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Some Vocal Characteristics and Call Variation in the Australian Corvids

CLARE LAWRENCE

School of Zoology, University of Tasmania, Private Bag 5, Hobart, Tasmania 7001
(Email: cllawren@postoffice.utas.edu.au)

Summary

Some vocal characteristics and call variation in the Australian crows and ravens were studied by sonagraphic analysis of tape-recorded calls. The species grouped according to mean maximum emphasised frequency (Australian Raven *Corvus coronoides*, Forest Raven *C. tasmanicus* and Torresian Crow *C. orru* with lower-frequency calls, versus Little Raven *C. mellori* and Little Crow C. *bennetti* with higher-frequency calls). The Australian Raven had significantly longer syllables than the other species, but there were no significant interspecific differences in intersyllable length. Calls of Southern *C.t. tasmanicus* and Northern Forest Ravens *C.t. boreus* did not differ significantly in any measured character, except for normalised syllable length (phrases with the long terminal note excluded). Northern Forest Ravens had longer normalised syllables than Tasmanian birds; Victorian birds were intermediate. No evidence was found for dialects or regional variation within Tasmania, and calls from the mainland clustered with those from Tasmania.

Introduction

Owing largely to the definitive work of Rowley (1967, 1970, 1973a, 1974), the diagnostic calls of the Australian crows and ravens *Corvus* spp. are well known in descriptive terms. The most detailed studies, with sonagraphic analyses, have been on the Australian Raven *C. coronoides* and Little Raven *C. mellori* (Rowley 1967; Fletcher 1988; Jurisevic 1999). The calls of the Torresian Crow *C. orru* and Little Crow *C. bennetti* have been described (Curry 1978; Debus 1980a, 1982), though without sonagraphic analyses. The Forest Raven *C. tasmanicus* is the least studied, and has scarcely been compared with the vocally most similar Little Raven with which it is sympatric in some areas (Debus 1982, 1985). The Forest Raven has not been studied in Tasmania, where it is the only corvid.

Recent reviews (Debus 1995, 1996), field-guides and handbooks, largely a précis of Rowley's and later work, have characterised the typical calls of the various species on the basis of pitch, tone, syllable length and tempo of territorial calls of moderate intensity ('mild territorial calls'). Sonagraphic analyses may reveal interspecific differences in spectral and temporal characters of calls, related to ecology, morphology or phylogeny. The five species fall into two phylogenetic groups — crows versus ravens — and two ecomorphological groups: large, resident species holding large, permanent territories (Australian and Forest Ravens, Torresian Crow), versus small, nomadic species holding small, temporary breeding territories (Little Raven, Little Crow) (Rowley 1970, 1973a,b). Furthermore, their habitats range from forest (Forest Raven) to woodland (Australian Raven, Torresian Crow), grassland (Little Raven) and desert (Little Crow), although all species forage in grassland. The various species may produce calls with optimal frequencies for the required distances and habitat structure (Morton 1975).

Calls may vary geographically, as suggested previously for most Australian corvids (Debus 1995, 1996; Schodde & Mason 1999). In particular, there may be differences between the calls of the two isolated subspecies of the Forest Raven:

Table 1

Number, source and location of corvid calls used in this study. N = number of calls analysed.

Species	*n*	*Recorder*	*Location(s)*
Australian Raven	12	F. van Gessel	NSW, Vic.
		J. Wiles	NSW
Southern Forest Raven	27	Clare Lawrence	Tas.
		F. van Gessel	Tas.
		R. Nagorcka	Tas., King Is.
		H. Plowright	Wilson's Prom. (Vic.)
Northern Forest Raven	13	F. van Gessel	NSW
		J. Wiles	NSW
Little Raven	5	F. van Gessel	NSW
		J. Wiles	Vic.
Little Crow	2	J. Wiles	NSW
		F. van Gessel	WA
Torresian Crow	12	F. van Gessel	Qld, NT
		J. Wiles	Brisbane (Qld)

the Southern *C.t. tasmanicus* (Tasmania and adjacent Australian mainland) and Northern *C.t. boreus* (New South Wales). The latter has been proposed (though not accepted) as a separate species, the New England or Relict Raven (Schodde & Mason 1999). Sonagraphic analyses may reveal regional variation in the calls of Forest Ravens, increasing with distance between populations, and measurable differences between the calls of the two subspecies.

