

# Learned vocalizations in budgerigars (*Melopsittacus undulatus*): The relationship between contact calls and warble song

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The budgerigar (*Melopsittacus undulatus*) has an extraordinarily complex, learned, vocal repertoire consisting of both the long rambling warble song of males and a number of short calls produced by both sexes. In warble, the most common elements (>30%) bear a strong resemblance to the highly frequency-modulated, learned contact calls that the birds produce as single utterances. However, aside from this apparent similarity, little else is known about the relationship between contact calls and warble call elements. Here, both types of calls were recorded from four male budgerigars. Signal analysis and psychophysical testing procedures showed that the acoustic features of these two vocalizations were acoustically different and perceived as distinctive vocalizations by birds. This suggests that warble call elements are not simple insertions of contact calls but are most likely different acoustic elements, created *de novo*, and used solely in warble. Results show that, like contact calls, warble call elements contain information about signaler identity. The fact that contact calls and warble call elements are acoustically and perceptually distinct suggests that they probably represent two phonological systems in the budgerigar vocal repertoire, both of which arise by production learning. © 2011 Acoustical Society of America. [DOI: 10.1121/1.3557035]

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## I. INTRODUCTION

Budgerigars (*Melopsittacus undulatus*) are small, highly social, gregarious parrots that have a complex, learned vocal repertoire. Although parrot vocal behaviors are generally less well studied than those of songbirds, some species, like the budgerigar, have been investigated extensively especially with regard to call learning (see review in Farabaugh and Dooling, 1996). As with songbirds, male budgerigars also produce a song, called warble, but much less is known about how learning is involved in this vocalization (Brockway, 1964b, 1969; Eda-Fujiwara and Okumura, 1992; Farabaugh *et al.*, 1992). Warble song is a melodic, multi-syllabic, non-stereotyped vocalization that can last well over several minutes (Brockway, 1969; Farabaugh *et al.*, 1992). It is primarily produced by males and directed toward females during mating behaviors but can be produced by males alone or in interaction with other males. Warble helps to maintain pair bonds, stimulates ovarian activity and egg-laying in females, and facilitates male gonadal development (Brockway, 1964b, 1965, 1969). Studies have shown that birds deafened when young or raised in acoustic isolation develop highly aberrant warble song (Eda-Fujiwara and Okumura, 1992), and individuals living together share a higher proportion of similar elements in their warble than those living apart (Farabaugh *et al.*, 1992).

Among the various warble elements that compose an entire warble bout, a strikingly large proportion (>30%) are

short (100–200 ms), frequency-modulated elements (Farabaugh *et al.*, 1992; Gramza, 1970), here referred to as warble call elements, which resemble the contact calls—a learned vocalization that is produced as a single utterance. Contact calls are by far the most frequently produced vocalization by budgerigars. They are short (approximately 100–300 ms), narrowband (2–4 kHz), and strongly frequency-modulated, typically used to coordinate, localize, and synchronize the flock during flight or when an individual is isolated from a social group or mate (Brockway, 1964a; Farabaugh *et al.*, 1994; Wyndham, 1980). Both male and female budgerigars with normal auditory feedback are able to learn contact calls through social interactions (Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter *et al.*, 2003). During the course of only a few days of interaction, the contact calls of social companions converge to a common type so that birds are producing nearly identical contact calls (Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994). Birds can also learn new contact calls under operant control and normal auditory feedback (Dooling *et al.*, 1997; Manabe *et al.*, 2008; Osmanski and Dooling, 2009). These are examples of production learning—new vocalizations acquired by modification of the bird's vocal apparatus through experience with other individuals (Janik and Slater, 2000).

Budgerigars seem to be unusual among birds in the extent to which call learning occurs under both social and operant circumstances and in the extent to which they can mimic novel and other environmental sounds and incorporate them into their warble (Brockway, 1969; Gramza, 1970)—a form of contextual vocal learning (Janik and Slater, 2000). Contact calls and warble call elements do share a number of acoustic features, and, taken together, they account for the majority of budgerigars' vocal repertoire. Although contact call learning has been extensively studied in many aspects for

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decades (see review in [Farabaugh and Dooling, 1996](#)), virtually nothing is known about how individual elements are learned in warble song or how elements might be combined to make complex temporal arrangements. So, as a step toward understanding warble, the present experiments investigate the relationship between contact calls and warble call elements in order to assess the contribution of these calls to the learned vocal repertoire in budgerigars.

One obvious possibility is that contact calls and warble call elements are essentially the same vocalization but that birds learn to use this vocalization in two different and distinct contexts. In such contextual learning, “new” vocalizations are acquired by a recombination of existing vocalizations or they are used in different circumstances ([Janik and Slater, 2000](#)). If this were the case in budgerigars, the acoustic features of contact calls and warble call elements taken from the same individual should be very similar and perceived as similar when presented alone without contextual cues. Alternatively, it may be that warble call elements are not related to a bird’s learned contact calls but rather are new acoustic elements created *de novo* and used solely in warble. If this is the case, contact calls and warble call elements should be different in demonstrable ways both acoustically and perceptually.

The acoustic complexity, non-repeating sequences, and unusual length of budgerigar warble make it extremely difficult to determine how and when vocal learning actually occurs in this species. The present experiments examine a relatively manageable part of this problem by providing a detailed comparison of the acoustic features and perceptual consequences of budgerigar contact calls and warble call elements in this species. The fact that warble call elements look and sound similar to the contact calls in this species offer the intriguing possibility of a new example of contextual learning where learned calls, used as single utterances in social situations, are incorporated in a much longer vocal stream and used almost exclusively in reproductive situations. This would also point to a surprising degree of cognitive flexibility in vocal production and would offer additional parallels between birdsong and human speech as when words produced alone may have one meaning and function, but can take on other functions and meanings when embedded in a running speech stream.

