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Alan B. Bond

University of Nebraska - Lincoln, abond1@unl.edu

Judy Diamond

University of Nebraska - Lincoln, jdiamond1@unl.edu

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Geographic and ontogenetic variation in the contact calls of the kea (*Nestor notabilis*)

Alan B. Bond¹ and Judy Diamond²

¹ School of Biological Sciences, University of Nebraska–Lincoln,
Lincoln, Nebraska, 68588 USA

² University of Nebraska State Museum, University of Nebraska–Lincoln,
Lincoln, Nebraska, 68588 USA

Corresponding author – A. Bond, abond@unl.edu

Summary

Regional and ontogenetic variation in the contact calls of the kea (*Nestor notabilis*), an omnivorous and socially complex New Zealand parrot, were examined throughout the range of the species. We recorded samples of kee-ah contact calls from sixteen resident adults and eleven juveniles and demonstrated significant differences between age classes in the acoustic form of the vocalization. Canonical correlation analysis revealed a gradient in the form of the kee-ah call in both adults and juveniles along and across the escarpment of the Southern Alps, the primary longitudinal mountain range on the South Island of New Zealand. Although the juvenile call varies geographically along the same axes as the adult version, the aspects of the call that vary geographically are strikingly different, suggesting that the variation results from independent processes of vocal learning in the two age classes. A similar analysis of squeal vocalizations, which are only produced by juveniles, found even greater levels of geographic variation. We suggest that the immediate social environment may serve as the primary factor shaping the vocal patterns of both juveniles and adults, producing localized homogeneity in call form within each age class.

Keywords: Psittaciformes, Aves, vocal communication, ontogeny, development, regional dialects

Introduction

Studies of the vocal behavior of wild parrots can provide a novel perspective on the adaptive significance of vocal communication in birds. Unlike many passerines, vocal learning in parrots is not generally

restricted to early stages of development; vocalizations in many species remain plastic throughout life, susceptible to modification or augmentation in response to social influences (Nottebohm, 1970; Farabaugh & Dooling, 1996; Brown & Farabaugh, 1997; Hile et al., 2000). Vocal mimicry, both intra- and interspecific, also appears to be far more common in parrots than in songbirds (Kroodsma & Baylis, 1982; Rowley & Chapman, 1986; Cruickshank et al., 1993). The neurological bases for vocal control and vocal learning in parrots differ significantly from those in songbirds (Ball, 1994; Striedter, 1994; Brenowitz, 1997), suggesting that vocal cognition has evolved independently in the two groups and may serve substantially different functions (Nottebohm, 1972).

Research on the vocal communication of parrots, particularly among wild birds, has been very limited, however (Baker, 2000, 2001; Bradbury, 2003). Of the more than 350 species of parrots (Juniper & Parr, 1998), the vocal behavior of less than a dozen has been systematically investigated in the field (e.g. Brereton & Pidgeon, 1966; Pidgeon, 1981; Martella & Bucher, 1990; McFarland, 1991; Fernández-Juricic et al., 1998; Fernández-Juricic & Martella, 2000; Venuto et al., 2000; Wirminghaus et al., 2000). Previous studies of parrot vocalizations show marked variation both between individuals and across geographic regions. Evidence for individual discrimination of contact calls has been shown in spectacled parrotlets (*Forpus conspicillatus*; Wanker & Fischer, 2001), white-tailed black cockatoos (*Calyptorhynchus funereus*; Saunders, 1983), galahs (*Cacatua roseicapilla*; Rowley, 1980), and budgerigars (*Melopsittacus undulatus*; Ito & Mori, 1999). Regional variation in the acoustic form of specific call types has been described in yellow-naped Amazons (*Amazonia auropalliata*; Wright, 1996; Wright & Wilkinson, 2001), orange-fronted conures (*Aratinga canicularis*; Bradbury et al., 2001), ringnecked parrots (*Bernardius zonarius*; Baker, 2000) and galahs (Baker, 2003). In several of these species, playback studies have subsequently demonstrated differential responding to local and distant dialects (Wright & Dorin, 2001; Vehrencamp et al., 2003).

Many parrots have a relatively prolonged juvenile phase, entailing persistent structured associations among young birds (Stamps et al., 1990; Garnetzke-Stollman & Franck, 1991; Munn, 1992; Wanker et al., 1996, 1998; Diamond & Bond, 1999, 2003). In species with an extended juvenile period and identifiable morphological and behavioral stages, we might expect to find evidence of juvenile vocalizations that are not just approximations to adult calls, but that exhibit their own characteristic

acoustic forms and that display geographic variation in parallel to those of adult birds. Vocal learning may, thus, play a different role in parrot societies than it does among oscine passerines, where the “subsong” of young birds is refined over the course of ontogeny by progressive convergence onto a prototypical adult vocal pattern (Marler & Peters, 1982).

