity to use a specific call type, and whether propensity to use a given call was age-dependent. Multiple comparisons were carried out using Dunn's tests.
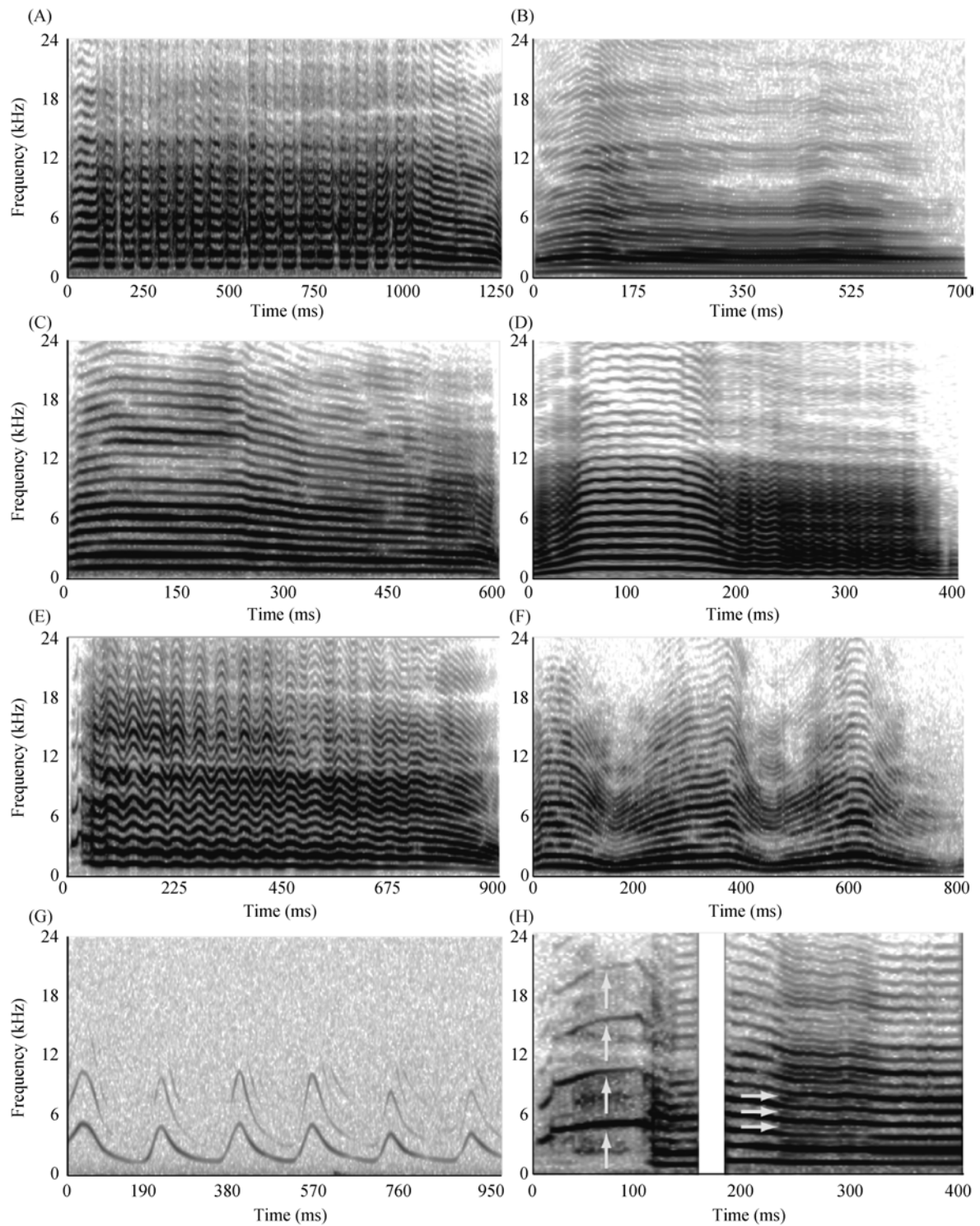
Fig. 1 Spectrograms of kea calls
A. Chatter. B. Mew. C. Screech. D. Screech-trill. E. Trill. F. Warble. G. Whistle. H. Within call harmonic variation (Arrows point at the anomalous harmonics). Note different timescales on X-axis.

1.4 Responses to different calls

As well as noting the sex and age of the caller for the calls of interest, we also noted the type of call of any responses to the call of interest, although we could not ascertain the sex and age of the responding bird. Calls from a different bird that occurred within 10 s of the call of interest were considered a response. The 10 s cut-off was chosen because kea are increasingly unlikely to be attending to a call after this period of time (based on work on the attention span of kea (Range et al., 2009)

and based on a field study on the vocalisations of the kea's closest relative, the kaka (van Horik et al., 2007)). For responses, we used Chi-square tests of independence to analyse whether these were affected by age and sex of the caller in all situations in which we had sufficient sample sizes.