## II. GENERAL METHODS

### A. Vocal recording

Contact calls and warble songs were recorded from four male adult budgerigars (Buzz, Ricky, Puffy, and Cosmo). They were initially housed together with approximately 40 other budgerigars and two other species of birds (i.e., canaries and zebra finches) in a large aviary at the University of Maryland. In selecting subjects for recording, the birds’ behaviors in the flock were observed for evidence of pair bonding between males and females, i.e., if a particular male was seen warbling to a specific female on several occasions, those two individuals were labeled as a pair and selected for recording. Approximately 4 weeks prior to the start of recording, the pairs were moved to a large flight cage in another room and housed together. Animals had *ad libitum* access to both food and water at all times.

Prior to recording, a pair of budgerigars was separated and placed in two small animal acoustic isolation chambers (Industrial Acoustic Company, Bronx, NY, IAC-1) individually. After an isolation period of at least 1 hour, the doors of the chambers were opened and a recording session was begun. Contact calls and warble were always recorded on separate days. Animals were returned to the flight cage following each recording session. All vocalizations were acquired over the course of 2 to 3 days.

During contact call recording sessions, the two birds remained in their individual chambers and two directional Audio-Technica Carotoid microphones PRO35A (Audio-Technica, Inc., Stow, OH) were aimed at each animal’s cage. Microphones were attached to a Marantz solid state digital recorder PMD670 (Marantz America, Inc., Mahwan, NJ) and each bird’s vocal behavior was stored on a separate channel of a PCM WAV file at a sampling rate of 48 kHz. The birds could interact acoustically but were not in visual contact with one another. The recording period was terminated after approximately 100–200 calls were recorded from each bird. Although we collected vocalizations from both the male and the female, only the male’s calls were used in subsequent analyses.

During warble song recording sessions, the cages of each pair member were placed in close proximity within one isolation chamber and a single directional microphone was aimed at the male’s cage. Here, the birds could interact both visually and acoustically, which helped to stimulate males to produce warble song. The male’s warble recording was uncontaminated by vocalizations from the female because females do not typically vocalize during warble production, although they orient toward the male and adopt specific body postures while he sings. The vocalization of the male was stored on a single channel of a PCM WAV file at a sampling rate of 48 kHz. To facilitate warbling, we played a recording of the animals’ home flock sounds at very low amplitude during this recording period. Each recording session was terminated after the male stopped singing of his own accord. A total of more than 1 hour of warble for each male was collected over approximately 4 hours of recording.

### B. Segmentation of vocalizations

Each recording session was transferred from the Marantz PMD670 digital recorder to a computer. A MATLAB program then segmented each WAV file into separate vocal segments (i.e., contact calls or warble elements, depending on the session). This program advanced through each WAV file and selected acoustic signals that exceeded user-defined values for minimum intensity (based on the overall amplitude of the recording), minimum duration, and minimum inter-syllable interval. Each selected signal was presented both acoustically and visually (as a spectrogram) to a rater familiar with budgerigar sounds who then either accepted or rejected the signal as a vocalization.

In the case of warble song, the final processing step was to remove elements that were not similar to contact calls by first eliminating those segments that did not fall between 100 and 200 ms in duration ([Ali et al., 1993](#)). Elements were then excluded by visual inspection for spectrographic

features that are stereotyped in contact calls (e.g., tonal sound, high frequency modulation, etc.) by an observer familiar with budgerigar warble sounds. Each element was treated as an individual event and was not compared to each other. This process ensured that alarm calls, harmonic elements, and non-frequency-modulated elements were excluded from further analyses.

### III. EXPERIMENT 1: ACOUSTIC ANALYSIS OF VOCALIZATIONS

#### A. Methods

For each of the four individuals recorded (Buzz, Ricky, Puffy, and Cosmo), warble call elements were compared to normal contact calls in three ways. First, a spectral cross-correlation program generated a similarity index between all calls recorded from a bird. This program created a spectrogram for each signal using a 256-point Hanning window with 50% window overlap. These spectrograms were then compared using a MATLAB two-dimensional cross-correlation algorithm (MATLAB function XCORR2). This algorithm generated a series of correlation values representing all possible temporal offsets between the two spectrograms. The maximum correlation value was taken as the similarity index between the two vocalizations. A matrix of similarity values was constructed from all vocalizations produced by each bird and was analyzed using a MATLAB classical multidimensional scaling algorithm (MATLAB function MDSSCALE). The multidimensional scaling output grouped signals into a three-dimensional space where spectrographically similar vocalizations cluster together and dissimilar vocalizations separate. Two different kinds of multidimensional scaling (MDS) plots were generated. First, we created a plot for each of the four birds that contained that individual's contact calls and warble elements. Second, five contact calls, and five contact call-like warble elements were randomly selected from each bird, and a total of 40 vocalizations were pooled together to make a three-dimensional MDS summary plot of the vocalizations from all four birds to see whether certain vocalizations still clustered together across birds.

Next, a Multivariate Analysis of Variance (MANOVA) was performed on these measures using SPSS 16.0 software to reveal any acoustic differences between call categories of the same individual. A MATLAB-based signal analysis program was used to generate power spectra iteratively across each call in 5 ms windows (with 50% window overlap). Both the peak amplitude and the frequency at the peak amplitude were measured for each power spectrum. These two measures were then used to construct a peak frequency and peak amplitude contour across each call in addition to several different call parameters, including:

Eight frequency variables that describe the frequency changes across each call:

- (1) Peak frequency (Hz): Average of the overall peak frequency contour.
- (2) SD frequency (Hz): Standard deviation of the overall frequency contour.
- (3) Maximum frequency (Hz): Frequency contour maximum value.