In this study we examine regional and ontogenetic variation in the contact calls of the kea (*Nestor notabilis*), an omnivorous parrot endemic to alpine tussock grass and montane beech forests on the South Island of New Zealand (Jackson, 1960, 1963). In contrast to many other parrots, keas exhibit delayed maturation and a greatly extended juvenile stage (Diamond & Bond, 1991, 1999). Young birds are not directly fed by their parents after the first six months, but juveniles are treated leniently by even unrelated adults for two to three years after fledging. During this time the juveniles show evidence of an identifiable behavioral repertoire, a kind of “youth culture” that is independent of adult behaviors and is primarily associated with peer interactions. Juvenile keas spend much of their time in social play and object exploration, and like human gangs, they show a strong dominance structure in their flocks where outsiders are met with vigorous aggression (Diamond & Bond, 1999, 2003, 2004).

Keas are uncommon and thinly distributed throughout the national parks along the Southern Alps, the mountain range that divides the South Island into eastern and western geographical provinces (Bond & Diamond, 1992; Diamond & Bond, 1999; Elliott & Kemp, 1999). Food resources in this high alpine habitat are unreliable, evanescent, and sparse, so keas forage on nearly anything edible in their environment (Brejaart, 1988; Diamond & Bond, 1999; Higgins, 1999; Cuthbert, 2003). Unlike many other parrot species, keas are relatively conservative in their movements and do not form large, anonymous flocks, at least as adults, nor do they assemble in large numbers at traditional night roosts. Aside from temporary aggregations at carcasses, rubbish dumps, and ski resorts, keas generally form small feeding flocks of related or familiar individuals (Diamond & Bond, 1991, 1999; Higgins, 1999). In spite of intensive research on other aspects of their biology, however, kea vocalizations have never been systematically described (Higgins, 1999). This study compares the geographic variation and structure of the adult “kee-ah” contact call to that of the juvenile version of the same call. In addition, we examine the geographic variation of the “squeal,” a separate, juvenile-specific contact call that is not used by adults.

Methods

Recording

We recorded adult and juvenile vocalizations as part of a population survey of keas at sites in six national parks on the South Island of New Zealand in 2000-2003. Keas produce a broad range of vocalizations in different behavioral contexts, but the most frequent and characteristic vocalization in adults is the "kee-ah" call. This is the primary general-purpose contact call of the species, used to establish communication between widely separated individuals (Higgins, 1999).

To obtain a motivationally consistent, statistically comparable sample of kee-ah calls from adults over a broad geographic range, we elicited responses from resident birds on their breeding territories by playback of recorded vocalizations (Marion et al., 1981; Falls, 1981; McGregor, 1992). The most effective playback stimulus proved to be a recording made from keas in Arthur's Pass National Park in 1991. The recording consists of a massed chorus of "bleat-trills," a call variant that indicates excitement or the imminent departure of a feeding flock (Diamond & Bond, 1999). The stimulus tape was broadcast for 30 s through a 20-watt remote-controlled game caller (Anchor Audio Mini-Vox), followed by a 5-min assessment period to listen for responses. If a kea responded to the playback, the playback stimulus was shut off, and the bird's subsequent actions and vocalizations were recorded on videotape. Vocalizations were recorded in CD-quality sound (48 kHz, 16-bit) using an Audio-Technica AT4071a shotgun microphone mounted on a Sony TRV900 digital video camera. In all, we acquired samples of five or six kee-ah calls from each of 16 adult individuals, covering virtually the entire geographic range of the species.

In the course of our survey, we also recorded vocalizations from fledgling and juvenile birds. Juveniles do not respond reliably to playback of kee-ahs or bleat-trills, except when in the company of their parents; the sample of juvenile subjects was, therefore, obtained primarily on the basis of spontaneous vocalizations. We acquired samples of five or six kee-ah vocalizations from each of 11 juveniles from across the geographic range of the species. "Squeal" calls, which constitute a major component of the vocalizations of small juvenile flocks, serve as an additional form of contact vocalization, in that they are invariably echoed by other juveniles in the vicinity. In the course of our survey, we recorded five successive squeal calls in single-bird ses-

sions from ten juveniles, six from Arthur's Pass National Park and four from Mt. Cook National Park.