I looked for interspecific differences in certain call parameters of the five species, and whether such variation correlates with body size, lifestyle, or the degree of relatedness or sympatry between species. I also investigated geographic variation in the primary territorial calls of the Forest Raven, at two scales: microgeographic (regional 'dialects' in contiguous populations), and macrogeographic (differences between isolated populations). A comparison between Northern and Southern Forest Ravens may shed light on the taxonomic question. Vocal characters examined were spectral and temporal: spectral is related to frequency (mean frequency of syllables, frequency range or changes in frequency over time), and temporal includes the length of syllables or the rate of delivery.

Methods

Interspecific comparisons

Tape-recorded calls were obtained for each of the five Australian species. The number of usable calls varied between species, as they were obtained from various sources using different equipment (Table 1). Only territorial calls, or calls that sounded similar to territorial calls, were used in this study. In a single call, phrases that were obscured by other sounds, and those which were obviously atypical of the call type, were omitted from the analysis. If a single syllable was obscured, the phrase in which it occurred was omitted completely. If a single syllable was atypical in an otherwise typical phrase, the full phrase was retained. Sample sizes used in all analyses were: Australian Raven 12 call sequences, Forest Raven 13, Little Raven five, Little Crow two, Torresian Crow 13.

For this analysis only the Northern Forest Raven was used, thus restricting the comparison to mainland populations only. Its calls did not differ significantly from those of the Wilson's

Promontory (Victoria) population of Southern Forest Ravens (see Results).

Time of day and year, and the gender of calling birds, were not controlled for in this study, as further selection from the already small number of available calls would provide insufficient samples for analysis.

Intraspecific comparison: Forest Raven

Territorial calls of Southern Forest Ravens were recorded in many locations throughout the species' range in Tasmania and Victoria (Table 1). In Tasmania a transect was defined running approximately north–south, bisecting the island, from North Bruny Island (just south of Hobart) to Deloraine on the centre of the north coast. Raven calls were recorded along this transect at approximately 10-km intervals, excluding zones of high traffic and residential areas. The sites were visited several times between June and August 2003 although, because of wind, inclement weather or the absence of Ravens, recordings were not made at each site every time. Recordings were made at different times of day, with most being made between mid morning and early afternoon. Many recordings were made at one site in Kingston (outer suburban Hobart) between June and September 2003, to test variation in the territorial calls of a single pair of Ravens.

Recordings were also made at four Tasmanian locations away from the transect (25 and 50 km either side in the south; on the north-eastern tip of Tasmania; and on Three Hummock Island off the north-western tip), as well as on Wilson's Promontory (Victoria) and on King Island in western Bass Strait. Recordings of calls from Northern Forest Ravens were obtained from New South Wales for comparison. Sites within Tasmania (including Three Hummock Island) were contiguous, as Ravens could fly between them. The Wilson's Promontory population was assumed to be isolated from those across Bass Strait.

Only territory-holding birds were recorded. I assumed that calls from other sources were also of territory-holding birds, although I could not verify this. I could not allow for the gender of calling birds, as males and females are morphologically similar and can only be distinguished by relative body size.

Most Tasmanian recordings were made using a Sony Mini-disc digital recorder with a Sennheiser K6 directional microphone and an amplifier, although some recordings were made by other people who used different equipment.

Only one call type, a common territorial call, was used in this study. This call is the most recognisable of the Forest Raven's vocalisations. Phonetically, the call may be described as a repeated hoarse *arr-arr-arrrrrr* with the last syllable drawn out and often descending. Several variations of this call exist, with some having more or fewer syllables, or having the last two syllables drawn out. In some cases this call is interspersed with phrases in which all syllables are of similar length with none descending. All variations of the basic territorial call were included in this study, as long as they were clearly recognisable.