- (4) Minimum frequency (Hz): Frequency contour minimum value.
- (5) Frequency range (Hz): Maximum frequency–minimum frequency. A measure of what spectral range a call is produced over.
- (6) Frequency change (Hz): The average of the difference between the peak frequency value measured in successive windows. A measure of how quickly and to what extent frequency is adjusted within a call.
- (7) Frequency modulation (Hz): The rate of modulation across the frequency contour.
- (8) 3-dB bandwidth (Hz): Frequency bandwidth 3 dB down from peak amplitude.

Eight amplitude variables that describe the amplitude changes across each call:

- (1) Peak amplitude (dB-Hz): Average of the overall peak amplitude contour.
- (2) SD amplitude (dB-Hz): Standard deviation of the overall amplitude contour.
- (3) Maximum amplitude (dB-Hz): Amplitude contour maximum value.
- (4) Amplitude range (dB-Hz): Maximum amplitude – minimum amplitude. A measure of what amplitude range a call is produced over.
- (5) Amplitude concentration 1 (%): Percentage of overall spectrum falling within 2–4 kHz.
- (6) Amplitude concentration 2 (%): Percentage of overall spectrum falling within 2.61–3.11 kHz.
- (7) dB-RMS: Overall amplitude derived from the root-mean-square of the signal.
- (8) Amplitude modulation (Hz): The rate of modulation across the amplitude contour.

Four “whole-call” variables:

- (1) Duration (ms): Length of the signal.
- (2) Wiener entropy: Unitless measure of disorder (pure tone =  $-\infty$ ; white noise = 0) (Tchernichovski *et al.*, 2001).
- (3) Tonal quality (%): Percentage of signal with 3 dB bandwidth within 0.3 kHz.
- (4) Phase linearity: Unitless measure of deviation from phase linearity (perfectly in phase =  $-\infty$ ).

Finally, contact call and warble call data from all four individuals were pooled together, and a principal components analysis (PCA) with varimax rotation was performed on the 20 measures to sort out the relative salience of the acoustic features budgerigars may use to discriminate call categories.

#### B. Results

All birds vocalized readily in both the contact call and warble recording sessions. Only vocalizations from males were processed and analyzed. Each bird produced an average of 130 contact calls (147, 146, 144, and 82 contact calls were produced by four budgerigars, respectively) and an average of 108 warble call elements (116, 109, 101, and 106 warble call elements were used produced by the same four budgerigars, respectively). Thus, a total of 519 contact calls and 432 warble call elements were used in the following analyses.



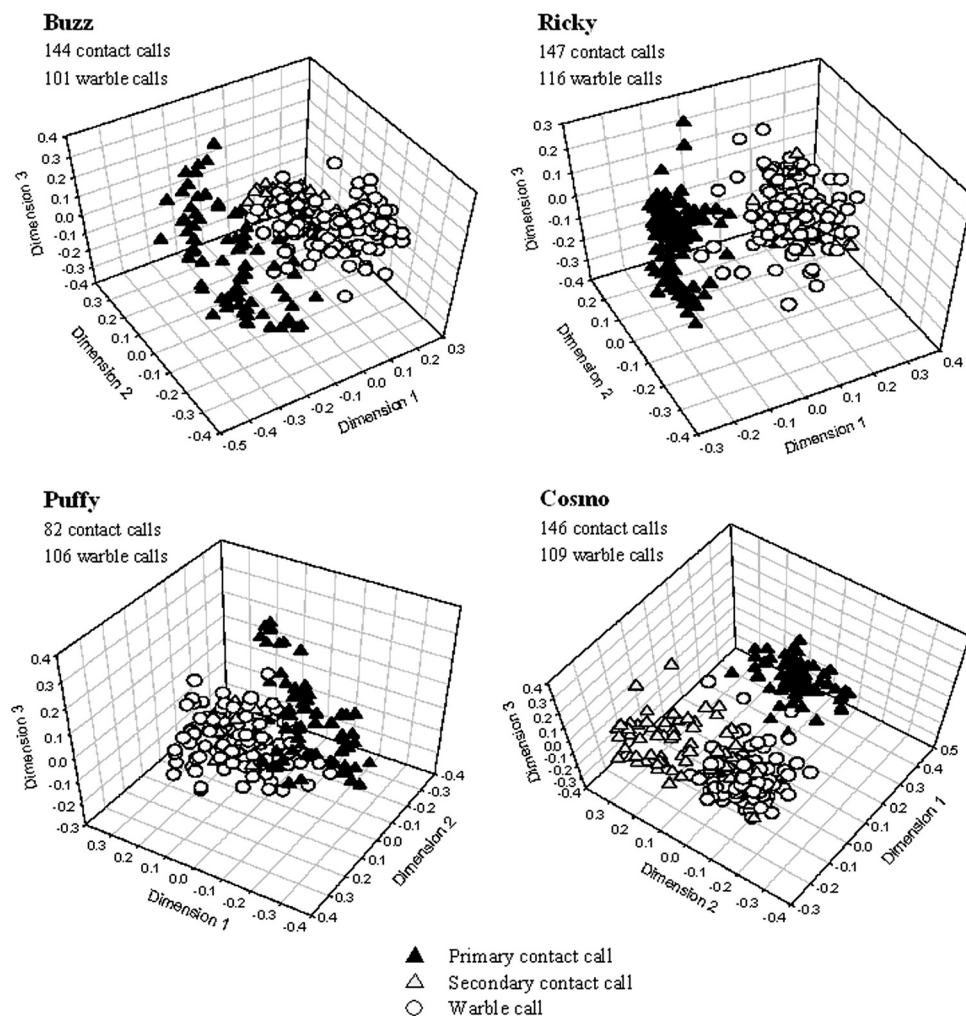


FIG. 1. Three-dimensional multidimensional scaling plots for each budgerigar showing clustering patterns for contact calls and warble call elements. Contact calls are shown as filled triangles. Each individual may have more than one primary contact call type, indicating by different colors. Warble call elements are shown as empty triangles. The two call classes are separated in all four birds, showing that the two call groups have distinct spectrotemporal acoustic features.

