Black-capped (*Poecile atricapillus*) and mountain chickadee (*Poecile gambeli*) contact call contains species, sex, and individual identity features

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The *tseet* contact call, common to both black-capped and mountain chickadees, is among the most frequently produced call of each species, but has remained little studied until now. In the current study, the authors characterized the *tseet* call of adult allopatric and sympatric black-capped and mountain chickadees in terms of nine acoustic features in a fashion similar to descriptive accounts of both species' *chick-a-dee* calls. Summary statistics, the potential for individual coding, and classification by linear discriminant analysis were used to describe the *tseet* call. The authors were able to correctly classify *tseet* calls in terms of which group or individual produced it with high accuracy. Furthermore, several acoustic features are highly individualized, indicating that the chickadees may use these features to identify signalers as individuals or members of a particular group. © *2010 Acoustical Society of America.* [DOI: 10.1121/1.3277247]

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I. INTRODUCTION

Bird calls are typically produced year round by both sexes and serve specific functional roles such as to deter predators, raise alarm within a flock, coordinate flock movement (Smith, 1991), announce or exchange food, and maintain group cohesion (Marler and Slabbekoorn, 2004). Previous studies have described the *chick-a-dee* call of black-capped chickadees (*Poecile atricapillus*), mountain chickadees (*P. gambeli*), Carolina chickadees (*P. Carolinensis*), and the closely related tufted titmice (*Baeolophus bicolor*). Quantitative analyses reveal that the note types within the *chick-a-dee* calls of all species are individualized, with significant differences between individuals (within each species) (Charrier *et al.*, 2004; Bloomfield *et al.*, 2004, 2005; Owens and Freeberg, 2007). However, whether other vocalizations common to both black-capped and mountain chickadees also contain features that convey information about the signalers' species, sex, or individual identity remain untested.

In addition to the *chick-a-dee* call, the *tseet* call is a contact call in the vocal repertoires of both black-capped and mountain chickadees. *Tseet* calls are the most frequently produced vocalization by black-capped chickadees (Odum, 1942) and, although not yet quantified, possibly by mountain chickadee as well (pers. obs.). Despite being the most commonly produced chickadee call-type, the *tseet* call has received little attention from researchers. In the present study, we examine the *tseet* calls of black-capped and mountain chickadees, the most closely related of the seven species of North American chickadees (Gill *et al.*, 2005).

The aim of the current study is to describe the *tseet* call of black-capped and mountain chickadees in a manner similar to previous work on the *chick-a-dee* call of these species. Specifically, we measure and examine nine acoustic features of the *tseet* calls of these species for evidence of individual identity features, and we classify calls according to the individual, species, and geographic origin for the birds that produced each call using linear discriminant analysis (LDA). We examine the *tseet* calls of (1) black-capped chickadees originating from regions that are also inhabited by mountain chickadees (sympatric group), (2) mountain chickadees from this same region, and (3) black-capped chickadees originating from regions where there are no mountain chickadees (allopatric group).

II. METHODS

A. Subjects

A total of 30 birds of at least 1 year of age (determined by the shape and coloring of outer tail retrices, Pyle, 1997) were captured between March 2002 and March 2004. Ten black-capped chickadees (5 male, 5 female) originated from several locations in Edmonton, Alberta, Canada (53° 06′N, 113° 04′W) and had no experience with mountain chickadees since both species are relatively non-migratory, and

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mountain chickadees do not inhabit the Edmonton area. Thus, black-capped chickadees originating from Edmonton are referred to as the allopatric group throughout. Ten mountain chickadees (5 male, 5 female) and ten black-capped chickadees (5 male, 5 female) were captured from several location in Kananaskis Valley (Alberta, Canada, 51° 02′N, 115° 03′W), approximately 300 km southwest of Edmonton. In Kananaskis, mountain and black-capped chickadees co-occur and can be observed foraging in close proximity of each other (pers. obs.), and hence, black-capped chickadees originating from Kananaskis are referred to as the sympatric group. Sex identification was conducted by DNA analysis (Griffiths and Double, 1998).