2 Results

2.1 Call types

Kea calls were grouped visually into the following seven mutually exclusive call types: chatter; mew; screech (often referred to as the 'kee-ah' call in the literature (Diamond and Bond, 1999; Bond and Diamond, 2005); screech-trill; trill; warble; and whistle. Most calls were under one second in length, had repeated frequency modulations and multiple harmonics (Δ frequency per harmonic ≈1000 Hz, most with discernable harmonics up to the recording bandwidth visible on the spectrogram), and carried most of the power in the second harmonic (≈ 8%–9% above the total call average) (Table 1). The unique aspects of each call type are described below as well as depicting the most common behavioural contexts during which the calls occurred. The behavioural categories are agonistic, alarm, altruistic, flying, foraging, play, preening and take-off. Calls made during inactivity (no discernable behaviour) were classified as broadcasting.

2.1.1 Chatter The chatter call (Fig. 1A) begins with a slight increase in frequency, followed by repeated frequency modulations, and ends in a smooth decrease in frequency. The most distinctive feature are gaps in the vocalisation between the frequency modulations, which can both be heard and clearly seen on the spectrogram, giving it a 'chattering' sound. The duration and number of modulations of this call are similar to those of screech-trill and trill calls (Table 1). Chatter calls have a fairly broad frequency range within the modulations of the call (ca. 1,400 Hz). Chatter calls were often associa-

ted with foraging (43%) and flight (18%) behaviour, and never with alarm or agonistic behaviour.

2.1.2 Mew The mew call (Fig. 1B) most often lacks frequency modulations, although these can sometimes be present. Mew calls resemble screech calls in structure and sound similar to a cat 'mewing'. Mews have the most densely generated harmonics (median 681.9 Hz), and are the second shortest (0.63 s) of all call types. For these reasons they only overlap with other call types on one of the parameters examined (Table 1), the ratio of power for the 2nd harmonic, as this is a characteristic of most kea calls (Table 1). Mews were most often associated with foraging behaviour (69%) and were generally recorded from single birds some distance (2–20 m) away from conspecifics. Because they were generally very quiet calls, it is likely that they were not intended for a receiver, but instead a sort of private 'vocal repetition'.

2.1.3 Screech The screech call (Fig. 1C) lacks repeated frequency modulations, beginning with an initial increase in frequency, followed by a longer decrease, which sounds like 'kee-aah', from which the species' name is derived. It is similar in harmonic density to chatters, screech-trills and warbles, but differs in all other aspects examined. The screech is most likely the kea's main contact call. It is the most frequent call during broadcasting (33%), as well flight (68%) and take-off (57%) behaviours, where group-cohesion is beneficial. It is also second most frequent call during agonistic (30%), foraging (29%) and play (30%) behaviours, where the location of conspecifics, although not paramount to the task at hand, is still of importance.

2.1.4 Screech-trill The screech-trill call (Fig. 1D) begins with an increase in frequency followed by repeated frequency modulations, although on some occasions the call begins with a decrease in frequency before the repeated frequency modulations. The repeated frequency modulations of screech-trill calls are similar to

Table 1 Characteristics of kea calls

	Chatter	Mew	Screech	Screech-trill	Trill	Warble	Whistle	Test statistic (H)
Call length (s)	0.83_a	0.63_b	0.62_b	$0.96_{a,c}$	0.88_a	0.72_d	$1.53_{c,e,}$	481.7
Δ frequency 2nd H	1921_a	1255_b	1721_c	1956_a	1651_c	1971_a	4841_d	548.8
Power ratio 2nd H	1.08_a	1.09_b	1.09_b	$1.08_{a,b}$	1.08_a	1.09_b	1.04_c	171.9
Δ frequency FM	1317_a	0_b	0_c	944.8_d	$1110_{d,e}$	1894_f	$4319_{f,g}$	2350.0
Length FM	0.06_a	0_b	0_c	0.02_d	$0.05_{a,d}$	0.09_e	$0.16_{e,f}$	2415.0
# FM	6_a	0_b	0_c	18_d	$12_{d,e}$	5_f	$9.5_{a,d,e}$	2260.0
Δ frequency H-H	1004_a	681.9_b	$999.8_{a,f}$	$1006_{a,f,e}$	$946.1_{d,e,h}$	$968.9_{a,f,h,}$	2568_g	589.1

Medians of quantitative measures by call type. Values in the same row not sharing the same subscript significantly different at $P < 0.05$ (Kruskal-Wallis tests; df = 6). FM: frequency modulation. H: harmonic. Δ frequency H-H: Difference in frequency between two harmonics.

those of trill calls (Δ frequency ≈ 1000 Hz), as is the total duration of the call (Δ time ≈ 0.96 s). Screech-trill calls differ from both screeches and trills in that they are more broadband, and so match the chatter and warble calls more closely (Table 1). The number of repeated frequency modulations is the highest for any call type. Most screech-trills occurred during foraging (66%), which might underline the intermediate nature of this call type between screech and trill calls, the two most common call types during foraging.

2.1.5 Trill The trill call (Fig. 1E) mainly consists of repeated frequency modulations with a short smooth decrease in frequency at the end - if there is a clearly audible increase of frequency at the beginning, the call is categorised as a screech-trill. It is most similar to the screech-trill, with the only significant dissimilarity being the bandwidth of the second harmonic (Δ frequency ≈ 950 Hz), which is more similar to that of a screech call. They also share some similarities with chatter (Table 1). The trill is most likely an alarm call, with 50% of trills uttered in alarm contexts, such as when humans access a nest (99% of calls in such contexts were trills). It also seems to be used in agonistic encounters, where 34% of all calls were trills, and in foraging situations, where 31% off all calls were trills, perhaps because group foraging at a shared food source can quickly lead to agonistic encounters.