The three-dimensional multidimensional scaling plots of vocalizations for each bird are shown in Fig. 1, where filled symbols represent contact calls and empty symbols represent warble call elements. Each bird has one primary contact call type that is used for most of the time and one or more secondary contact call types that are less used. The two call categories are clearly separated for each of the four animals in three-dimensional space, indicating that the two groups are acoustically distinct based on the spectrotemporal features. In the summary, MDS plot (Fig. 2), the contact calls (filled), is grouped in separate clusters by individual bird; intriguingly, the warble call elements (empty) are seen as one large cluster and separate from the contact calls. This shows that contact calls are individually distinct, while warble call elements have common features presented in different budgerigars.

Results from Multivariate Analysis of Variance in all four birds showed that contact calls are significantly different from warble call elements on a number of acoustic dimensions (see Table I for summary). Which acoustic measures distinguish between contact calls and warble calls, and their relative importance varies somewhat across birds. In general, however, contact calls are longer, louder, and have a more restricted frequency range than warble call elements. Contact calls also have higher average peak frequency and less frequency-modulation compared to warble call elements.

The results of the principal components analysis are summarized in Table II. Five principal components that altogether accounted for 74.22% of the variation were extracted from the data. The first principal component (PC1) accounted for 19.08% of the variance in the dataset, and the second

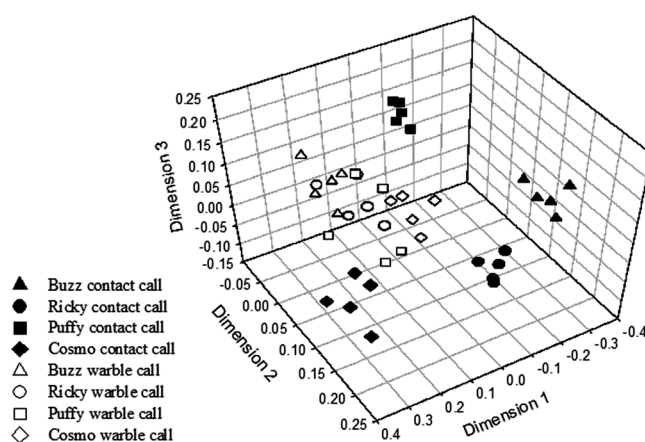


FIG. 2. Three-dimensional multidimensional scaling plot showing how the vocalizations from all four birds tend to cluster together. Five contact calls and five warble call elements were randomly selected from each bird for a total of 40 vocalizations. The contact calls (filled symbols), are seen grouping into separate clusters by bird (Buzz = triangle, Ricky = circle, Puffy = square, and Cosmo = diamond); the warble call (empty symbols), are seen as one large cluster and mostly distinct from the contact calls.

TABLE I. Summary of means and Multivariate Analysis of Variance results in each of the four budgerigars.

Measure	Buzz				Ricky			
	Contact call	Warble call	$F_{(1,243)}$	$p$	Contact call	Warble call	$F_{(1,261)}$	$p$
Peak frequency (Hz)	2815.24	2754.65	6.10	<0.05	2996.36	2382.33	329.05	<0.001
SD frequency (Hz)	584.87	664.52	4.87	<0.05	476.60	653.13	92.60	<0.001
Maximum frequency (Hz)	4045.56	3895.90	3.44	<i>n.s.</i>	3843.67	3724.38	1.56	<i>n.s.</i>
Minimum frequency (Hz)	1597.85	1127.93	22.14	<0.001	1886.84	1034.05	122.00	<0.001
Frequency range (Hz)	2447.70	2767.97	5.27	<0.05	1956.82	2690.33	40.24	<0.001
Frequency change (Hz)	227.79	266.81	4.37	<0.05	221.12	259.97	17.99	<0.001
Frequency modulation (Hz)	7.90	6.65	6.89	<0.01	8.24	7.63	1.21	<i>n.s.</i>
3dB bandwidth (Hz)	329.95	317.57	9.98	<0.01	311.80	334.97	56.82	<0.001
Peak amplitude (dB-Hz)	6.88	3.78	144.57	<0.001	9.59	3.51	485.76	<0.001
SD amplitude (dB-Hz)	3.88	3.48	5.87	<0.05	2.87	3.30	14.19	<0.001
Maximum amplitude (dB-Hz)	11.67	9.02	85.56	<0.001	14.18	8.07	476.93	<0.001
Amplitude range (dB-Hz)	15.67	14.49	4.05	<0.05	12.25	13.80	7.23	<0.01
Amplitude concentration 1 (%)	.98	.99	1.70	<i>n.s.</i>	.99	.99	4.27	<0.05
Amplitude concentration 2 (%)	.52	.39	23.27	<0.001	.26	.20	7.45	<0.01
dB-RMS (dB)	-20.17	-25.51	118.27	<0.001	-16.04	-26.94	442.99	<0.001
Amplitude modulation (Hz)	3.66	4.02	3.66	<i>n.s.</i>	5.02	3.96	24.44	<0.001
Duration (ms)	150.05	140.21	8.10	<0.01	160.34	131.25	143.64	<0.001
Wiener entropy	-0.53	-0.46	26.48	<0.001	-0.44	-0.47	3.92	<0.05
Tonal quality (%)	69.46	68.83	.41	<i>n.s.</i>	71.79	66.23	45.21	<0.001
Phase linearity	40.04	38.75	.27	<i>n.s.</i>	27.19	32.49	10.49	<0.05