Each species was housed separately at the University of Alberta in individual Jupiter Parakeet cages ($0.3 \times 0.4 \times 0.4$ m; Rolf C. Hagen, Inc., Montreal, Canada). Housing conditions allowed for auditory and visual contacts, but not physical contact with conspecifics. Birds had food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), water (vitamin supplemented on alternate days; Hagen, Rolf C. Hagen, Inc., Montreal, Canada), grit, and cuttle bone *ad libitum*. Birds were given three to five sunflower seeds daily. Birds also received one mealworm three times a week and a mixture of eggs and greens twice a week. Birds were maintained on a light-dark cycle that mimicked the natural cycle for Edmonton, Alberta.

B. Recordings

Birds were individually recorded in a sound attenuating chamber ($1.83 \times 1.83 \times 1.83$ m, Industrial Acoustics Corporation, Bronx, NY) using an AKG C 1000S condenser microphone connected to a Marantz PMD 670 digital recorder (frequency response: 10–20 000 Hz; Marantz Electronics, Eindhoven, The Netherlands). Digitized files (44 100 Hz) were downloaded to an Intel based PC and analyzed with SIGNAL 4.0 (Engineering Design, Berkeley, CA).

C. Acoustic analysis

Ten high quality (e.g., not distorted from cage noise), clearly classifiable (i.e., not another note type produced in isolation from a call) *tseet* notes were randomly selected from several recording sessions for each bird. To standardize all analyses with similar resolution, each individual call was saved as a separate file with a duration of 300 ms by adding leading and trailing silence to each file. Three temporal and three spectral measures were taken from the sound spectrograms (cut-off amplitude of −35 dB relative to peak amplitude) and fast Fourier transforms (FFTs, settings for temporal measures: Hanning window=256 points, precision=5.8 ms; FFT settings for spectral measures: Hanning window=1024 points, precision=43 Hz).

The three temporal measures are (1) the ascending duration (AD), which is measured from the start of the call to the point where the rapid frequency modulation ends; (2) the descending duration (DD), which is measured from the highest frequency of the call where the call begins to descend in frequency, until the end of the call; and (3) the total duration (TD) of the call. The three frequency measures are (1) the

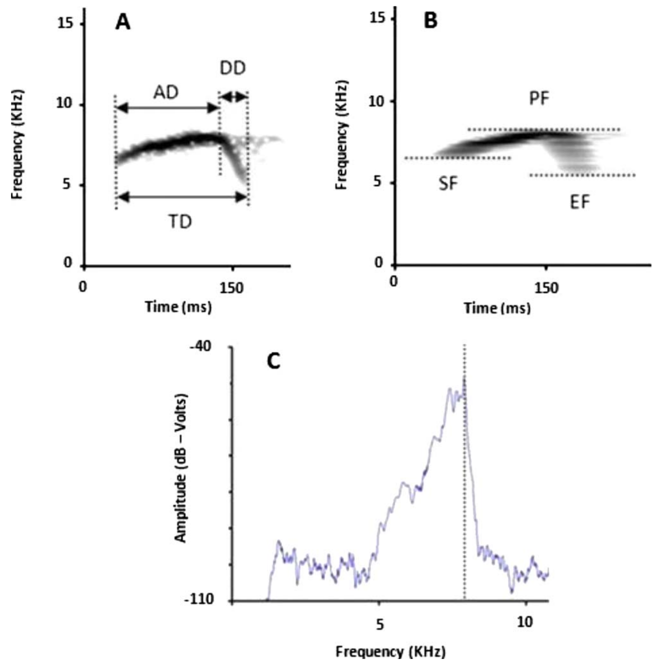

FIG. 1. (Color online) Sound spectrogram and spectrum illustrating note-type features measured in *tseet* calls. Panel A: Frequency (*y*-axis) by time (*x*-axis) sound spectrogram (FFT window=256 points) of a *tseet* call. Vertical lines represent approximate boundaries for ascending duration (AD), descending duration (DD), and total note duration (TD). Panel B: Frequency (*y*-axis) by time (*x*-axis) sound spectrogram (FFT window=1024 points) of a *tseet* call. Horizontal lines illustrate the start frequency (SF), peak frequency (PF), and end frequency (EF). Panel C: Relative amplitude (*y*-axis) by frequency (*x*-axis) sound spectrum (window size=4096 points) of a *tseet* call. The vertical line illustrates the frequency at max amplitude (Fmax).

start frequency (SF), (2) the peak frequency (PF), and (3) end frequency (EF) of the call. Three additional features of the calls are (1) the maximum (i.e., loudest) frequency (Fmax), which was measured in a spectrum window (modal window size=4096 points; (2) the rate of rise for the ascending slope (FMasc), which was calculated using the formula (PF − SF)/AD; and (3) the rate of decay in the descending slope (FMdesc), which was calculated using the formula (EF − PF)/DD (see Fig. 1).