2.1.6 Warble The warble (Fig. 1F) is a highly variable call, which is associated with play behaviour (Diamond and Bond, 1999). This call has also been called a 'squeal' (Diamond and Bond, 1999; Bond and Diamond, 2005). Although it is one of the shorter calls (0.72 s), it always contains a few (median 5) large repeated frequency modulations (Δ time of modulation ≈ 0.09 s, Δ frequency of modulations ≈ 1,900 Hz). Elements from other call types can be found in many warble calls. The warble was most often uttered during play behaviour, with 51% of all warbles occurring during play and 54% of all calls recorded during play being warbles.

2.1.7 Whistle The whistle (Fig. 1G) is the most rarely recorded of all kea calls, representing only 1% of the calls available for analysis from more than 20 h of recordings. It consists of repeated frequency modulations, which are longer (0.16 s) than those of other calls. These calls also have a much broader frequency range (4,319 Hz) than any other call, yet they are also the only calls that have no discernable harmonics above 16-18 kHz. Whistle calls are also the longest of all call types (1.53 s) and have the smallest power ratio between second harmonic and the whole call (1.04). Although

the rarest of kea calls, whistles had the highest frequency of association with preening and allo-feeding behaviour of all call types, with 26% of calls during preening and 100% of calls during allo-feeding being warbles.

Most types of kea calls (excluding whistles and mews) were occasionally produced containing within-call changes in the number of harmonics (Fig. 1H). When this happened, typically the bird began the call with only a few harmonics present, but the number increased as the call progressed, sometimes ending with four times as many harmonics as at the start of the call. The other relatively common change in harmonics occurred when the bird doubled the number of harmonics within the call for a short period and then returned to the original number of harmonics. The two types were not mutually exclusive, but only occurred at low frequencies (< 10% of calls) overall.

Individuals were found to vary across many different parameters for most call types; the exception of the screech-trill call might be due to limited sample size (Table 2). Based on all the call parameters measured, no call type was exclusively sexually dimorphic. However, there were sex differences in between one and four of the call characteristics for each of the calls (Table 3). There were also multiple call characteristics for which the variance could be explained by the age group categories (Table 4). In just under 70% of these cases there was a pattern in the changes that followed in a linear manner with increasing age, such that age groups divided by one or more age classes often no longer shared a common set of parameters, and sometimes there were differences in call characteristics that were evident at all stages, from fledgling to juvenile to sub-adult to adult.

In terms of call sequencing, it was apparent that calls were overwhelmingly preceded and followed by the same type of call, although chatter was often preceded and followed by a screech, which was the only other call to be used with any regularity either before or after any given call of interest (Fig. 2).

2.2 Use of vocalisations by kea of different sexes and ages

In total, we obtained 1,802 analyzable calls for which we could reliably determine sex (1,044 for females and 758 for males). Of the seven call types, we only found sex differences in their frequency of use for chatter ($U = 373,346$, $P = 0.049$), where males produced chatter calls proportionally more than females (Fig. 3).

We obtained 1011 analyzable calls for fledglings, 378 calls for juveniles, 108 calls for subadults and 995 calls for adults. Of the seven types of calls described here, we

Table 2 Individual variation in kea call types

		Male			Female		
		Fledgling	Juvenile	Adult	Fledgling	Subadult	Adult
Chatter	Call length (s)	13.733	8.295		13.733		21.104
	Δ frequency 2nd H	13.004			13.004		
	Δ frequency FM	8.351			8.351		20.708
	Length FM	20.271	9.454		20.271		20.652
	# FM	24.671			24.671		15.806
	Δ frequency H-H						
Mew	Call length (s)						
	Δ frequency 2nd H						
	Δ frequency FM						
	Length FM						
	# FM						
	Δ frequency H-H						7.288
Screech	Call length (s)					17.949	28.912
	Δ frequency 2nd H	62.859					41.627
	Δ frequency FM						
	Length FM						
	# FM						
	Δ frequency H-H					21.98	39.97
Trill	Call length (s)	4.654	5.762	85.334			160.297
	Δ frequency 2nd H	10.029	10.714	110.876	10.029		78.523
	Δ frequency FM	13.357		38.741	13.357		69.121
	Length FM	17.477	8.641	67.325	17.477		34.199
	# FM	10.071	7.344	46.755			178.428
	Δ frequency H-H	7.579		71.689			40.309
Warble	Call length (s)						
	Δ frequency 2nd H						
	Δ frequency FM						11.245
	Length FM						
	# FM						
	Δ frequency H-H						

Test statistic values within indicated category different at $P < 0.05$ (Kruskal-Wallis tests; all df ≥ 2 depending on number of individuals/category). FM: frequency modulation. H: harmonic. Δ frequency H-H: Difference in frequency between two harmonics. No effects in 'screech-trill' and 'whistle'; no effect among subadult males or juvenile females (columns not included).