Data extraction

Sound recordings were converted to computer files and rectified with SoundForge (version 6.0, Sound Forge, Inc., 2003) sound editing and noise reduction software to remove recording artifacts and, in some cases, to reduce the levels of low-frequency background noise. Calls were selected for formal analysis only if they were clear and distinct, with minimal background noise and no confounding, overlapping vocalizations from other birds. We discriminated acoustic structures based on a set of descriptive measures extracted by hand from sonagrams that were generated from all sampled calls with SoundForge (Williams & Slater, 1991). To maximize resolution of the fine structure of the calls, we used a 1024-point FFT with 50% overlap and a Blackman-Harris smoothing window, taking 10,000 samples per fixed, five-second interval and displaying a frequency range between 0 and 12,000 Hz.

Kea vocalizations are harmonically rich, with most of the acoustic energy being carried in the second (rarely the third) harmonic. To maintain comparability across individual samples, we extracted coordinates of critical points from the second harmonic of each sampled call, using SigmaScan (version 5.0, SPSS, Inc., 1999). For kee-ah calls, we digitized the beginning and end points of the call, as well as the points at which the call crossed a superimposed grid spaced at 75 ms intervals. As descriptive measures, we calculated the duration of each call, the highest and lowest frequencies exhibited, and the temporal position of the highest frequency value (relative to the beginning of the call). In addition, we calculated slope values between each pair of successive gridded points and extracted the maximum, minimum, median, and interquartile range of the slope values, along with their temporal position in the call, a total of ten descriptive measures.

Because of their large, irregular frequency modulations, squeal vocalizations required a somewhat different strategy for data extraction. Squeals were analyzed by digitizing the successive local frequency maxima and minima, as well as the beginning and end points of the call. From these data, we extracted the call duration, the beginning and ending frequencies, the frequency range, the slope of the relationship between frequency and duration, the median and interquartile range of

the amplitudes and wavelengths of frequency modulations within each call, and the correlations between amplitude, wavelength, and time since the beginning of the call, a total of eleven descriptive measures.

Analysis methods

To test for developmental differences in the kee-ah call, we selected eleven adults and eleven juveniles from locations across the range of the species. To avoid confounding geographic and ontogenetic effects, the adult birds were chosen so as to balance the juvenile sample with respect to geographic location. We tested for ontogenetic effects using a canonical discriminant analysis (SAS CANDISC version 8.0, SAS, Inc., 1999) of the ten descriptive measures from the individual calls, generating a weighted linear combination of response variables that maximally separated adult and juvenile groups. Using individual calls as the unit of analysis produces the most accurate estimates of the variable weights and avoids the possibility of distortions due to variation in average call morphology across individuals. Because this approach pools observations from different individuals, however, and because the number of calls sampled per individual were not uniform, the Type I error rate could conceivably have been inflated due to lack of independence (Leger & Didrichsons, 1994; Moskowitz & Hershberger, 2002). We therefore conducted a validation analysis, comparing the scores from adults and juveniles in a nested one-way ANOVA, using hierarchical linear modeling (HLM version 5.0, SSI, Inc., 1999; Osborne, 2000; Raudenbush & Bryk, 2002).

We quantified geographic variation in kee-ah calls from adults and juveniles separately using canonical correlation analysis (SAS CANCORR version 8.0, SAS, Inc., 1999; Bradbury et al., 2001; Baker, 2003), which generates weighted linear combinations (termed “canonical variates”) of the input variables that maximize the correlation between sets of predictor and response variables. For predictors, the latitude and the longitude of each location were determined with GPS and converted to Euclidean distances. Because initial results suggested that call variation tended to occur along the Alpine Fault, the plate boundary that defines the primary escarpment of the Southern Alps, we rotated the location coordinates to express linear distances along vs. across the fault line. For response variables in the analysis of kee-ah calls, we used the ten descriptive measures from each call recorded from the sampled individuals. As in the ontogeny analysis, we subsequently validated our

findings, comparing the scores from individuals from the northwest of the Alpine Fault to those from the southeast using hierarchical linear modeling. Because our sample of squeal calls came from just two different locations, we tested for geographic variation in squeals using a canonical discriminant analysis of the eleven descriptive measures from the individual calls, and, as in the kee-ah analyses, we subsequently validated the discriminant results using hierarchical linear modeling.