III. RESULTS

A. Classification of *tseet* calls by individuals

Bloomfield and Sturdy (2008) demonstrated that black-capped chickadees can memorize up to 15 individual black-capped and mountain chickadee *chick-a-dee* calls, each from a unique individual. For birds to be able to discriminate among individuals based on their *tseet* calls, one or more of the nine acoustic features outlined above may contain information specific to each individual within a group. One or more acoustic parameter(s) must have high individual stereotypy and thus may be used by conspecifics for individual identification. If this is the case, then acoustic variation in a single feature among all *tseet* calls in a group (e.g., SF for all mountain chickadees) must be greater than the acoustic variation in that same feature within an individual's calls (e.g., average SF for an individual mountain chickadee). To identify the acoustic parameters that may contain individual identity in the *tseet* call, we examined the potential for individual coding (PIC) (Charrier *et al.*, 2004). The PIC value is the ratio of the coefficient of variation between individuals (CV_b) to the average of the coefficients of variation within an individual (CV_w) for a particular group (e.g., allopatric chickadees). In this formulation, $CV_b=(SD/X)\times 100$, where SD is the standard deviation of the group (e.g., allopatric chickadees), X is the group mean for an acoustic feature (e.g., PF), and CV_w is the average of the coefficients of variation for each individual in that group. Acoustic features that yield a PIC value greater than 1 are potentially used for individual recognition since the inter-individual variability (for that specific acoustic feature) is greater than the intra-individual variability (Sokal and Rohlf, 1995).

Table I shows the means, standard deviations, coefficients of variations within and between individuals, and the PIC. While all PIC values are greater than 1 (i.e., for each species, allopatric or sympatric and each sex), the *tseet* call of males tended to have more individualized acoustic features than the *tseet* call of their female counterparts. Across all sympatric birds the acoustic features with the highest PIC values are the spectral features of start and end frequencies. For allopatric chickadees, the acoustic feature with the highest PIC value is the total duration.

We employed stepwise LDAs (SPSS 15.0 for Windows) to classify each *tseet* call in terms of which individual or group of chickadees produced it. If it is possible for chickadees to use a feature, or a combination of features from *tseet* calls to identify individuals as belonging to a particular group, then it follows that the LDA should be able to predict group membership with a high degree of accuracy (see Dawson *et al.*, 2006). Several different LDAs were preformed; each LDA could use the nine different acoustic features, outlined in the acoustic analysis section above, as independent variables to classify *tseet* calls into groups according to which chickadee produced the call.

Analyzing errors in the LDA predictions (i.e., when the LDA identifies a *tseet* call as being produced by the incorrect individual or group of chickadees) is a useful tool to understand subtle similarities and differences between the *tseet* calls produced by the different individuals, groups, and sexes. In LDA the squared canonical correlation (R_c^2) can be interpreted as the proportion of variation that is accounted for by the independent variables. The standardized discriminant function coefficient is used to assess the relative importance of each independent variable through its unique contribution to a particular discriminant function (Betz, 1987; Klecka, 1980). The limitation of interpreting the standardized discriminant function coefficient is that variables that are highly correlated share contributions to the discriminant score. Therefore we have also included the structure coefficients, the bivariate correlation between the variable and discriminant function which therefore are not influenced by covariances with other variables. Structure coefficients identify the aspect of the discriminant function that discriminates between groups (Klecka, 1980).

Nine stepwise LDAs were conducted to classify *tseet* calls in terms of which individual produced it. A separate LDA was conducted for each group of birds (male allopatric, female allopatric, male sympatric, female sympatric, male mountain, female mountain, all allopatric, all sympatric, and all mountain chickadees). The purpose of these LDAs is twofold: (1) to determine the ability of the model to correctly classify each *tseet* call in terms of which individual produced it and (2) to determine the correspondence between the feature with the highest PIC and the feature that was loaded most heavily on (standardized coefficient) or correlated with (structure coefficient) the first discriminant function for each group of birds. In this way, we used two complimentary statistical techniques for assessing individualization of *tseet* calls.