I compared the calls from populations of Southern Forest Ravens from Kingston and Wilson's Promontory, and Northern Forest Ravens from the New England region of New South Wales. I investigated whether individual phrases could be grouped according to recording site, by comparing four sites: three in south-eastern Tasmania (Bruny Island, Howden and Kingston; nine, six and 22 phrases respectively), and one at Mount Field in western Tasmania (nine phrases). I also compared the mean values of all recording sites in Tasmania, King Island (two phrases), Victoria (nine phrases) and New South Wales (15 phrases).

Sonagram analysis

Each recording was converted to a sonagram using Syrinx sound-analysis software (John Burt, www.syrinxpc.com). Three parameters were determined for each phrase: mean syllable length, mean intersyllable length and mean maximum emphasised frequency (= dominant frequency; see below and Figure 1 for definitions). Mean syllable length was also calculated with terminal drawn-out syllables omitted, so all phrases effectively contained only 'normal' length syllables.

The Syrinx program displays the frequency and time of a selected part of a sonagram, and measures the time interval between two cursors. Dominant frequency was the least subjective part of a sonagram to measure. To ensure consistency, one person performed all measurements, repeating many several times each, always with very similar if not identical results for repeated measures of a given parameter.

Definitions for sonagram analysis

Syllable: an individual sound or note (see Figure 1).

Phrase: a discrete group of syllables. In most cases phrases are easily identifiable on a sonagram by sight.

Call: a group of phrases. Here each recording is considered a single call, although a recording may not cover a call in its entirety.

Emphasised frequency: the most intense frequency of a syllable (Morton 1975). On a sonagram this is seen as the darkest part of the syllable. Most corvid syllables have two dark bars, although some have more or fewer (Figures 1–6). For this analysis the frequency value was taken as the maximum frequency of the second dark bar of each syllable. Bars (emphasised frequencies) above the second were in some cases harmonics (Figures 2, 5) and may have influenced how the syllable sounded.

Syllable length: the duration of each syllable.

Intersyllable length: the interval between neighbouring syllables.

Long syllable: any syllable, usually at the end of a phrase, that is obviously longer than the others in the phrase. In many cases long syllables descend in frequency.

Normalised syllable length: the length of syllables in a phrase, with the long terminal syllable(s) omitted from the data.

Quantitative analysis

I compared mean maximum emphasised frequency, syllable length, normalised syllable length and intersyllable length by One-way Analyses of Variance (ANOVA), using SAS data-analysis software, with species or population as the independent variable and the phrase mean for each parameter as the dependent variables. Pair-wise comparisons were made between species or populations using Ryan-Einiot-Gabriel-Welsch (REGW) multiple-range tests in the SAS software package.

I used Principal Components Analysis (PCA) in PRIMER statistical software to compare species or populations based on combined values of frequency, normalised syllable length and intersyllable length. Preliminary regressions indicated no relationship between any of these characters. Data were normalised in PRIMER, as the characters used were measured in different units. The data were otherwise untransformed.

Cluster analyses were performed in PRIMER using the same data as for PCA. Cluster analyses were based on Normalised Euclidean Distance measures with Complete Linkage. Data were not transformed. Graphical outputs from PCA and Cluster Analysis are presented elsewhere (Lawrence 2003).