Measure	Puffy				Cosmo			
	Contact call	Warble call	$F_{(1,186)}$	$p$	Contact call	Warble call	$F_{(1,253)}$	$p$
Peak frequency (Hz)	2830.91	2625.42	28.50	<0.001	2798.86	2657.56	27.32	<0.001
SD frequency (Hz)	591.23	647.85	5.05	<0.05	492.98	613.98	39.81	<0.001
Maximum frequency (Hz)	3932.82	4081.21	1.92	<i>n.s.</i>	3744.25	4062.93	11.53	<0.01
Minimum frequency (Hz)	1926.28	1463.32	74.58	<0.001	1909.76	1698.46	36.18	<0.001
Frequency range (Hz)	2006.56	2617.88	28.28	<0.001	1834.49	2364.47	29.20	<0.001
Frequency change (Hz)	194.87	255.10	15.39	<0.001	188.23	206.70	3.31	<i>n.s.</i>
Frequency modulation (Hz)	8.60	9.43	.73	<i>n.s.</i>	7.49	9.05	10.22	<0.01
3dB bandwidth (Hz)	312.69	323.77	6.90	<0.01	310.58	300.41	9.64	<0.01
Peak amplitude (dB-Hz)	7.44	3.07	101.29	<0.001	8.18	3.95	297.92	<0.001
SD amplitude (dB-Hz)	2.72	2.88	1.48	<i>n.s.</i>	3.25	2.97	9.80	<0.01
Maximum amplitude (dB-Hz)	11.75	7.41	88.65	<0.001	12.88	9.12	181.37	<0.001
Amplitude range (dB-Hz)	11.31	12.09	1.85	<i>n.s.</i>	14.03	11.88	32.31	<0.001
Amplitude concentration 1 (%)	.99	.96	17.43	<0.001	1.00	1.00	9.45	<0.01
Amplitude concentration 2 (%)	0.14	.26	23.15	<0.001	.36	.24	33.48	<0.001
dB-RMS (dB)	-20.26	-28.03	73.62	<0.001	-18.38	-26.48	253.58	<0.001
Amplitude modulation (Hz)	5.11	4.68	.82	<i>n.s.</i>	2.99	5.22	133.01	<0.001
Duration (ms)	129.42	126.67	.61	<i>n.s.</i>	190.39	123.59	326.14	<0.001
Wiener entropy	-0.47	-0.48	.75	<i>n.s.</i>	-0.50	-0.51	1.74	<i>n.s.</i>
Tonal quality (%)	69.89	68.49	1.11	<i>n.s.</i>	73.14	72.32	.62	<i>n.s.</i>
Phase linearity	33.74	38.31	4.65	<0.05	32.74	41.21	14.06	<0.001

(PC2), third (PC3), fourth (PC4), and fifth (PC5) components accounted for 18.55, 17.33, 11.85, and 7.42%, respectively. Measures of amplitude (e.g., peak amplitude, maximum amplitude, and decibels-root-mean-square) loaded highly on PC1, while PC2 showed high correlations with frequency measures. PC3 was highly correlated with amplitude range, PC4 was related to tonal quality and 3 dB bandwidth, and PC5 was heavily dependent on the energy falling within the frequency range of 2.61 and 3.11 kHz.

### C. Discussion

Acoustic analyses showed that contact calls and warble call elements are different on a number of spectrotemporal

properties, supporting the notion that they are acquired through production learning rather than contextual learning. Contact calls are louder than warble call elements, which fits with both the context of their occurrence and their social function. Contact calls are typically produced at very high amplitudes when an individual is isolated from a social group or mate (Farabaugh *et al.*, 1994; Wyndham, 1980), while warble songs are produced at low amplitudes, primarily by males, and directed toward females at close distances (usually close enough to be accompanied by stereotyped preening, beak touching, and other tactile behaviors between the male and female) during courtship (Brockway, 1964b).

TABLE II. Summary of PCA results. Measures larger than  $\pm .7$  were printed in bold.

Measure	PC1	PC2	PC3	PC4	PC5
Peak frequency	0.632	0.262	-0.169	-.039	0.437
SD frequency	-0.249	<b>0.741</b>	0.345	0.235	-0.250
Max frequency	0.134	<b>0.900</b>	0.076	0.014	0.132
Min frequency	0.422	-0.122	-0.600	-0.268	.452
Frequency range	-0.178	<b>0.760</b>	0.455	0.188	-.199
Frequency change	-0.104	<b>0.803</b>	0.093	0.327	-.205
Frequency modulation	-0.029	0.577	-0.454	-0.055	.179
3dB bandwidth	-0.002	0.110	0.206	<b>0.885</b>	-.042
Peak amplitude	<b>0.950</b>	-0.147	-0.083	-0.084	0.040
SD amplitude	0.070	0.083	<b>0.765</b>	0.441	0.276
Maximum amplitude	<b>0.943</b>	-0.106	0.129	0.045	0.097
Amplitude range	0.124	0.067	<b>0.804</b>	0.360	0.176
Amp concentration 1	0.065	- <b>0.771</b>	0.126	0.057	-0.038
Amp concentration 2	0.079	-0.113	0.179	-0.071	<b>0.721</b>
dB-RMS	<b>.946</b>	-0.083	0.064	0.055	0.082
Amplitude modulation	-0.181	0.082	-0.665	-0.002	.043
Duration	0.580	-0.046	0.426	-0.078	-0.134
Wiener entropy	-0.119	-0.095	-0.545	-0.391	-0.470
Tonal quality	0.066	-0.110	-0.022	- <b>0.895</b>	0.066
phase linearity	-0.090	0.119	0.509	-0.091	0.063
Eigenvalue	5.213	4.219	2.851	1.367	1.194
Cumulative variance (%)	19.076	37.631	54.956	66.801	74.224