Table II shows a summary of the LDAs conducted to classify *tseet* calls in terms of which individual in a distinct group produced the call. The original and cross-validation of correctly identified cases, along with the eigenvalue and the canonical correlation, the standardized discriminant function coefficient, and structure coefficient for the first discriminant functions are listed. For four groups of birds, the feature with the largest standardized discriminant function coefficient and largest structure coefficient for the first discriminant function matches the feature which yielded the highest PIC: TD for female allopatric black-capped chickadees, SF for female sympatric chickadees, SF for male and female sympatric chickadees combined, and EF for male and female mountain chickadees combined, although the combined group is likely driven by the males in the mixed sex mountain group. There was almost a perfect match, with the exception of female mountain chickadees, for the type of feature (temporal vs spectral) with the highest PIC value and highest structure coefficient, suggesting that these features account for the majority of the individual differences in *tseet* calls within each group.

B. Classification of *tseet* calls into groups

Another LDA classified *tseet* calls into three groups, namely, calls produced by allopatric chickadees, calls produced by sympatric chickadees, and calls produced by mountain chickadees. The purpose of this LDA was to classify each call in terms of the bird (allopatric, sympatric, and mountain chickadees) that produced it using the nine acoustic measures. Two discriminant functions (function 1 eigenvalue=3.716, $R_c^2=0.889$; function 2 eigenvalue =1.216, $R_c^2=0.6741$) correctly classified *tseet* calls in terms of species and geographic origin in 87.7% of cases (see Table III). A z-test for the differences between two proportions shows that the predictions yielded by the LDA are significantly better than predictions expected by chance for allopatric black-capped ($z=9.01$, $p<0.05$), sympatric black-capped ($z=6.07$, $p<0.05$), and mountain chickadees ($z=9.28$, $p<0.05$, Betz, 1987; Glass and Stanely, 1970). All but one of the nine acoustic measures (AD) contributed to the discriminant functions (see Table IV). From examining group centroid loadings on the discriminant functions, we see that function 1 separates allopatric black-capped from mountain chickadees and the acoustic measure with the largest standardized coefficient for function 1 is end frequency. The second discriminant function separated the sympatric black-

TABLE I. Means, standard deviations, between-bird coefficients of variation (CV_b), within-bird coefficients of variation (CV_w), and PIC for each acoustic feature measured in *tseet* calls. ΣPIC is the sum of the PIC values for that group.