Results

Frequency

Typical territorial calls of each species are displayed as sonagrams (Figures 1–6). All five species had mean maximum emphasised frequencies of 2.1–2.7 kHz (Table 2). There was no significant variation in emphasised frequency between the five species (ANOVA: $F_{4,40} = 1.98$, $P = 0.12$). One data point was an obvious outlier, so the analysis was repeated with this data point omitted and a significant difference was found ($F_{4,39} = 12.26$, $P = 0.0001$). Pair-wise comparison of means using a REGW multiple-range test placed the five species into two groups based on call frequency. The Australian Raven, Forest Raven and Torresian Crow did not differ significantly from one another, but had lower emphasised frequencies than the Little Raven and Little Crow. However, the Australian Raven and Torresian Crow had bands of harmonics extending above 8 kHz and 6 kHz respectively, whereas the other three species had harsher calls with most energy

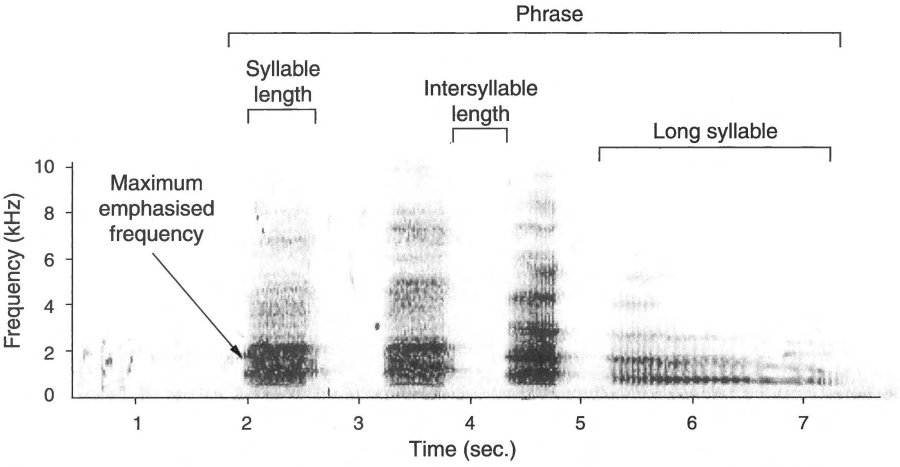

Figure 1. **Sonagram of the common territorial call of the Forest Raven** *Corvus tasmanicus tasmanicus* **from Wilson's Promontory, Victoria, showing call characters used in the analysis (Howard Plowright).**

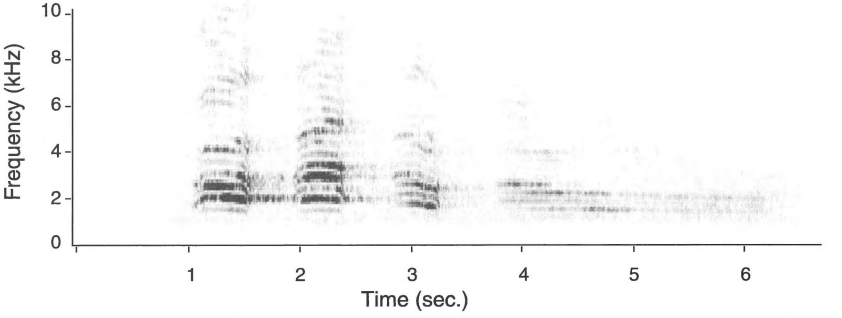

Figure 2. **Sonagram of the common territorial call of the Australian Raven** *Corvus coronoides* **from Glen Davis, New South Wales (Fred van Gessel).**

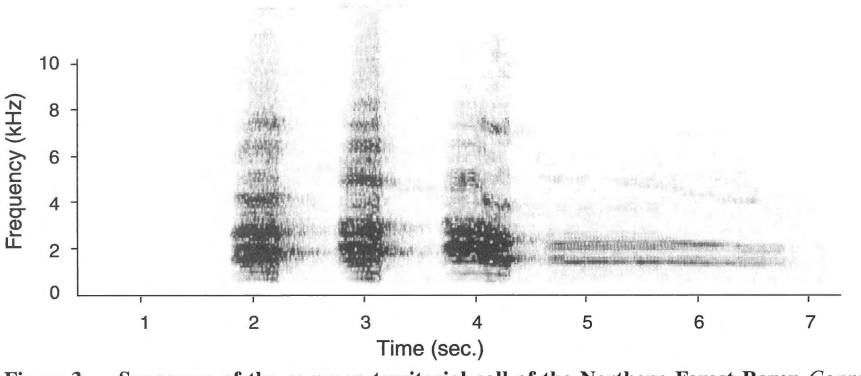

Figure 3. **Sonagram of the common territorial call of the Northern Forest Raven** *Corvus tasmanicus boreus* **from Smiths Lake, New South Wales (Fred van Gessel).**