Table 3 Sexual variation in kea call types

	Chatter	Mew	Screech	Screech-trill	Trill	Warble	Whistle
Call length (s)	1.028/0.855*	0.634/0.564*	0.669/0.603*	1.206/1.111	0.955/0.932	0.766/0.696*	2.017/1.169
Δ frequency 2nd H	1842/2063*	1223/1163	1760/1685	2181/2000	1802/1582*	1677/1491*	4827/5183
Δ frequency FM	1394/1324	721.1/1021		1769/939*	1198/1059*	1893/1923	4202/4389
Length FM	0.057/0.054*	0.039/0.040		0.044/0.022*	0.051/0.061*	0.104/0.085*	0.181/0.150*
# FM	11/7*	0/0	0/0	8/36*	13/12*	5/5	11/8
Δ frequency H-H	987.9/1000	641.5/703.6*	933/1013*	1150/1103	931.9/963.7	1005/964.9*	2731/2537

Medians of quantitative measures by call type in males/females. Asterisk: distribution between sex categories different at $P < 0.05$ (Mann-Whitney U Test). FM: frequency modulation. H: harmonic. Δ frequency H-H: Difference in frequency between two harmonics.

Table 4　Developmental variation in kea call types

	Chatter	Mew	Screech	Screech-trill	Trill	Warble	Test Statistic (H)
Call length (s)	0.72/0.76	0.62/0.93	0.59/0.68	0.68/0.75	0.62/0.82	0.72/0.67	340.2
	0.91/1.1**	0.76/0.56*	0.66/0.68**	1.05/1.21**	0.70/0.98**	0.82/0.73**	
Δ frequency 2nd H	1921/1975	1288/830.7	1704/1807	2241/1680	1482/1710	1522/1822	47.7
	1809/1927	1325/1314**	1570/1858	1575/2174*	1570/1695**	1511/1746**	
Δ frequency FM	1340/1214	767.3/844.5		1037/1070	1304/917.3	1904/1894	98.3
	1234/1354	1109/1075		1894/833.1*	1081/1119	1965/1849	
Length FM	0.06/0.05	0.07/0.02		0.04/0.02	0.05/0.03	0.10/0.08	96.1
	0.06/0.05**	0.02/0.11*		0.05/0.02	0.04/0.05*	0.08/0.1	
# FM	4/3	0/0	0/0	9/8	7/16	5/5	383.4
	9/12**	0/0*	0/0	8/40**	11/13*	5/5	
Δ frequency H-H	973.5/984.4	682.5/665.8	1011/913.7	962.6/785.1	1002/860.0	968.9/918.2	51.9
	1052/1001	808.7/627.4	1098/977.8*	1071/1167**	880.4/947.5**	1083/989.4*	

Medians of quantitative measures by call type for age categories (fledglings/juveniles/ subadults/adults). Asterisk: distribution between age categories different at $P < 0.05$ (Kruskal-Wallis tests, $df = 3$). Double asterisk: distribution between age categories different at $P < 0.05$ and conforming to a linear developmental pattern (see text for details). FM: frequency modulation. H: harmonic. Δ frequency H-H: Difference in frequency between two harmonics.
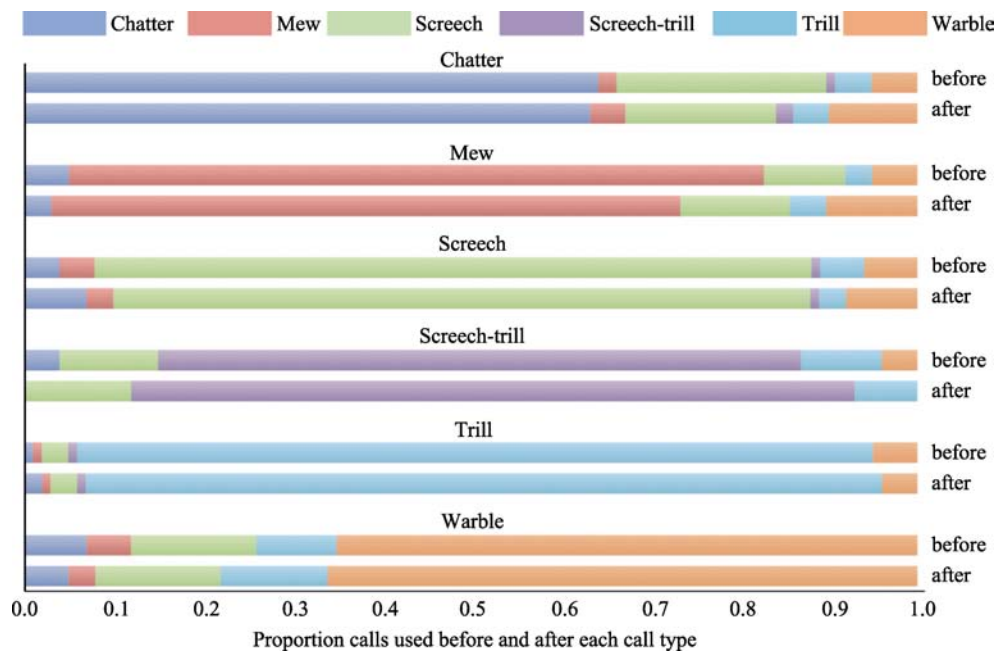