		TD	AD	DD	SF	PF	EF	Fmax	FMasc	FMdesc
					Male allopatric					
ΣPIC=15.34	X	54.67	36.70	12.04	6009.12	7590.27	4264.49	7127.07	46.43	−284.01
	SD	7.66	10.38	3.57	434.67	564.05	651.31	478.49	17.45	91.99
	CV_b	14.01	28.29	29.63	7.23	7.43	15.27	6.71	37.58	−32.39
	CV_w	4.84	15.18	20.58	5.35	3.69	11.16	4.32	28.07	−21.37
	PIC	2.89	1.86	1.44	1.35	2.01	1.37	1.55	1.34	1.52
					Female allopatric					
ΣPIC=11.44	X	48.61	36.43	10.85	5907.02	7619.89	4678.73	7153.96	48.20	−275.79
	SD	7.37	6.34	1.78	367.27	299.35	600.00	371.97	12.05	63.64
	CV_b	15.17	17.41	16.43	6.22	3.93	12.82	5.20	24.99	−23.08
	CV_w	10.42	12.05	13.03	5.53	3.19	9.36	3.94	23.19	−19.96
	PIC	1.46	1.44	1.26	1.12	1.23	1.37	1.32	1.08	1.16
					Male sympatric					
ΣPIC=16.20	X	52.56	19.62	11.08	5959.33	7736.13	6785.75	7734.68	68.43	−148.26
	SD	6.80	9.20	4.55	836.86	334.06	394.38	263.52	20.26	88.76
	CV_b	12.94	46.91	41.08	14.04	4.32	5.81	3.41	29.61	−59.87
	CV_w	6.85	32.09	30.69	5.17	2.07	4.00	1.30	27.41	−38.43
	PIC	1.89	1.46	1.34	2.72	2.08	1.45	2.62	1.08	1.56
					Female sympatric					
ΣPIC=15.85	X	47.97	33.87	12.95	5006.43	7306.42	5559.13	7371.12	47.18	−228.28
	SD	4.61	5.41	1.86	831.48	405.82	630.32	303.79	9.52	35.80
	CV_b	9.62	15.97	14.34	16.61	5.55	11.34	4.12	20.17	−15.68
	CV_w	8.10	13.68	9.96	4.65	2.60	5.73	2.11	19.08	−11.62
	PIC	1.19	1.17	1.44	3.57	2.14	1.98	1.96	1.06	1.35
					Male mountain					
ΣPIC=17.33	X	79.72	39.67	17.92	5600.30	6901.08	5621.67	6705.55	40.09	−68.75
	SD	18.46	13.99	6.69	1137.85	511.96	1133.88	482.63	32.62	21.14
	CV_b	23.15	35.27	37.35	20.32	7.42	20.17	7.20	81.37	−30.75
	CV_w	12.84	29.88	22.02	9.44	3.67	6.58	3.58	43.37	−20.23
	PIC	1.80	1.18	1.70	2.15	2.02	3.06	2.01	1.88	1.52
					Female mountain					
ΣPIC=11.79	X	61.95	30.03	15.04	6416.82	7364.21	6527.00	7125.56	32.08	−58.41
	SD	9.61	15.04	4.98	493.66	348.72	506.42	329.86	16.41	17.47
	CV_b	15.52	50.07	33.12	7.69	4.74	7.76	4.63	51.16	−29.91
	CV_w	12.41	37.64	24.66	3.94	2.64	4.25	2.49	54.44	−30.32
	PIC	1.25	1.33	1.34	1.95	1.79	1.83	1.86	0.94	0.99
					Allopatric					
ΣPIC=13.70	X	51.64	36.57	11.45	5958.07	7605.08	4471.61	7140.52	47.32	−279.90
	SD	8.08	8.56	2.87	403.62	449.49	656.87	426.60	14.94	78.81
	CV_b	15.64	23.41	25.06	6.77	5.91	14.69	5.97	31.58	−28.16
	CV_w	7.63	13.61	16.80	5.44	3.44	10.26	4.13	25.63	−20.67
	PIC	2.05	1.72	1.49	1.25	1.72	1.43	1.45	1.23	1.36
					Sympatric					
ΣPIC=19.21	X	50.26	26.74	12.02	5482.88	7521.27	6172.44	7552.90	57.80	−188.27
	SD	6.23	10.38	3.58	958.18	428.22	808.44	336.79	19.03	78.43
	CV_b	12.39	38.80	29.83	17.48	5.69	13.10	4.46	32.92	−41.66
	CV_w	7.48	22.88	20.32	4.91	2.33	4.87	1.70	23.25	−25.02
	PIC	1.66	1.70	1.47	3.56	2.44	2.69	2.62	1.42	1.66
					Mountain					
ΣPIC=16.47	X	70.83	34.85	16.48	6008.56	7132.65	6074.34	6915.55	36.08	−63.58
	SD	17.15	15.24	6.05	964.26	494.04	985.02	462.27	26.00	19.98
	CV_b	24.21	43.73	36.69	16.05	6.93	16.22	6.68	72.06	−31.43
	CV_w	12.67	33.70	23.50	7.19	3.53	5.89	3.41	47.28	−24.80
	PIC	1.91	1.30	1.56	2.23	1.96	2.75	1.96	1.52	1.27

TABLE II. The original (Orig) and cross-validated (Cross) percent of cases correctly classified by individual identity by stepwise linear discriminant analysis for all groups of birds, M=male, F=female, allop =allopatric black-capped chickadee, sym=sympatric black-capped chickadee, mo=mountain chickadee. The eigenvalue (Eigen) and canonical correlation (R_c^2), acoustic feature with the highest standardized canonical function coefficient (Std coeff), and highest structure coefficient (Str coeff) for the first discriminant function. PIC represents the acoustic feature, which yielded the highest PIC value. TD=total duration, AD=ascending duration, DD=descending duration, Fmax=frequency at loudest amplitude, SF=start frequency, EF=end frequency, and PF=peak frequency.