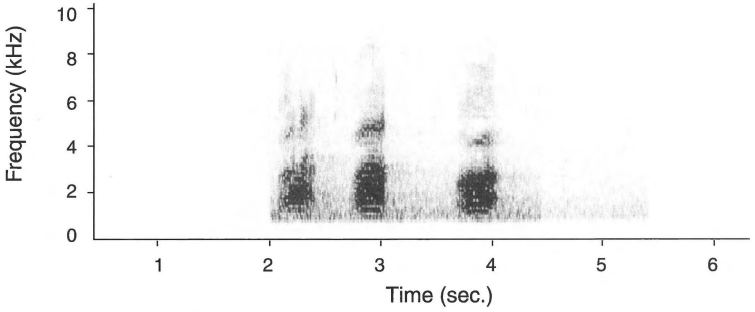

Figure 4. **Sonagram of the common territorial call of the Little Raven *Corvus mellori* from Menindee, New South Wales (Fred van Gessel).**

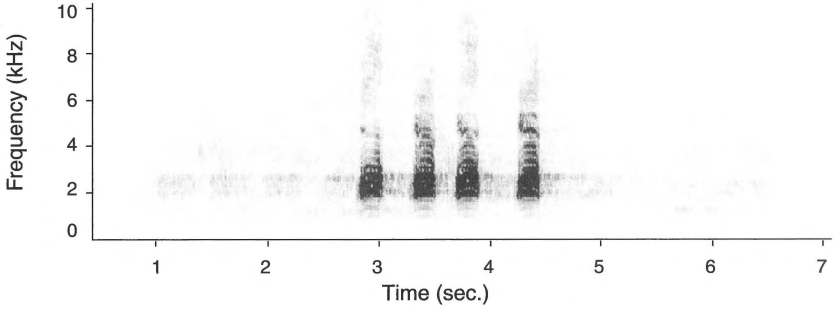

Figure 5. **Sonagram of the common territorial call of the Torresian Crow *Corvus orru* from Douglas Daly, Northern Territory (Fred van Gessel).**

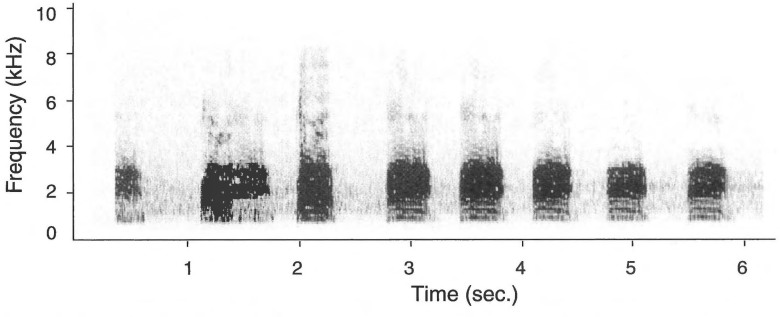

Figure 6. **Sonagram of the common territorial call of the Little Crow *Corvus bennetti* from Mullawa, Western Australia (Fred van Gessel). Note: the top of the sonagram is truncated, but this does not affect the analysis.**

Table 2

Properties of the calls of the five species of Australian corvid: mean ± standard deviation. AR = Australian Raven, FR = Forest Raven (Australian mainland), TC = Torresian Crow, LR = Little Raven, LC = Little Crow. Frequency = dominant frequency (mean maximum emphasised frequency: see Methods text and Figure 1). Sample sizes in parentheses; superscript indicates REGW grouping for each parameter (species in the same group are not significantly different).