Fig. 2　Proportion of use of each call type (whistles were rare and typically singular events and so are not plotted) prior to and following any given type of call, showing that the sequencing of calls was typically of the same call type

found significant differences in the frequency with which different age groups used five of them (Fig. 4): chatter ($H_3 = 25.09$, $P < 0.001$), mew ($H_3 = 87.21$, $P < 0.001$), screech ($H_3 = 100.20$, $P < 0.001$), trill ($H_3 = 427.50$, $P < 0.001$), and warble ($H_3 = 90.80$, $P < 0.001$). For example, more than half of all calls recorded from adults were trill calls, which comprised less than 25% of all calls in all other age categories. Screeches were more commonly used by the younger age groups of kea than by subadults and adults. Subadults tended to use chatter and warble calls more frequently than other age groups (Fig. 4). No differences between age groups were discernable (Fig. 4) for screech trill ($H_3 = 3.72$, $P = 0.293$) and whistle ($H_3 = 6.81$, $P = 0.078$), although these were

very rare vocalisations and we may have been limited by sample size.

2.3　Responses to different calls

With the exception of warbles and screeches, calls were infrequently responded to with the same type of call. Additionally, depending on the sex (Fig. 5) and age (Fig. 6) of the caller, responses to any given call often differed. Screech-trills and mew calls were not common enough to analyse, but we analysed the other calls to determine whether respondents differed in the use of response calls depending on sex and age of the caller. Sex of the caller had an effect on the responding calls when these were screeches ($\chi^2_5 = 23.29$, $P < 0.001$), trills ($\chi^2_5 = 12.27$, $P = 0.031$) and chatter calls ($\chi^2_4 = $
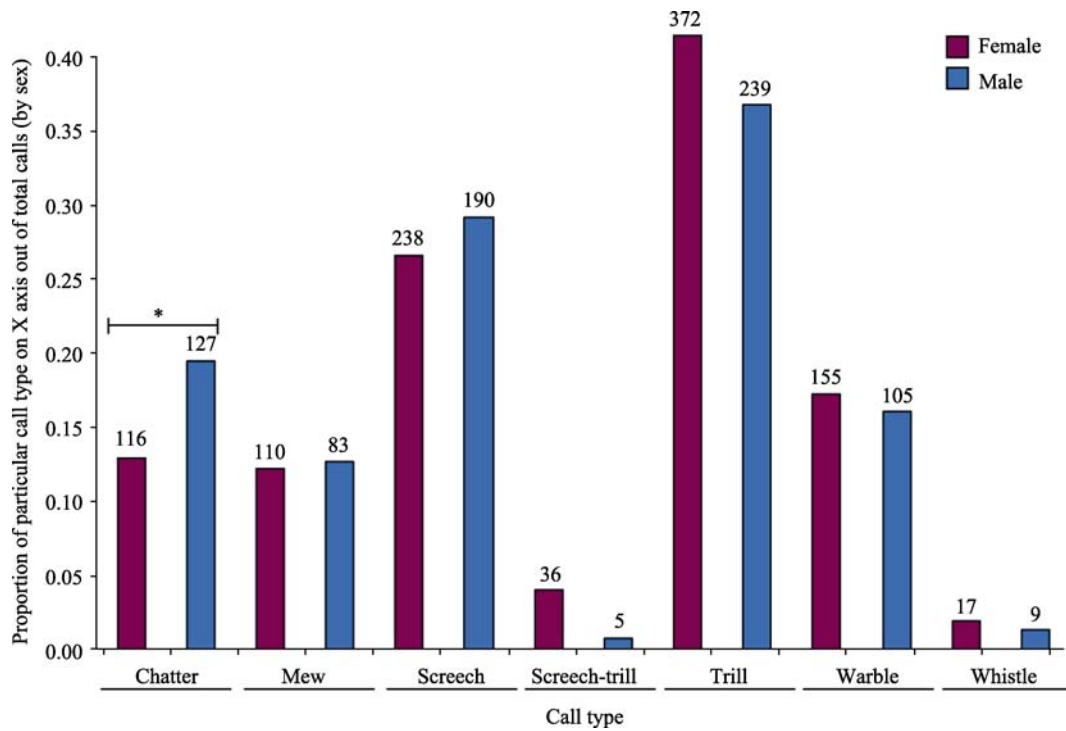
Fig. 3 Proportion of each of the seven different calls types used by either male or female kea from the total number of calls given by each sex