On average, the peak frequency of contact calls is higher than that of warble call elements. This is most likely due to budgerigars actively modulating air flow and tension on the tympaniform membranes of the vocal production apparatus (i.e., the syrinx), rather than an effect of coarticulation due to streams of utterances. If so, this would be an evidence for budgerigars actively learning new warble call elements by altering the state of their sound-producing structures as opposed to simply inserting pre-existing contact calls into warble streams.

Contact calls are also longer in duration than warble call elements. Shorter warble call elements may be related to the fast delivery rate of warble song (over 150 elements per minute) which might restrict the production window for different warble elements. This might be analogous to the human speech principal that the greater the number of “subunits” in a unit of speech, the shorter each subunit becomes (Lindblom, 1963; Pickett, 1999).

In summary, acoustic analysis has shown that while there are overlapping similarities, contact calls and warble call elements are significantly different in amplitude, frequency, and duration. This suggests that they are not the same vocal signals and are not used interchangeably such that contact calls are directly inserted into warble and changing their function according to the context.

#### IV. EXPERIMENT 2: PERCEPTUAL TESTING OF VOCALIZATIONS

To test whether contact calls and warble call elements belong to two separate phonological systems, a psychophysical paradigm was used to test budgerigars’ perception of these two types of calls independent of context. The question asked is whether birds can attend to the acoustic differences between contact call and warble call vocalizations while

ignoring the inherent acoustic variation within these two categories due to which bird is vocalizing, etc.

## A. Methods

### 1. Subjects

Subjects were four budgerigars different from the animals used in experiment 1. They were never housed together with those individuals whose vocalizations were recorded as stimuli and, therefore, did not have auditory experience with those vocalizations.

### 2. Apparatus

Birds were trained and tested in a small wire cage ( $23 \times 25 \times 16 \text{ cm}^3$ ) mounted in a sound-attenuated chamber (Industrial Acoustics Company, Bronx, NY, IAC-3). Inside the test cage, a perch was mounted on the floor in front of a small light bulb (the hopper light) and an opening on the floor through which food was accessible when a hopper was raised by activation of a solenoid. A control panel with two microswitch response keys was mounted vertically in front of the perch and the food opening was within a reachable distance for the bird on the perch. The keys were approximately 5 cm apart and each key had an 8 mm light emitting diode (LED) attached.

The experiments were controlled by a principal component microcomputer controlling Tucker-Davis Technologies (TDT, Gainesville, FL) System III modules. Stimuli were stored digitally and output via a two-channel signal processor (TDT, Model RX6) at a sampling rate of 24.4 kHz. Each signal was then output at a mean level of about 70 dB sound pressure level (sound pressure level) with a 3 dB rove across presentations from a separate channel of the digital-analog (digital-to-analog) converter to a separate digital attenuator TDT, Model PA5 (Tucker-Davis Technologies, Gainesville, FL), combined in an analog summer (Model SM5, Tucker-Davis Technologies, Gainesville, FL) and then amplified (Model D-75, Crown Audio, Inc., Elkhart, IN) to a loudspeaker (KEF Model 80V, GP Acoustics, Inc., Marlboro, NJ) in the sound-attenuated chamber. All test sessions were conducted using custom-designed MATLAB software driving the external hardware as described earlier. Data were stored digitally and analyzed using both MATLAB and commercially available statistics software.

### 3. Vocal stimuli

The vocal signals used here were the same as those used in the acoustic analysis. Four male adult budgerigars were recorded, resulting in eight “call groups:” Buzz contact calls, Buzz warble call elements, Ricky contact calls, Ricky warble call elements, Puffy contact calls, Puffy warble call elements, Cosmo contact calls, and Cosmo warble call elements.

Stimuli were calibrated individually with a Larson-Davis sound level meter (Model 825, Provo, UT) with a 20-foot extension cable attached to a  $\frac{1}{2}$  in. microphone. The microphone was positioned in the place normally occupied by the listening bird’s head during testing.

There were 100 trials in each running session, consisting of 80 target trials and 20 sham trials where no target was



presented. The 80 target trials consisted of 10 calls from each of these eight call groups, each served as target only once in a test session to prevent the subjects from memorizing these sounds. The background used in each session consisted of 70 random calls from one call group. As a result, in each test session, there were 10 trials in which the target was from the same call group as the background, and there were another 10 trials in which the target was from the different call group of the same individual as the background. These 20 trials from each session were the focus of our analysis. Since eight different call groups served as backgrounds (one per session), each subject was required to run eight sessions to complete the experiment.

#### 4. Testing procedure

The birds were trained to peck one key (observation key) repeatedly during a continuous presentation of multiple tokens from one call group (background) and to peck the other key (report key) when they detected a token from a different call group (target) that was presented alternately with the background tokens. Note that multiple tokens from the same group were used to train the birds so that they discriminated at the level of “call groups” instead of comparing them as individual sounds.