Group	Orig	Cross	Eigen	R_c^2	Std coeff	Str coeff	PIC
M allop	86	82	8.888	0.948	PF	TD	TD
F allop	60	56	1.211	0.74	TD	TD	TD
M sym	92	88	11.92	0.961	Fmax	Fmax	SF
F sym	98	96	36.021	0.986	SF	SF	SF
M mo	84	70	12.25	0.962	Fmax	EF	EF
F mo	88	70	5.316	0.917	Fmax	AD	SF
Allop	63	48	3.448	0.88	PF	DD	TD
Sym	95	88	18.895	0.975	SF	SF	SF
Mo	75	58	10.097	0.954	EF	EF	EF

capped chickadees from allopatric black-capped and mountain chickadees. The feature with the largest standardized coefficient for function 2 is Fmax. Both functions combined yielded Wilks's lambda=0.095, distributed as $\chi^2(16,N=299)=691.514$ and $p<0.001$, indicating that the group centroids differed significantly from each other and indicating that the model is successfully discriminating among the groups.

The last LDA classified *tseet* calls into six groups, namely, calls produced by either male allopatric, female allopatric, male sympatric, female sympatric, male mountain, and female mountain chickadees, also based on the nine acoustic measures obtained from our sample of *tseet* calls. Five discriminant functions correctly classified *tseet* calls in terms of sex, species, and geographic origin in 67.7% of all cases (see Table V). While all five functions combined yielded Wilks's lambda=0.033, distributed as $\chi^2(35,N=299)=996.358$ and $p<0.001$, the first two discriminant functions accounted for the majority (88.7%) of the variance accounted for overall. In the first discriminant function both EF (2.396) has large standardized function coefficients, while Fmax (−0.641) has the largest standardized function coefficients in the second discriminant function (see Table VI). A z-test for the differences between two proportions show that the predictions yielded by the LDA are significantly better ($p<0.05$) than predictions expected by chance for all groups (male allopatric, $z=20.48$; female allopatric, $z=22.33$; male sympatric, $z=32.86$; female sympatric, z

TABLE III. Matrix of classification by group membership of the actual groups of chickadees *tseet* calls and the LDA predicted group classification based on nine measured acoustic features. Correct LDA classification are presented (in percentages) along the diagonal in bold. Misclassifications are presented (in percentages) in corresponding rows and columns. Allopatric =allopatric black-capped chickadees, Sympatric=sympatric black-capped chickadees, and Mountain=mountain chickadees. Overall, 89.3% of original cases are classified correctly and 87.7% of cross-validated cases are classified correctly.

	LDA predicted group classification		
Actual group	Allopatric	Sympatric	Mountain
Allopatric	**91**	4	5
Sympatric	18	**76**	6
Mountain	0	4	**96**

TABLE IV. Group centroids, discriminant structure matrix, and the standardized canonical discriminant function coefficients for discriminant analysis of the acoustic measures used to classify *tseet* calls in terms of the group of birds producing each call. BC=black-capped chickadee, Allop =allopatric, Sym=sympatric, MO=mountain chickadee, TD=total duration, DD=descending duration, PF=peak frequency, EF=end frequency, FMasc =rate of rise in ascending slope, FMdesc=rate of fall in descending slope, and Fmax=frequency at loudest amplitude.

	Discriminant function	
	1	2
Group	Group centroids	
BC Allop	−2.404	−0.734
BC Sym	0.084	1.551
MO	2.320	−0.817
Variable	Discriminant structure matrix	
FMdesc	0.699	−0.147
DD	0.239	−0.204
PF	−0.216	0.155
Fmax	−0.106	−0.553
EF	0.418	−0.445
TD	0.345	−0.428
FMasc	−0.110	0.344
SF	0.008	−0.263
Variable	Standardized coefficients	
FMdesc	0.302	−0.124
DD	0.500	−0.136
PF	0.051	−0.714
Fmax	−0.388	1.059
EF	1.150	0.393
TD	0.402	−0.125
FMasc	0.302	−0.124
SF	−0.327	−0.482

TABLE V. Matrix of classification by group membership and sex of the actual groups of chickadee *tseet* calls and the LDA predicted group classification based on nine measured acoustic features. Correct LDA classifications are presented (in percentages) along the diagonal in bold. Misclassifications are presented (in percentages) in corresponding rows and columns. Allopatric=allopatric black-capped chickadees, sympatric=sympatric black-capped chickadees, and mountain=mountain chickadees. Overall, 70.7% of original cases are classified correctly and 67.7% of cross-validated cases are classified correctly.