Results

Structure of kee-ah and squeal calls

Kee-ah contact calls are among the most frequent vocalizations of keas in the field. They are produced by birds of all age groups, but they are most conspicuously associated with resident adults. Keas commonly reply with kee-ahs in response to contact calls from other individuals, even birds that are hundreds of meters away, and they readily respond to playback of calls recorded from distant regions. Throughout the 600-km range of the species, resident adults responded to our playback of Arthur's Pass calls as vigorously and consistently as they did to the spontaneous calls of keas from their own districts. In adults, broadcast kee-ah calls are produced at very high volume and sustained duration (averaging about 800 ms; Table 1) and are repeated at roughly 6-8 s intervals. The vocalization exhibits an initial, rapid frequency rise (the "kee") to a peak of about 2700 Hz in the second harmonic, with a subsequent, gradual downward modulation (the "ah"), terminating at about 1400 Hz (Table 1; Figure 1a). The downward portion is generally negatively curved, with the steepest declines at or near the end of the call (mean position of minimum slope = 81%; Table 1).

Juvenile keas produce kee-ah calls that are generally similar both in acoustic structure and in context to those of adults (Table 1; Figure 1b), but juvenile calls are usually shorter in duration (about 700 ms; Table 1) and more variable in their frequency modulation (Table 1; Figure 1b). Kee-ah calls are not predictably elicited from juveniles by playback in the absence of resident adults. Squeals, in contrast, are by far the most frequent contact calls produced by young birds, and they are highly facilitative, in that they are invariably echoed by other juveniles in the vicinity. We found that playback of squeal calls was particularly attractive to juvenile keas, drawing them in to the speaker and eliciting extensive squeals in response.

Table 1. Age differences in the structure of kee-ah calls. Means and 95% confidence limits of the descriptive measures of the calls, separated by age class, along with their correlations with the canonical discriminant variate. Measures with correlations accounting for more than 5% of the variance are shown in boldface

Measure	Adults (<i>N</i> = 59)	Juveniles (<i>N</i> = 58)	Correlation
Med Slope	-0.87 ± 0.15	-1.12 ± 0.19	0.282
QR Slope	1.63 ± 0.18	3.29 ± 0.67	-0.602
Duration (s)	0.857 ± 0.050	0.697 ± 0.034	0.645
Max Freq (kHz)	2.745 ± 0.085	2.616 ± 0.063	0.324
Min Freq (kHz)	1.436 ± 0.070	1.280 ± 0.051	0.467
Posn Max Freq	0.075 ± 0.020	0.078 ± 0.018	-0.032
Max Slope	15.60 ± 5.54	11.54 ± 2.55	0.180
Min Slope	-13.34 ± 2.72	-12.88 ± 2.38	-0.034
Posn Max Slope	0.034 ± 0.007	0.038 ± 0.006	-0.120
Posn Min Slope	0.814 ± 0.059	0.531 ± 0.061	0.778
Prop. of Variance (Ttl)			0.184

Squeals appear to be produced exclusively by fledglings and juveniles; we have never recorded a confirmed instance of squealing by adults or even subadults. The calls are characterized by a series of uneven oscillatory frequency modulations with a very low periodicity

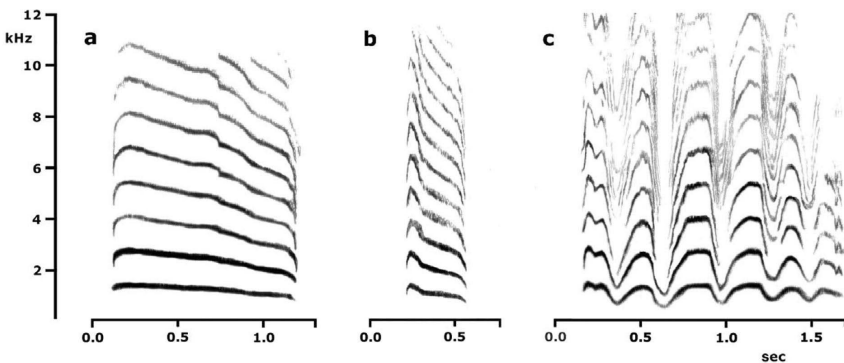


Figure 1. Typical forms of kea contact calls. (a) Adult kee-ah, recorded February 26, 2000, in Kahurangi National Park in response to playback; (b) Juvenile kee-ah, recorded January 12, 1991, in Arthur's Pass National Park; (c) Juvenile squeal, recorded January 14, 1991, in Arthur's Pass National Park.

(about 5-8 cps; Figure 1c) and an amplitude of 500-600 Hz (Table 4). The duration of the call averages 800-900 ms, and the median frequency is level (at about 2000 Hz) or very slightly declining across the course of the call (average frequency slope = -0.6; Table 4). The amplitude of the oscillatory modulations generally tends to increase from the beginning to the end of the vocalization (average correlation between amplitude and time = 0.3; Table 4).