Significant sex differences indicated, *P < 0.05. N above each bar.
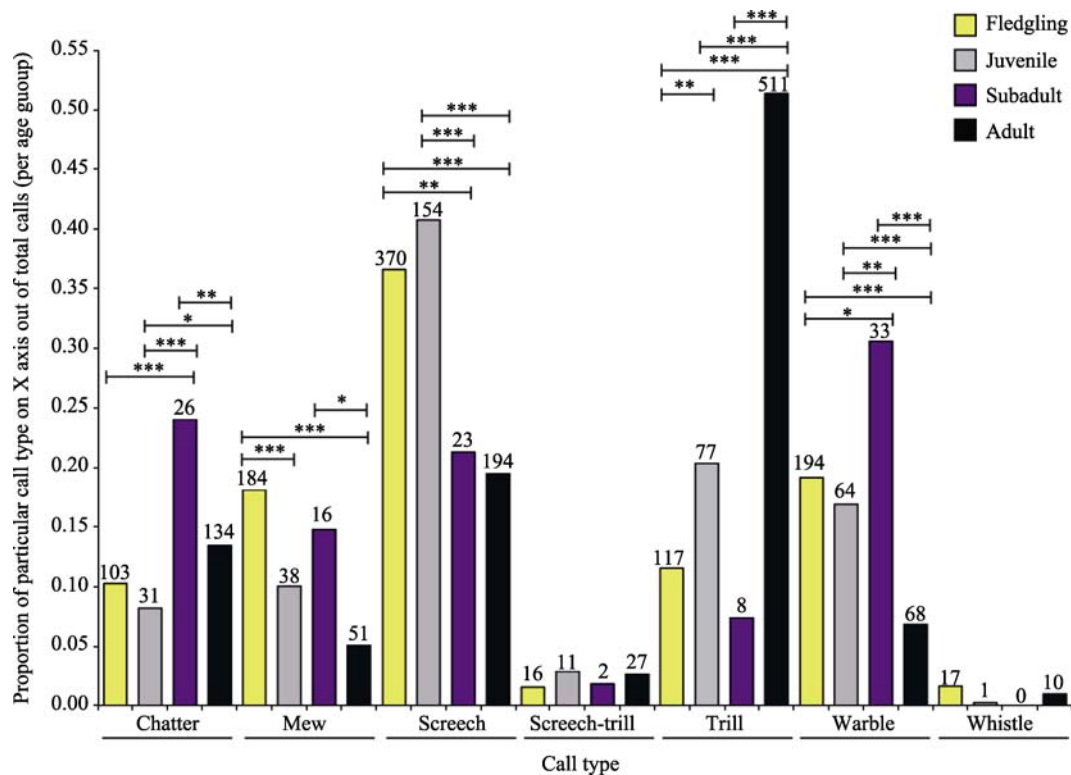

Fig. 4 Proportion of each of the seven different calls types used by different age groups of kea from the total number of calls given by each age group

For each call type, significant pairwise comparisons are indicated, *P < 0.05, **P < 0.01, ***P < 0.001. N above each bar.

24.15, $P < 0.001$), but not when the responses were warbles ($\chi^2_4 = 2.61$, $P = 0.626$). Age also had an effect on the response calls used when these were screech (χ^2_{15} = 36.58, $P = 0.002$) and chatter calls ($\chi^2_{15} = 46.82$, $P < 0.001$), but not warbles ($\chi^2_{12} = 16.35$, $P = 0.176$) or trills ($\chi^2_{15} = 15.34$, $P = 0.427$).
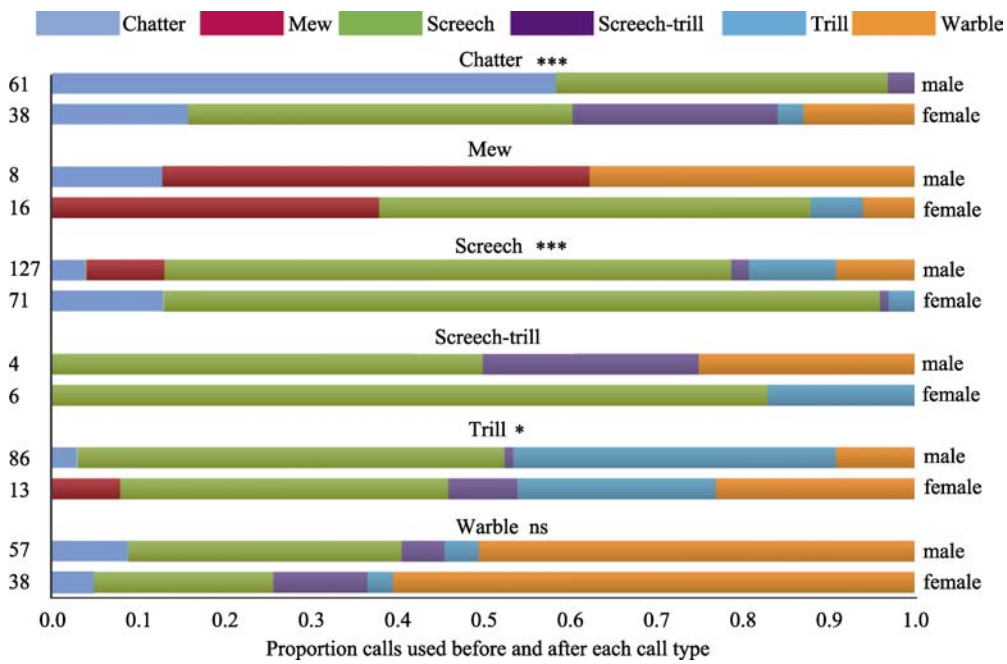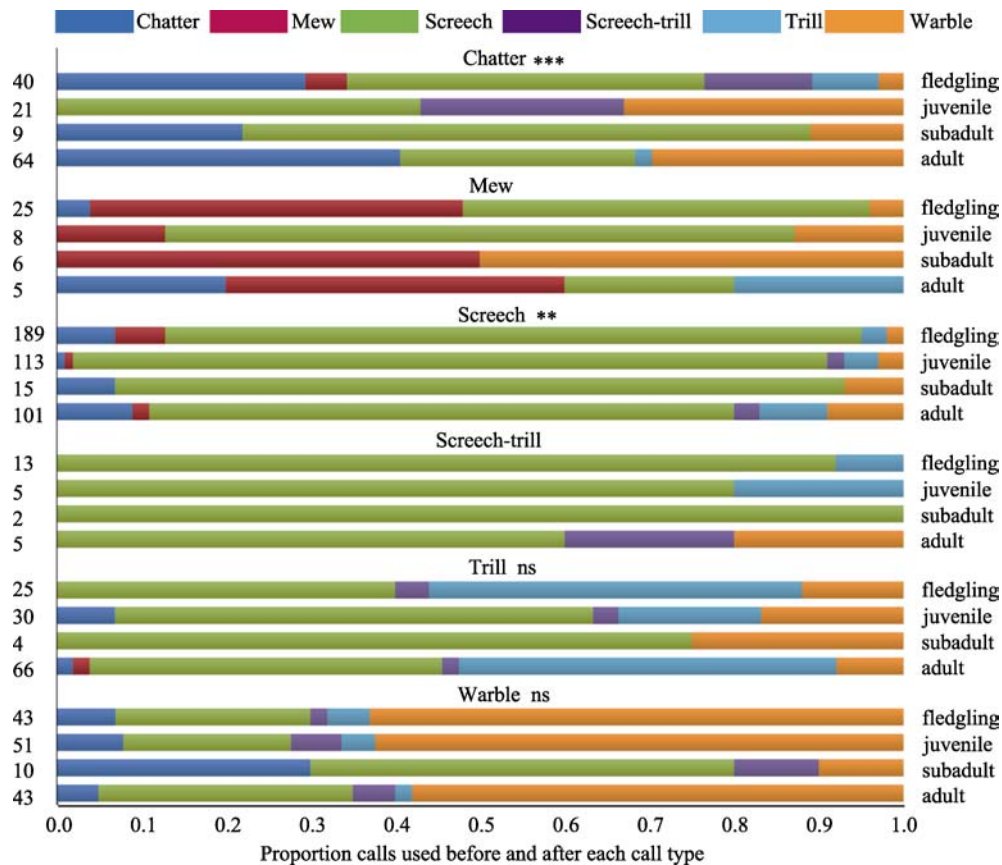
Fig. 5   Proportion of use of each call type (whistles were rare and typically singular events and so are not plotted) used as a response to any given type of call, showing the initial caller's sex
Responses to calls appear to differ depending on whether the caller is a male or a female, especially when the call is a chatter, mew or screech-trill call. Sample size permitting, results of Chi-square tests of independence for sex differences are indicated, *$P < 0.05$, ***$P < 0.001$, ns: not significant. *N* to the left of each bar.