	LDA predicted group classification					
Actual group	Male allopatric	Female allopatric	Male sympatric	Female sympatric	Male mountain	Female mountain
Male allopatric	**56**	42	2	0	0	0
Female allopatric	28	**60**	0	10	2	0
Male sympatric	0	0	**82**	10	0	8
Female sympatric	2	36	0	**62**	0	0
Male mountain	0	0	2	0	**58**	40
Female mountain	0	0	4	0	8	**88**

=23.24; male mountain, z=21.40; and female mountain, z =35.75).

IV. DISCUSSION

Bioacoustic analyses can provide insight into the particular features of vocal signals that may potentially convey species, sex, geographic origin, and individual identity. Here we use bioacoustic analyses as a first step toward characterizing temporal and spectral regularities found in chickadee *tseet* calls produced by different species, sexes, and individuals from different geographic regions. These differences in signal characters are potentially useful for discrimination

TABLE VI. Eigenvalues, canonical correlations (R_c^2), group centroids, discriminate structure matrix, and standardized canonical discriminant function coefficients for discriminant analysis of the acoustic measures used to classify *tseet* calls in terms of the group of birds producing each call. M=male, F=female, allop =allopatric black-capped chickadee, sym=sympatric chickadee, mo=mountain chickadee, FMdesc=rate of fall in descending slope, AD=ascending duration, DD=descending duration, TD=total duration, SF=start frequency, EF=end frequency, PF=peak frequency, and FMasc=rate of rise in ascending slope.

	Discriminant function				
	1	2	3	4	5
Eigenvalue	5.069	1.46	0.491	0.31	0.034
R_c^2	0.914	0.77	0.574	0.487	0.181
Group			Group centroids		
M allop	−2.931	0.629	0.526	0.145	−0.279
F allop	−2.598	0.179	0.264	−0.179	0.334
M sym	1.667	−2.056	0.647	0.432	0.003
F symp	−0.827	−0.908	−1.415	−0.084	−0.059
M mo	2.291	1.703	−0.257	0.717	0.054
F mo	2.398	0.453	0.236	−1.031	−0.053
Variable			Discriminant structure matrix		
EF	0.513	−0.496	0.047	−0.358	0.163
TD	0.307	0.637	0.061	0.606	−0.330
DD	0.168	0.335	−0.246	0.109	−0.346
AD	−0.109	0.433	−0.307	0.098	0.257
SF	0.048	0.076	0.734	−0.471	−0.131
FMasc	−0.030	−0.375	0.211	0.544	0.266
Fmax	−0.020	−0.668	0.148	−0.091	−0.350
Variable			Standardized coefficients		
EF	1.396	−0.211	−0.150	−0.173	0.502
TD	0.569	0.242	0.222	0.819	−0.528
DD	0.530	0.179	−0.199	−0.498	−0.117
AD	−0.145	0.326	−0.073	0.313	0.728
SF	0.018	0.390	1.085	−0.366	0.218
FMasc	0.154	−0.268	0.636	0.616	0.846
Fmax	−0.406	−0.614	−0.058	0.474	−0.913

among black-capped and mountain chickadees, male and female chickadees, and individual chickadees within each group.