Ontogeny of kee-ah calls

To analyze for differences in the structure of adult and juvenile kee-ah calls, we controlled for geographical effects by reducing the comparison sample of adults to 11 individuals that balanced the juvenile sample with respect to geographic location. Canonical discriminant analysis between these adult and juvenile samples demonstrated a significant age-dependent difference in the form of the kee-ah contact call (Wilks' λ : $\eta^2 = 45\%$, $F(10, 106) = 8.52$, $p < 0.001$). Confirmatory hierarchical linear modeling of the canonical variate found that a significant proportion of the variance among calls was accounted for by age-related differences (43%, $\chi^2(1) = 37.4$, $p < 0.0001$), indicating that the results of the discriminant analysis could not be attributed to sampling artifacts.

Canonical redundancy analysis indicated that there were clear ontogenetic differences in six of the ten measures (Table 1): Adult calls were longer in duration than those in juveniles, and both the maximum and the minimum frequencies were also generally higher. Most strikingly, however, adult kee-ah calls were flatter, showing less frequency modulation, and the later, descending portion of the call was usually roughly linear or downwardly curved. Juvenile kee-ah calls commonly showed an upward curvature in the descending phase, with the result that the position of the minimum slope in adults occurred much later in the call than in juveniles. The proportion of aggregate variance in the descriptive measures that was explained by ontogenetic differences was over 18%, indicating that the differences in form were pervasive across individuals at all locations. These results suggest that juvenile kee-ah calls are not simply amorphous approximations of the adult version, but that they show consistent and distinctive features that are not present in the corresponding adult vocalization.

Table 2. Geographic differences in the structure of adult kee-ah calls. Means and 95% confidence limits of the descriptive measures of the calls, separated by region, along with their correlations with the geographic canonical variate. Measures with correlations accounting for more than 5% of the variance are shown in boldface.

Measure	NW Region (<i>N</i> = 27)	SE Region (<i>N</i> = 54)	Correlation
Med Slope	-0.64 ± 0.18	-1.03 ± 0.15	0.339
QR Slope	1.30 ± 0.25	1.80 ± 0.23	-0.421
Duration (s)	0.957 ± 0.063	0.813 ± 0.061	0.287
Max Freq (kHz)	2.634 ± 0.129	2.717 ± 0.077	-0.140
Min Freq (kHz)	1.443 ± 0.081	1.419 ± 0.070	-0.062
Posn Max Freq	0.107 ± 0.033	0.066 ± 0.016	0.114
Max Slope	15.77 ± 6.07	14.96 ± 5.85	0.093
Min Slope	-12.49 ± 3.27	-11.72 ± 2.65	-0.187
Posn Max Slope	0.035 ± 0.007	0.032 ± 0.007	0.032
Posn Min Slope	0.881 ± 0.094	0.788 ± 0.069	0.178
Prop. of Variance (Ttl)			0.049

Table 3. Geographic differences in the structure of juvenile kee-ah calls. Means and 95% confidence limits of the descriptive measures of the calls, separated by region, along with their correlations with the geographic canonical variate. Measures with correlations accounting for more than 5% of the variance are shown in boldface.

Measure	NW Region (<i>N</i> = 19)	SE Region (<i>N</i> = 40)	Correlation
Med Slope	-0.65 ± 0.25	-1.32 ± 0.22	0.409
QR Slope	3.21 ± 1.54	3.39 ± 0.67	-0.041
Duration (s)	0.726 ± 0.061	0.687 ± 0.041	0.109
Max Freq (kHz)	2.457 ± 0.076	2.689 ± 0.075	-0.422
Min Freq (kHz)	1.321 ± 0.048	1.257 ± 0.070	0.199
Posn Max Freq	0.097 ± 0.038	0.075 ± 0.023	0.155
Max Slope	13.94 ± 4.81	10.53 ± 2.91	0.231
Min Slope	-14.77 ± 4.20	-11.89 ± 2.82	-0.165
Posn Max Slope	0.036 ± 0.009	0.039 ± 0.007	-0.279
Posn Min Slope	0.661 ± 0.064	0.476 ± 0.079	0.375
Prop. of Variance (Ttl)			0.072