Fig. 6   Proportion of use of each call type (whistles were rare and typically singular events and so are not plotted) used as a response to any given type of call, showing the initial caller's age group
Responses to calls appear to differ depending on caller age, particularly when the caller is a subadult kea. Sample size permitting, results of Chi-square tests of independence for age differences are indicated, **$P < 0.01$, ***$P < 0.001$, ns: not significant. *N* to the left of each bar.

3 Discussion

The vocal repertoire of kea is comprised of seven distinct call types, falling within the typical range of five to fourteen distinct vocalisations for most birds (Gill, 2007). More specifically, the number of call types is very similar to those found in other parrots, such as the blue-fronted amazon (Fernández-Juricic et al., 1998), the ground parrot (Chan and Mudie, 2004), the yellow-faced parrot (de Araújo et al., 2011) and the kaka (van Horik et al., 2007), the latter being the kea's closest relative (Grant-Mackie et al., 2003). Given the suggestion that complex communication is linked with cognitive ability (Wanker et al., 1998; Pepperberg, 1999; Bradbury et al., 2001; Wanker and Fischer, 2001; Byrne and Bates, 2007), we might expect a bird with cognitive abilities (Huber and Gajdon, 2006; Auersperg et al., 2009) rivalling those of chimpanzees *Pan troglodytes* to have a larger repertoire than we describe here. There are several factors that might explain the apparent paucity of call types among kea. This is only the first comprehensive study of the variety of vocalisations in this species, and it is possible that more calls exist which have yet to be described. However, this study is based on an unusually large sample size, so this explanation does not seem especially likely. More likely is that subtle differences, which we were unable to gauge, are used by kea to differentiate between call types, such as those in the contact and pre-flight calls of other parrot species, as suggested by Bradbury (2003). Our analysis produced no measurable differences, and calls from both behavioural categories were classified as 'screech' calls.

The calls of some animals that exhibit large repertoires are alarm calls for specific predators, because the required behavioural responses necessary for escape are different (Seyfarth and Cheney, 1986; Evans et al., 1993; Evans and Evans, 2007). However, kea evolved in the absence of terrestrial predators (Diamond and Bond, 1999), leaving them vulnerable only to avian predators and thus decreasing the need for multiple evasive strategies, and potentially the use of multiple alarm call types. Furthermore, the only potential predators present during most of its evolutionary history (Holdaway and Worthy, 1997) were the Haast's eagle (*Aquila moorei*, formerly *Harpagornis moorei*), the New Zealand falcon *Falco novaeseelandiae*, the laughing owl *Sceloglaux albifacies*, and the Eyles's harrier *Circus eylesi*. The kea was most likely too small a prey for the three metre (wing span) Haast's eagle (Bunce et al., 2005), which preyed on moa (*Dinornis* ssp.), and too large a prey for

the laughing owl and for New Zealand falcons, as even in modern times no account of a predation event has been recorded for falcons (Diamond and Bond, 1999). With potentially only a single predator, Eyles's harrier, the kea would have little need for more than one alarm call.