If the bird pecked the report key during the background-target alternation, the food hopper was activated for 1.5 s and the bird received access to food. This was recorded as a “hit.” If the bird failed to detect the target and did not peck the report key, it was recorded as a “miss.” If the bird did not peck the report key during sham trials where no target was presented, it was recorded as a “correct rejection.” Pecks to the report key during sham trials were recorded as “false alarms” and punished with a blackout period (2–10 s) during which all of the room lights were turned off and no sound was played back. Any other incorrect report key pecks were also recorded and punished with blackouts. The same trial (or next trial if it were a false alarm) resumed after the blackout period.

Birds were tested twice a day, 5 days a week. To minimize response biases and practice effects, birds ran on different experimental conditions in a random order. Earlier work has shown that response latency can be reliably used as a measure of stimulus similarity where long latencies reflect greater stimulus similarity and short latencies reflect greater stimulus differences (Dooling *et al.*, 1987a; Dooling and Okanoya, 1995; Dooling *et al.*, 1987b; Okanoya and Dooling, 1988). Here, response latencies were recorded for all trials. If the result of the trial was a miss, a maximum response latency of 2000 ms was recorded. A repeated-measures analysis of variance (ANOVA) was performed on these response latencies to test budgerigars’ discriminability between call groups using SPSS 16.0 software. Response latencies were expected to be longer when background and targets came from the same calls group of the same budgerigar (i.e., more difficult to discriminate) than when they were from different call groups of the same budgerigar (i.e., easier to discriminate).

Acoustic analysis showed that contact calls from different birds were distinctively different while warble call elements from these same birds clustered together in one large

group (Fig. 2). In other words, in a combined multidimensional scaling analysis, the difference between the contact calls of different birds was much greater than the differences between the warble call elements of these birds. While these results address acoustic differences among the vocalizations, they do not answer the question of whether these differences are discriminable. To determine whether budgerigars can discriminate contact calls and warble call elements of different individuals, the response latencies for detecting contact calls and warble call elements of individuals other than the individual providing the background calls were also analyzed by ANOVA and a least significant difference test (LSD) by SPSS 16.0 software.

#### B. Results

Figure 3 shows that the interaction between the call group identity of background and that of targets was highly significant in the vocalizations of all four budgerigars (Buzz: target  $F_{(1,39)} = 5.26$ ,  $p < 0.05$ ; background  $F_{(1,39)} = 7.12$ ,  $p < 0.05$ ; interaction  $F_{(1,39)} = 44.25$ ,  $p < 0.001$ ; Ricky: target  $F_{(1,39)} = 15.02$ ,  $p < 0.001$ ; background  $F_{(1,39)} = .23$ ,  $p = 0.63$ ; interaction  $F_{(1,39)} = 185.00$ ,  $p < 0.001$ ; Puffy: target  $F_{(1,39)} = 157.11$ ,  $p < 0.001$ ; background  $F_{(1,39)} = 12.54$ ,  $p < 0.01$ ; interaction  $F_{(1,39)} = 302.19$ ,  $p < 0.001$ ; Cosmo: target  $F_{(1,39)} = 0.05$ ,  $p = 0.83$ ; background  $F_{(1,39)} = 0.00$ ,  $p = 0.97$ ; interaction  $F_{(1,39)} = 39.82$ ,  $p < 0.001$ ). All subjects responded faster (i.e., easier discrimination) when the background and the target sounds are from different call groups of the same individual. However, this effect was not so obvious when Puffy’s warble call elements were in the background.

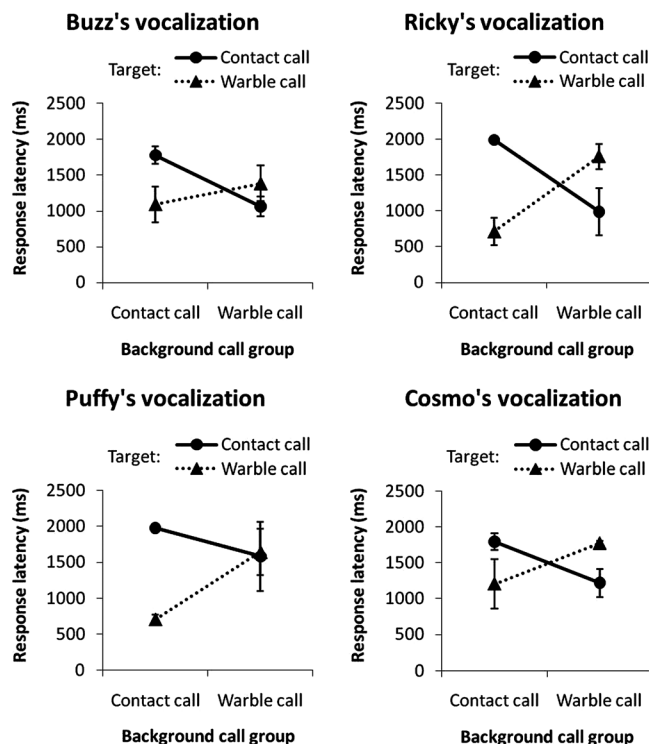


FIG. 3. Results of the psychophysical test on calls of each individual budgerigar. Significant interactions showed that response latencies were longer when the vocalizations of the targets and the background were from the same call group than when they were from different call groups. (Error bars indicate standard errors among four subjects.)