Parameter	*AR (12)*	*FR (13)*	*TC (12)**	*LR (5)*	*LC (2)*
Frequency (kHz)	$2.366^{A} \pm 0.19$	$2.378^{A} \pm 0.09$	$2.176^{A} \pm 0.09$	$2.632^{B} \pm 0.20$	$2.595^{B} \pm 0.06$
Syllable length (sec)	$0.78^{A} \pm 0.24$	$0.48^{B} \pm 0.12$	$0.34^{B} \pm 0.07$	$0.41^{B} \pm 0.26$	$0.42^{B} \pm 0.01$
normalised	$0.65^{A} \pm 0.16$	$0.47^{A} \pm 0.34$	$0.33^{A} \pm 0.08$	$0.36^{A} \pm 0.16$	$0.40^{A} \pm 0.01$
Intersyllable length (sec)	$0.41^{A} \pm 0.24$	$0.45^{A} \pm 0.09$	$0.46^{A} \pm 0.23$	$0.43^{A} \pm 0.04$	$0.47^{A} \pm 0.33$

*with one outlying data point removed from sample.

below 6 kHz. The Australian Raven and Torresian Crow also had their dark (intense) bands extending to 4 kHz, whereas the other three had their dark bands concentrated below 4 kHz.

Syllable length

There was a significant difference in syllable length between species (ANOVA: $F_{4,40} = 11.45, P = 0.0001$). Pair-wise comparison showed that the Australian Raven had significantly longer syllables than the other four species (Table 2). When long terminal syllables were omitted from the data a significant difference was still found between species ($F_{4,40} = 3.86$, $P = 0.01$), although pair-wise comparisons using REGW analysis did not distinguish between species.

Intersyllable length

Intersyllable length did not vary significantly between species ($F_{4,40} = 0.11$, $P = 0.98$). The order of species for intersyllable length did not correlate with species order for syllable length: the Little Crow had the longest intersyllable length, the Torresian Crow had the second-longest, and the Australian Raven had the shortest (Table 2).

Principal components analysis

PCA suggested some interspecific variation in calls. Species groups were evident, although groups overlapped and there were several outliers. The three large resident species — Australian Raven, Forest Raven and Torresian Crow — clustered together, with the Little Raven to one side although two Little Raven calls fell within the Forest Raven group. The sample size was too small to group the Little Crow.

The Australian Raven, Forest Raven and Torresian Crow had lower-frequency calls than the Little Raven and Little Crow, and the Australian Raven had the longest syllables. PCA also suggested some variation between species in intersyllable length. The two principal components (frequency + syllable length vs intersyllable length) accounted for 69% of variation between the five species.

Table 3

Properties of the calls of the Forest Raven from three populations: mean ± standard deviation. T = Tasmania (Kingston), V = Victoria (Wilson's Promontory), N = New South Wales (Smiths Lake). Frequency = dominant frequency (mean maximum emphasised frequency: see Methods text and Figure 1). Sample sizes in parentheses; superscript indicates REGW grouping for each parameter (species in the same group are not significantly different).

Parameter	*T (22)*	*V (9)*	*N (15)*
Frequency (kHz)	$2.324^{A} \pm 0.28$	$2.447^{A} \pm 0.10$	$2.304^{A} \pm 0.24$
Syllable length (sec)	$0.72^{A} \pm 0.28$	$0.77^{A} \pm 0.13$	$0.78^{A} \pm 0.27$
normalised	$0.46^{A} \pm 0.14$	$0.51^{A} \pm 0.11$	$0.59^{A} \pm 0.06$
Intersyllable length (sec)	$0.36^{A} \pm 0.25$	$0.35^{A} \pm 0.11$	$0.26^{A} \pm 0.13$

Cluster analysis

Cluster analysis could not clearly assign calls to species. Some close relationships were evident between two to four conspecific calls, but these groups were often clustered with one or more heterospecific calls.