A. Classification by individuals

The *tseet* call seems to be a reliable indicator of individual identity for most but not all of the groups in our study. For allopatric black-capped chickadees, who live in areas devoid of mountain chickadees, males *tseet* calls are more highly individualized and easier to classify than female *tseet* calls. However, for both sympatric black-capped and mountain chickadees, *tseet* calls of both males and females can be classified with high accuracy, suggesting that the *tseet* call is highly individualized in both sexes in these populations. This could perhaps be due to the different habitats of sympatric and mountain chickadees compared to allopatric chickadees. The population of allopatric chickadees were captured in the North Saskatchewan River valley in Edmonton, Alberta, while the sympatric and mountain chickadees originated from Kananaskis, Alberta, which is a more densely wooded, expansive forest compared to the Edmonton location. Perhaps individual identification of vocalizations has a higher benefit in the latter; thus the *tseet* call has evolved to be more highly individualized in both sexes in both groups of chickadees that reside in Kananaskis. An alternative theory for the high individuality of *tseet* calls in the Kananaskis population could be explained by acoustic character displacement. Acoustic character displacement is the results of a process by which features (morphological, acoustic, etc.) diverge over time so that two or more closely related species which cohabitat becomes increasingly dissimilar (Brown and Wilson, 1956). Although we would need to examine the *tseet* calls of allopatric mountain chickadees to confirm this claim, it does appear that the *tseet* calls of closely related heterospecifics are more highly individualized compared to a population of one species that live in an area of allopatry.

Overall, we see a correspondence between LDA and PIC with regard to which feature (temporal or spectral) is more unique to each individual. Of course, the next step is to test the birds in a categorization experiment, manipulating individual features or sets of acoustic features of within the *tseet* calls. Charrier and colleagues (Charrier *et al.*, 2005; Charrier and Sturdy, 2005) conducted a similar classification study on black-capped chickadees by manipulating sets of acoustic features for different note types of the *chick-a-dee* call. The performance of the birds on an acoustic discrimination task demonstrated an increase in misclassification of certain note types as they were shifted into the frequency space occupied by other note types.

Predictions yielded from the current data set would suggest that shifting the peak, end and loudest frequencies higher in mountain chickadee *tseet* calls would result in these calls being classified as *tseet* calls produced by sympatric black-capped chickadees. These types of studies could provide insight into featural evolution that could be the result of acoustic character displacement between sympatric black-capped and mountain chickadees.

B. Classification by species and geography

We were able to use the acoustic features contained in *tseet* calls to correctly, statistically, and significantly classify birds on the basis of both species and geographic region of origin with a high degree of accuracy. The best classified groups were allopatric and mountain chickadees. When allopatric black-capped chickadees were misclassified in this analysis, they were equally misclassified as mountain and sympatric black-capped chickadees. Although this is unexpected initially that allopatric black-capped chickadees would be classified as mountain chickadees, it follows if (1) both groups are thought to descend from a common chickadee ancestor and (2) neither are under any current pressure to modify their vocalizations, thus allowing the *tseet* call to remain in a more common ancestral form.

Allopatric chickadees from our study population reside in areas with limited contact with congeners—there are no mountain chickadees and few, widely dispersed boreal chickadees. In contrast to allopatric and mountain chickadees, sympatric black-capped chickadees are classified correctly with less accuracy than the other groups and are misclassified three times as often as allopatric black-capped chickadees compared to mountain chickadees. Of all three groups, sympatric chickadees are in the most constant contact with congeners; sympatric chickadees are in contact with altitudinal-migrating mountain chickadees both in the winter and also during the spring and summer, as well as boreal chickadees. We hypothesize that these differences in the amount of contact with congeners may have given rise to the differences observed in *tseet* call production.

C. Classification by species, geography, and sex

Classification of *tseet* calls according to more specific groupings of male and female for allopatric, sympatric, and mountain chickadees was correct in only 68% of cases overall. Nonetheless, the relatively poorer level of classification by the model allows us to look at misclassifications to examine subtle similarities of *tseet* calls produced by the different sexes within and between populations. Male allopatric black-capped and male mountain chickadees were most frequently misclassified as in-group (i.e., within the same species) females and rarely misclassified as out-group birds. In contrast, male sympatric chickadees were nearly equally misclassified as in-group females and female mountain chickadees. Although the classification results at the level of sex within group are less clear than those observed for individuals within group or species by location, it is too early at this point to determine whether this differentiation is simply too difficult to achieve using the current methodology or, alternatively, whether more accurately classifying by species, geography, and sex requires a larger sample of birds and their calls.

Although all nine features we measured were initially included in the LDA, a stepwise analysis revealed that only seven features contributed significantly to the model. Thus, although a linear analysis can use all acoustic features to classify calls, all features are not required. This supports the notion that some acoustic features may be more critical than others not only in a statistical classification procedure but in the field when birds are discriminating on the basis of this vocalization.

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