Geographic variation in kee-ah calls

We found a significant relationship between the form of both adult and juvenile kee-ah calls and their geographic location across the full range of the species on the South Island. However, the pattern of geographic variation in the call was distinctly different in the two age groups. The first canonical variate of the geographic predictor measures correlated strongly with distance both along (adult $r^2 = 0.68$; juvenile $r^2 = 0.76$) and across (adult $r^2 = 0.92$; juvenile $r^2 = 0.77$) the Southern Alps. The canonical correlation between the predictor and response variates was significant (Wilks' λ : adult $\eta^2 = 33\%$, $F(20, 138) = 2.37$, $p < 0.002$; juvenile $\eta^2 = 55\%$, $F(20, 92) = 3.11$, $p < 0.001$), indicating a strong relationship between geographic position and the linear composite of the call measures. For both age groups, these were the only canonical variates with significant interpretive value, implying that call variation occurred only along a single multivariate dimension. Canonical redundancy analysis indicated that the proportion of variance in the descriptive measures that was explained by the geographic predictor variate was roughly 5% in adults and 7% in juveniles (Tables 2 and 3).

To confirm that the apparent geographical effects were actually attributable to differences between individuals across locations, we conducted a nested analysis of variance, comparing birds from northwest of the Alpine Fault to those from the southeast using hierarchical linear modeling. A significant proportion of the variance between calls was accounted for by regional differences (adults 17%, $\chi^2(1) = 7.78$, $p = 0.006$; juveniles 41%, $\chi^2(1) = 19.2$, $p < 0.001$), indicating that the results of the canonical correlation analysis could not be attributed to sampling artifacts. Mean values of the canonical response variates by individual are plotted in Figure 2, separately for adults and juveniles, in approximately the locations from which they were recorded.

To determine which descriptive measures of the kee-ah call varied geographically, and whether the pattern of variation was consistent across age groups, we examined correlations within age groups between each of the ten descriptive measures and the predictor variate (Tables 2 and 3). The direction of the correlations between the descriptive measures and the geographic variate were roughly correspondent in adults and juveniles, but the magnitudes of the correlations were often strikingly different, with juveniles showing clear geographic effects in five of the ten measures, only one of which was shared with the

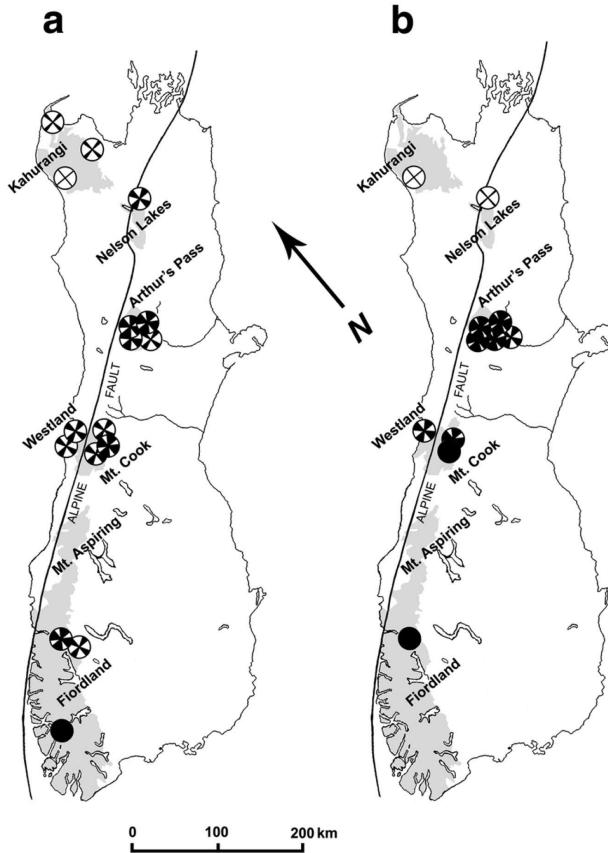


Figure 2. South Island of New Zealand, showing data collection locations at a range of sites in six national parks along the Southern Alps. Kee-ah contact calls were recorded from each of 16 resident adult keas and 11 juveniles, and ten descriptive measures were extracted from each call. Pie symbols indicate the relative magnitude of the mean scores for each individual on the first canonical variate of the descriptive measures, plotted at the approximate recording location for adults (**a**) and juveniles (**b**). Note the gradation in scores from southeast to northwest.

adults. In adults, kee-ah calls from the northwest were generally longer in duration than those from the southeast and flatter and less variable in their frequency profiles, with less extreme median slopes and smaller slope quartile ranges (Table 2). The median slope difference also showed up in juveniles (Table 3), but the other juvenile geographic differences were in an entirely different set of measures. Juvenile kee-ahs from the northwest were lower in their maximum frequency than those

Table 4. Geographic differences in the structure of juvenile squeal calls. Means and 95% confidence limits of the descriptive measures of the calls, separated by region, along with their correlations with the canonical discriminant variate. Measures with correlations accounting for more than 5% of the variance are shown in boldface.