Forest Raven

No significant difference was detected in mean call frequency for Southern Forest Ravens from Tasmania and Victoria, and Northern Forest Ravens (ANOVA: $F_{2,43} = 1.00, P = 0.35$: Table 3; also compare Figures 1 and 3). REGW analysis did not discriminate between populations.

No difference was detected in syllable length among the three populations when long syllables were included in the analysis (ANOVA: $F_{2,43} = 0.26, P = 0.77$; Table 3). When long syllables were omitted from the analysis a significant difference was found between populations ($F_{2,43} = 4.40, P = 0.0001$). REGW analysis showed the Tasmanian population of Forest Ravens and the Northern Forest Raven to differ, but the Victorian population of Forest Ravens did not differ significantly from either the Tasmanian or Northern populations (Table 3).

No difference was detected in intersyllable length between the three populations (ANOVA: $F_{2,43} = 1.42, P = 0.25$). REGW analysis also did not discern any difference between pairs of sites (Table 3).

PCA did not show any clear groupings of phrases based on recording site. Most phrases from the four sites were similar in the parameters measured, with some outliers on both axes (frequency vs intersyllable length). Some groupings according to these two parameters were apparent, but these groups reflected phrases within a single call. These two principal components accounted for 80% of total variation between phrases.

Cluster analysis showed some close groupings of phrases within a site; however, close groupings also occurred between phrases from different sites. The analysis did not suggest any effect of increased geographical distance between sites.

PCA revealed no clear pattern in the calls of Forest Ravens throughout their range. Most sites away from the Tasmanian transect clustered with those from within the transect. Three Hummock Island and King Island were within the

Tasmanian cluster; Wilson's Promontory and New South Wales, although slight outliers, were less so than outliers representing sites within Tasmania. The two principal components (intersyllable length + normalised syllable length, vs frequency) accounted for 81% of variation.

Several Tasmanian sites were obvious outliers in the PCA ordination. One site on the transect was characterised by long intersyllables and short syllables; the habitat did not appear to differ substantially from the sites around it. A site in western Tasmania, separate from the other sites, was characterised by high call frequencies.

Cluster analysis also did not show any pattern in site means. Close groupings existed between pairs of sites that are geographically isolated from each other: for example, north coast of Tasmania and King Island; southern Tasmania and Wilson's Promontory (Victoria). In addition, the Northern Forest Raven was not apparently different from the Southern Forest Raven.

Preliminary comparison of calls from a single pair of Forest Ravens found great individual variation in a single call type, namely the mild territorial call.

Discussion

Interspecific comparisons

The results of this study suggest slight differences in the calls of each species, with considerable overlap. There were significant differences in emphasised frequency and syllable length, but not intersyllable length. The results group these birds into large species with low-frequency (deep) calls versus small species with slightly higher-frequency (rather higher-pitched) calls, and the Australian Raven with long syllables versus the others with shorter syllables. This outcome departs somewhat from statements in the literature on relative pitch and tempo of the calls of the various species: for instance, that the Australian Raven and Torresian Crow are 'tenors', the Little Raven and Little Crow 'baritones', and the Forest Raven a 'bass'; or that the Australian and Forest Ravens have slow calls (e.g. Debus 1995, 1996). However, the harmonics in Australian Raven and Torresian Crow calls produce purer tones, which give the calls of these species a clearer, higher sound to the human ear than the harsh calls of the other three species.

It is apparent that syllable length, rather than intersyllable length, characterises the tempo of calls. Thus, although the Forest Raven does utter some slow and drawn-out calls, on average its normalised syllables are not significantly longer than those of the smaller species.