In addition to providing evidence of individual variation in kea calls, the clear patterns of differences for call characteristics based on sex and age are suggestive that calls may encode not only information concerning the individual, but also encode its age and sex. Most of the parameters showed age-based differences in all calls, except in whistles. Perhaps as a potential appeasement call, information relating to age is unnecessary. Sex differences were found in one to four parameters per call type, and these were often in functionally relevant parameters: all five frequency-modulated call types were sex differentiated in the length of frequency modulation, whilst the two non-frequency modulated call types differed in parameters affecting the tone, instead of the structure, of the call.

The distribution of discernable differences between individuals does not seem to follow any particular pattern. The proposed contact call, the 'screech', exhibits remarkably little individual variation, suggesting these common calls be not be individually discriminable. In contrast, the trill call, the proposed alarm call, contains significant individual variation. This may be important for young birds to adaptively respond to their parent's alarms, or even, as social birds to discriminate callers that may cry wolf. The second most 'identity discernable' call type was the 'chatter', which was most often associated with 'foraging' behaviour, which is another highly important behaviour both for young birds learning about foods from their parents and for birds foraging in a group, as kea often do (Young et al., 2012).

We found that young birds favoured the screech (contact call) as their 'default' call type (i.e., the most likely call to be uttered). As the least modulated call, this might point towards the screech being the simplest call type to produce and thus the first that a fledgling kea masters. Additionally, the lack of modulations is likely to carry the call further in windy conditions, enabling birds to maintain contact over long distances. Another explanation, compatible with the former hypotheses, is that, as a possible 'contact call' (as suggested by Bond and Diamond, 2005) produced to locate group members (Farabaugh and Dooling, 1996; Bradbury et al., 2001), the screech may be of greater importance to the more vulnerable young birds (fledglings and juve-

niles). The relatively greater use of trill calls by adults can be explained in similar fashion, with its complexity restricting its use to older birds. Alternatively, the trill might be an alarm call produced more often by adults because they are more likely to take up a sentinel position and call in response to possible threats (Diamond and Bond, 1999).

Subadults often engage in play behaviour, unlike adults. This is consistent with our finding that subadults use warbles more often than other age groups, as warbles have been coupled with play behaviour (Diamond and Bond, 1999). That younger birds also engage in play, but do not produce as many warble calls, may be associated with the difficulty of producing the frequency modulated call. Alternatively, this could simply be an age effect: fledglings and especially juveniles vocalise much more frequently than sub-adults and adults. During play, all age categories of kea vocalise almost continuously, so there should be a relative decrease in the proportion of warbles for the younger birds, which vocalise at higher frequencies during all other times when compared to the older birds.

Interestingly, the fledglings' and juveniles' warble calls were most likely responded to with warble calls, while subadults were rarely responded to using these calls. This may be a statistical artefact due to the small number of sub-adult warbles being responded to, but could also be an effect of their relatively detached role within kea society (Diamond and Bond, 1991, 1999). Certainly, it is apparent that sub-adults use calls very differently than other age groups. Nevertheless, it appears that responses to different call types are influenced by two strong trends: matching call type and 'defaulting' to a screech (contact call). The adults were generally more likely to be responded to by the same call type, which might indicate that the context in which they produced each call type was more appropriate. Nonetheless, at all ages, call types were matched as a large proportion of the responses. Correspondingly, although screech was the most frequent response to the calls of young birds (fledglings and juveniles), a large proportion of the responses to calls of all age groups was the screech call. This may be due to the habitat in which the birds live. Our measurements show that, on average wind speed was 10 ms^{-1} (RS, unpubl. data), which is more than twice the speed known to severely affect sound transmission (Foss, 1979). This could indicate that a large proportion of screech responses are due to the receiver's inability to hear the sender's call type, and they therefore respond with a possible contact call.

This is supported by the fact that kea calls contain energy at frequencies higher than those generally used by other parrots - between 2–6 kHz (e.g., Fernández-Juricic et al., 1998; Venuto et al., 2000; Chan and Mudie, 2004; Berg et al., 2011). Although the kea's congener, the kaka, produces calls with energy at frequencies up to 10 kHz (van Horik et al., 2007), all kea calls (with the exception of the whistle) were found to contain energy at frequencies above 10 kHz. As wind and other low-frequency sounds (such as waterfalls, which are common in kea habitat) are known to affect transmission of low frequency components of a signal (Foss, 1979; Slabbekoorn and den Boer-Visser, 2006), it is possible that the high frequency harmonics of kea vocalisations enable the transmission of the signal in an acoustically noisy environment. On-going research into attenuation levels of kea calls over distance and the hearing thresholds of kea should shed light on this possibility.

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