Measure	Mt. Cook (<i>N</i> = 20)	Arthur's Pass (<i>N</i> = 29)	Correlation
Med FM Amp (kHz)	0.593 ± 0.107	0.531 ± 0.109	0.175
Med FM Wvlen (s)	0.231 ± 0.035	0.160 ± 0.018	0.761
QR FM Amp (kHz)	0.496 ± 0.113	0.502 ± 0.098	-0.017
QR FM Wvlen (s)	0.133 ± 0.032	0.102 ± 0.016	0.409
Duration (s)	0.821 ± 0.103	0.954 ± 0.149	-0.294
Freq Slope	-0.654 ± 0.314	-0.644 ± 0.212	-0.012
Start Freq (kHz)	2.290 ± 0.140	2.228 ± 0.154	0.126
End Freq (kHz)	1.920 ± 0.145	1.742 ± 0.114	0.419
Freq Range (kHz)	0.436 ± 0.120	0.515 ± 0.124	-0.193
Amp / Time Corr	0.306 ± 0.178	0.341 ± 0.141	-0.069
Wvlen / Time Corr	0.141 ± 0.229	0.207 ± 0.158	-0.110
Prop. of Variance (Ttl)			0.101

from the southeast and showed a more abrupt initial rise. In addition, the upward curvature in the descending phase of the call that is characteristic of juvenile kee-ahs (Table 1) was less conspicuous in juveniles from the northwest, with the result that the position of the minimum slope in these birds occurred later in the call than in juveniles from the southeast (Table 3). In spite of the fact that both adults and juveniles showed geographic differences in call structure, therefore, there was little evidence of a common pattern across age groups in geographic variations in call morphology.

Geographic variation in squeal calls

Canonical discriminant analysis within juveniles, contrasting birds from Mt. Cook National Park with birds from Arthur's Pass, revealed a significant relationship between the form of the squeal contact call and the geographic location (Wilks' λ : $\eta^2 = 41\%$, $F(11, 37) = 2.36$, $p < 0.03$). Confirmatory hierarchical linear modeling of the canonical variate found that a significant proportion of the variance among calls was accounted for by geographic location (37% , $\chi^2(1) = 15.7$, $p < 0.001$), indi-

cating that the results of the canonical discriminant analysis could not be attributed to sampling artifacts. Overall, about 10% of the variance was explained by geographic differences. The canonical structure (Table 4) indicated that, in comparison to birds from Mt. Cook, juvenile keas from Arthur's Pass National Park displayed shorter and more uniform wavelengths in their oscillatory frequency modulations and produced longer duration calls that terminated at a lower frequency. That juvenile squeal calls exhibited geographic variation of this magnitude is particularly striking, given that the two locations were only 150 km apart and on the same side of the Southern Alps.

Discussion

This study found significant geographic variation in the acoustic form of the kee-ah contact call, which is produced, in different forms, by both adults and juveniles. Keas of both age classes from the northern and western parts of the South Island differed significantly in the forms of their vocalizations from those from more southern areas. Birds from Kahurangi, Westland, and Nelson Lakes National Parks, which lie to the north and west of the Alpine Fault, produced kee-ah calls that were significantly different, along several dimensions, from those of birds from the southeast, including Arthur's Pass, Mt. Cook, and Fiordland National Parks (Figure 2). Consistent differences were also evident in the form of the squeal vocalizations produced by juveniles in Arthur's Pass and Mt. Cook National Parks. The distribution pattern of the call form across the entire 600-km range of the species suggested clinal variation, rather than discrete dialects. This was most apparent in the calls from birds from geographically intermediate locations, such as Westland or Nelson Lakes National Parks, which were generally intermediate in form, rather than adhering to one or another distinctive prototype.

Comparable levels of geographic variation have been recorded from several other species of wild parrots (Wright, 1996; Baker, 2000, 2003; Bradbury et al., 2001). In their pattern of geographic variation, keas appear to be more similar to orange-fronted conures (Bradbury et al., 2001), which also display a graded variation in call form, than to yellow-naped amazons (Wright, 1996), which show clear distinctions in call forms between neighboring regions and relative uniformity within regions. Whether this distinction in the continuity of the geographic

gradient reflects a meaningful difference in call function is not clear (Bradbury et al., 2001). One indication of the adaptive significance of variation in vocal morphology is provided by the responses of individuals to local and distant call variants. In this regard, keas appear to be far more tolerant of deviant vocal forms than either of the Central American parrot species. Playback studies of both amazons (Wright & Dorin, 2001) and conures (Vehrencamp et al., 2003) found maximal responding only to local contact calls; vocalizations from other, more distant regions were responded to at far lower intensities. It is noteworthy that resident adult keas from throughout the range of the species responded with equal vigor and persistence to playback of a single call tape recorded from Arthur's Pass National Park.