The species-groupings identified in this study correlate with lifestyle (resident versus nomad), not with phylogeny (crows versus ravens); they are perhaps most simply explained by body size. Larger individuals tend to have deeper voices, call frequency being a function of the relative mass of the vibrating structures that produce sound in a bird's syrinx (Ryan & Brenowitz 1985). Lower-frequency calls are also the more appropriate for long-distance sound transmission, and for transmission in forested or wooded versus open habitats (Morton 1975; Wiley & Richards 1982; Ryan & Brenowitz 1985). Nevertheless, the mean emphasised frequency of all the Australian corvids is typical for forest birds (Morton 1975), and these species all forage in open habitats at least some of the time (Rowley

1970). If habitat structure were an important influence on frequency then sympatric species (e.g. Australian Raven and Little Raven, or Torresian Crow and Little Crow) should have similar emphasised frequencies, but the converse applies. Rather, it appears that such character divergence in sympatry is related to species recognition (Rowley 1970, 1973a,b).

Little Ravens and Forest Ravens are closely related (Rowley1970) and have been proposed as a superspecies (Schodde & Mason 1999). In morphology and acoustic characters Forest Ravens are thought to be simply a larger version of the Little Raven (G. Chapman pers. comm.). The results of this study do not support such a conclusion. On body size alone, Forest Ravens should have deeper calls (as found). Although the two species do not differ significantly in syllable length or intersyllable length, they are no more similar to each other than to the other species (except that they, like the two crows, have shorter syllables than the Australian Raven).

The interspecific comparisons in this study are limited by small sample sizes, especially for the Little Raven and Little Crow, and by variation in the calls (and their sources and recording equipment) and hence in their resulting sonagrams. Although commonly used in such comparative studies, sonagrams do not reveal how a call sounds to the human ear (e.g. its tone) or how it may be transcribed phonetically (Thorpe 1961). Such characters may confer important interspecific differences, but cannot be used in statistical analyses as can frequency or temporal characters. This study, examining only measurable parameters, may not reflect the true and discernible level of variation between the five Australian species; further work, using larger samples in a more standardised approach, is required.

Intraspecific comparison: Forest Raven

The results of this study suggest that the territorial calls of Forest Ravens do not vary significantly across their range in Tasmania, the Bass Strait islands and southern Victoria. Furthermore, the territorial calls of the two isolated subspecies (Northern and Southern) are not significantly different. Of the four characters analysed only one — normalised syllable length — differed significantly between populations. The Tasmanian population had significantly shorter syllables than those of Northern Forest Ravens; the Victorian population of Southern Forest Ravens was intermediate in this character. No difference was found in mean maximum emphasised frequency, non-normalised syllable length, or intersyllable length between sites. This similarity is despite long isolation of Northern Forest Ravens, since the Late Pleistocene (Rowley 1973b), and despite significant morphological divergence (Northern being slightly the larger: Schodde & Mason 1999). Contrary to expectation, and to suggestions that the subspecies have slight vocal differences (Debus 1995, 1996), the subspecies were not found to differ in the pitch of their calls. There was also no evidence of regional dialects within Tasmania, nor any discernible pattern of call variation with distance. Victorian and Northern calls clustered with those from Tasmania. Thus, the results of this study do not support the elevation of the Northern Forest Raven to specific rank.

An unresolved question is why mainland Forest Ravens should have slightly longer normalised syllables than Tasmanian birds. This aspect may be related either to character divergence in sympatry with the Little Raven so that both species emphasise their differences and avoid interbreeding, or to character convergence in sympatry with the Australian Raven so that both large species can recognise and efficiently signal to each other during interspecific competition for territories.

The longer syllables of Northern Forest Ravens, which are sympatric with both the ecologically different Little Raven and ecologically similar Australian Raven and Torresian Crow, may be evidence of character shift. The deep calls of the Forest Raven are well suited to transmission in forest (Morton 1975; Ryan & Brenowitz 1985), which is consistent with the postulated origin of the species in temperate, humid south-eastern Australia (Rowley 1973b).

The intraspecific comparisons in this study are limited by small sample sizes, and by variation in the calls, sources and equipment. Similarly, further work is required using a standardised approach that incorporates knowledge of the functions of, and behaviour corresponding to, corvid calls, and takes into account the motivational state of the caller.

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