When warble call elements were in the background, subjects were significantly slower in detecting warble call elements from the same individual and significantly faster at detecting warble call elements from other individuals (Buzz:  $F_{(3,156)} = 12.35$ ,  $p < 0.001$ ; Ricky:  $F_{(3,156)} = 17.49$ ,  $p < 0.001$ ; Puffy:  $F_{(3,156)} = 11.03$ ,  $p < 0.001$ ; Cosmo:  $F_{(3,156)} = 41.84$ ,  $p < 0.001$ ). This was in spite of the fact that warble call elements across individuals are acoustically similar (Fig. 4). Similarly, when contact calls were in the background, subjects responded significantly faster to contact calls of other individuals than those of the individual in the background (Buzz:  $F_{(3,156)} = 64.96$ ,  $p < 0.001$ ; Ricky:  $F_{(3,156)} = 118.09$ ,  $p < 0.001$ ; Puffy:  $F_{(3,156)} = 121.63$ ,  $p < 0.001$ ; Cosmo:  $F_{(3,156)} = 30.74$ ,  $p < 0.001$ ).

### C. Discussion

These results show that budgerigars are able to: (1) discriminate among contact calls and warble call elements from the same individual and (2) recognize that there are common features among warble call elements from the same individual. In an aggregate multidimensional scaling analysis (Fig. 2), warble call elements from different birds are acoustically more similar to each other than are the contact calls from those same birds. In spite of this overall similarity in warble call elements of different individuals, response latency data show birds are able to extract certain constant features, so far unidentified, as the “vocal characteristics” of each individual. These data suggest that budgerigars, like humans, can form perceptual categories based on voice characteristics.

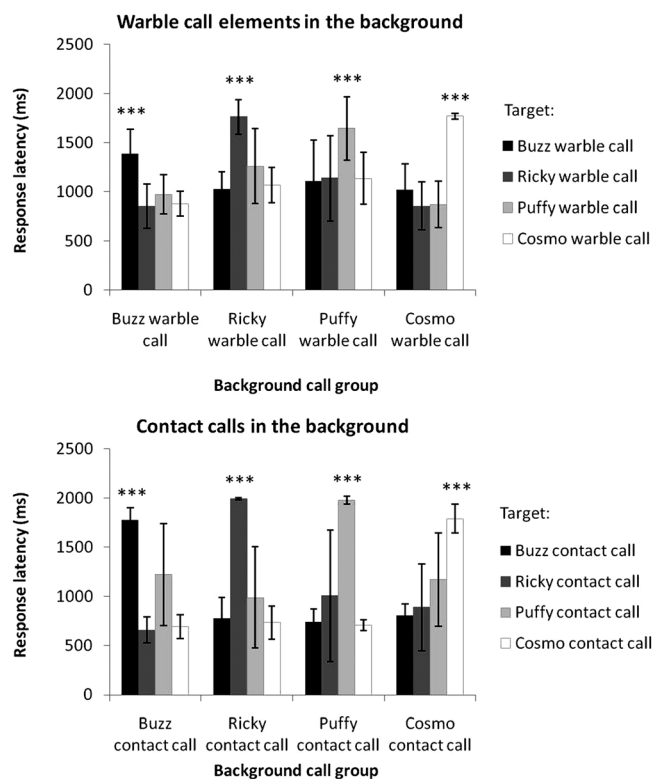


FIG. 4. Differences in response latencies when detecting warble call elements against a background of warble call elements (upper plot) and when detecting contact calls against a background of contact calls (lower plot). The responses were significantly slower when the background and the targets were from the same individual. (Error bars indicate standard errors among four subjects;  $p < 0.001$  is indicated with \*\*\*)

### V. GENERAL DISCUSSION

The warble song of budgerigars is composed of a number of acoustic elements, including warble call elements that look and sound very similar to learned contact calls. Together, contact calls and warble call elements comprise more than half of the vocalizations produced by budgerigars and must certainly play a significant role in budgerigar vocal communication. Both of these vocalizations are highly discriminable, falling in the sweet spot of best hearing and spectral resolving power of this species (Dooling *et al.*, 1987b; Farabaugh and Dooling, 1996). The present experiments provide converging evidence from acoustic analyses and from psychophysical testing showing that contact calls and warble call elements are acoustically and perceptually distinct and therefore probably belong to two different phonological systems in the budgerigar vocal repertoire both of which involve learning.

The present analysis of contact calls and warble call elements stimulates speculation about the role of learning in vocal communication in budgerigars. Earlier work has shown that contact calls can be acquired through production learning (Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994). There is no equivalent evidence that warble call elements are learned in a similar fashion and thus the etiology of these elements in warble remains obscure. Male birds that live together show more similarity in some of these warble elements than those who do not (Farabaugh *et al.*, 1992). One possibility is that warble call elements are a kind of precursor to contact calls that are used as single utterances. In this scenario, warble song functions as an arena for vocal practice for new or emerging contact call variants before they become accurate copies and are used in other contexts as single utterances. We have shown that budgerigars' secondary contact calls seem to be much closer to the warble call elements than the primary contact calls (Fig. 1), which is supportive to this hypothesis. To be fair, one argument against this hypothesis is that female budgerigars generally do not produce warble but can learn new contact calls, although they do so more slowly compared to males and typically have smaller repertoires (Hile and Striedter, 2000).

Among bird vocalizations, budgerigar warble is interesting for length, complexity, and repetition of a limited set of elements produced in apparently random sequences. It is also a critical part of a complex sequence of intimate courtship behaviors in budgerigars (Brockway, 1964b, 1965; Farabaugh *et al.*, 1992). Beyond this we know little about how information is encoded in this vocalization, how much of it is learned, and how much is production learning and how much is contextual learning. The fact that warble is composed of a finite set of element categories, is produced in long sequences, and is used in intimate contexts offers the possibility of intriguing new parallels with human speech in that information may be coded in the sequences of these learned elements.

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