What was most striking in our findings was the presence of juvenile-specific vocalizations that were different from the contact calls of adults, but that nevertheless exhibited a similar gradient of geographic variation. The juvenile kee-ah call differs significantly from that of adults, and although it varies geographically along the same gradients as the adult version, the components of the call that vary geographically are also different in juveniles and adults. The difference in pattern of distribution suggests that the variation results from an independent process of vocal learning. The squeal call is produced only by juveniles and also shows geographic variation, even over relatively short distances. Variation in the form of both the juvenile kee-ah call and the squeal vocalization suggests that local features of contact calls are acquired very early in keas, perhaps within several months of leaving the nest. More importantly, because adults do not produce squeals and do not show juvenile characteristics in their kee-ah calls, this vocal learning in juveniles must be based on the calls, not of local adults, but of juvenile peers, a form of call convergence within juvenile society (similar to budgerigars: Brittan-Powell et al., 1997). The alternative interpretation, that the vocal differences between populations reflect an underlying genetic gradient, rather than a process of local learned convergence in contact calls, tends to be neglected in groups such as parrots that are widely known as good imitators. Wright & Wilkinson (2001) conducted a careful evaluation of the population genetics of yellow-fronted amazons and found no indication that their dialects were based on genetic differences. A similar test of geographic variation in kea genetics would, however, be valuable, especially given the apparent correspondence in the directions of the juvenile and adult vocal gradients.

If kea calls are, in fact, learned by social convergence, however, the occurrence of a distinctive juvenile vocal repertoire implies that the form of the adult kee-ah call, which also varies geographically, must be acquired at a later stage. The developmental process thus appears to occur in several successive waves: Fledglings have a predisposition to produce a generalized kee-ah contact call. When they first achieve independence in juvenile flocks, they adopt the form of call that is being used by other juveniles in the area. Later, when they have dispersed to a new location and settled down as adults, their kee-ah call is reformed by "social conformity" (Bradbury et al., 2001) to resemble that of the resident population of breeding adults. Similar call convergence among adult individuals is known or at least suspected in other species of parrots (Nottebohm, 1970; Brown & Farabaugh, 1997; Bartlett & Slater, 1999; Hile et al., 2000; Vehrencamp et al., 2003), as well as in several other groups of birds (Brown et al., 1988; Nowicki, 1989; Price, 1998; Hopp et al., 2001).

The functional significance of vocal social conformity is not clear, but traditional arguments for the maintenance of adult dialects based on access to food resources or successful pair formation (Catchpole & Slater, 1995) appear inadequate when applied to kea flocks, particularly to flocks of juveniles. In interactive playback experiments, Vehrencamp et al. (2003) found indications that some wild conure flocks had begun to converge on the vocal forms provided in their experimental playback stimuli. They interpreted these changes as evidence that the form of the contact call was a signal of flock affiliation, and that short-term call "morphing" by recipient birds reflected a desire or intention to join the new flock. If this is true, then vocal forms may be even more pliant and variable in parrots than our rough geographic and ontogenetic categories can reflect. There are clear analogies to human societies, where adoption of novel linguistic patterns is commonly required for acceptance into local social groups, particularly among adolescents. The immediate social environment and the effort to be accepted into it can, thus, be viewed as the primary factors shaping the vocal patterns of both juveniles and adults, producing localized homogeneity in call form within each age class. These socially induced patterns would then be modified by diffusion and dispersal between local populations, generating a continuous gradient.

Unlike conures, however, keas exhibit delayed maturation, breeding for the first time at roughly four or five years of age (Jackson, 1962, 1963). Before they settle down and begin reproduction, young keas

thus spend a considerable period flocking with other juveniles, exploring, foraging, fighting, and playing together (Diamond & Bond, 1999). In these circumstances, the consequence of enforcing local vocal conformity is to produce a youth culture, a parallel social system to that of adults with its own unique vocal repertoire. Exactly how the mechanism of call convergence operates in wild parrots and how it might function to mediate novel social affiliations is of considerable interest, as it bears on our understanding of the evolutionary significance of vocal imitation in this group of birds (Kroodsmma & Baylis, 1982). Further field studies of kea vocal behavior, quantifying short-term changes and convergences in vocal patterns and relating them to specific social interactions among flock members, would be exceedingly valuable.

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