

Statistical Classification of Black-Capped (*Poecile atricapillus*) and Mountain Chickadee (*Poecile gambeli*) Call Notes

Michael R. W. Dawson, Laurie L. Bloomfield, Isabelle Charrier, and Christopher B. Sturdy
University of Alberta

Both black-capped (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*) produce a chick-a-dee call that consists of several distinct note types. In some regions, these 2 species live sympatrically, and it has been shown that 1 species will respond weakly to songs of the other. This suggests that chickadee song, and potentially other of their vocalizations, contains species-specific information. We tested the possibility that call notes were acoustically sufficient for species identification. Black-capped and mountain non-D notes were summarized as a set of 9 features and then analyzed by linear discriminant analysis. Linear discriminant analysis was able to use these notes to identify species with 100% accuracy. We repeated this approach, but with black-capped and mountain D notes that were summarized as a set of 4 features. Linear discriminant analysis was able to use these notes to identify species with 94% accuracy. This demonstrates that any of the note types in these chickadee calls possesses sufficient information for species classification.

Keywords: songbirds, vocalizations, classification, bioacoustics

Songbirds are a model of choice for understanding vocal communication using learned vocalizations (Slater, 2003). Songbirds are particularly useful not only because of the important role that vocal communication plays in their survival, but also because they learn many of their communication sounds in a manner considered analogous to human vocal learning (Doupe & Kuhl, 1999). This is based on several pieces of evidence, including the fact that songbirds learn vocalizations from a model, that they do so early in development during a critical period, and that they require auditory feedback to acquire and maintain their vocalizations. Thus, by understanding the mechanisms that underlie songbird vocal com-

munication, we may also gain insight into human acoustic communication.

Not only do songbirds learn many of their vocalizations, but they use learned communication sounds in several contexts (for a review, see Catchpole & Slater, 1995). Male songbirds learn and produce song, typically thought to be the most complex vocalization songbirds produce, and use song to attract females and repel rivals. Some female songbirds, in turn, perceive male song to gauge fitness and use song quality as a guide with which to choose a mate. Song is not the only acoustic signal that songbirds use or acquire through imitative learning and as such should not be the end point to studies of acoustic communication in songbirds.

In addition to learned song, songbirds also learn, produce, and perceive species-specific calls (e.g., Hughes, Nowicki, & Lohr, 1998; see Marler, 2004, and Vicario, 2004, for reviews). Calls are used in a number of specific, well-defined behavioral circumstances. In contrast to songs, calls are generally regarded as less acoustically complex. As such, the study of calls is frequently overlooked in the more general study of songbird communication. To gain a truly comprehensive understanding of songbird acoustic communication, research must extend to the detailed understanding of learned calls and not simply be limited to the study of learned song.

This study explores the species-specific chick-a-dee calls of two different species of North American chickadees. In particular, it investigates the extent to which the different notes that make up these calls possess sufficient acoustic information to permit species identification and thus to perform a biologically relevant task of natural categorization. In other words, we set out to determine whether there was an acoustical–statistical basis for sorting call notes by species based solely on the acoustic properties of the call notes themselves. Evidence suggests (e.g., Bloomfield, Sturdy, Phillmore, & Weisman, 2003) that chickadees treat chick-a-dee calls as open-ended categories and can quickly and easily sort call exemplars by species in operant conditioning tasks. The mecha-

Michael R. W. Dawson, Laurie L. Bloomfield, and Isabelle Charrier, Department of Psychology, University of Alberta, Edmonton, Alberta, Canada; Christopher B. Sturdy, Department of Psychology and Centre for Neuroscience, University of Alberta, Edmonton, Alberta, Canada.

Isabelle Charrier is now a member of the Bioacoustics Team, Université Paris Sud, Orsay, France.

This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) discovery grant, start-up funding from the University of Alberta, an Alberta Ingenuity New Faculty grant, NSERC and Social Sciences and Humanities Research Council of Canada research grants, NSERC Grant PGS-B, an Alberta Ingenuity Studentship, an Isaac Walton Killam Memorial Trust postdoctoral fellowship, and an Alberta Ingenuity Fund postdoctoral fellowship. This research was approved by the University of Alberta Biological Sciences Animal Care Committee (Protocol No. 351201) and University of Calgary Life and Environmental Sciences Animal Care Committee (Protocol No. BI2001-028). Birds were captured under Environment Canada, Canadian Wildlife Service Scientific Permit WSA-1-02; Alberta Fish and Wildlife Research Permits 4619 GP, 4621 GP, and 8734 GP; and Collection Licenses 088 CN, 089 CN, and 147 CN.

Correspondence concerning this article should be addressed to Christopher B. Sturdy or Michael R. W. Dawson, P-217 Biological Sciences Building, Department of Psychology, University of Alberta, Edmonton, AB T6G 2E9, Canada. E-mail: sturdy@ualberta.ca or mdawson@ualberta.ca

nism behind this ability remains unknown. As a preliminary step, we use statistical techniques to discriminate between chick-a-dee call notes produced by black-capped and mountain chickadees and thus to begin to understand the mechanism underlying a biologically relevant categorization task that chickadees, and in fact all animals that use acoustic communication, must perform with accuracy in the wild.

The black-capped chickadee is one of seven chickadee species native to North America. Of these seven species, the mountain chickadee represents the species most closely related to the black-capped chickadee (Gill, Mostrom, & Mack, 1993). Whereas the black-capped chickadee inhabits the northern United States and most of Canada, the mountain chickadee inhabits the western edge of North America, from the Yukon to New Mexico (McCallum, Grundel, & Dahlsten, 1999; Smith, 1993). In some regions, however, such as in the Canadian Rocky Mountains, both of these species can be found.

In contrast to many songbird species, black-capped chickadee song is significantly less complex than their learned chick-a-dee calls (Hughes et al., 1998). The chick-a-dee call is one of the most well-studied vocalizations of the black-capped chickadee and is the basis for which the species was named (Ficken, Hailman, & Hailman, 1994). This call contains four note types, labeled A, B, C, and D, and is interesting because, although its component notes are generated in a fixed order ($A \rightarrow B \rightarrow C \rightarrow D$), in a particular call note types can be either repeated or omitted. As a result, a seemingly unlimited variety of different chick-a-dee calls can potentially be produced (e.g., ACCCCD, ABDDD). Indeed, the combinatorial nature of the chick-a-dee call has been used to draw interesting analogies between it and human speech (Hailman, Ficken, & Ficken, 1985).

The chick-a-dee call of the mountain chickadee is acoustically similar to that of the black-capped chickadee and is also used when the bird is mildly alarmed or in flock movement (Gaddis, 1985). One difference between this and the black-capped chickadee's chick-a-dee call is the number of component note types: Bloomfield, Charrier, and Sturdy (2004) classified the components of the mountain chickadee's call into six distinct note-type categories (A, A/B, B, C, Dh, D). Most calls consisted of four notes, which differed from black-capped chick-a-dee calls, which have an average of six notes per call (Hailman et al., 1985). A second difference between the calls is that the syntactic organization of call notes within the chick-a-dee calls of the mountain chickadee appears to be more flexible. Bloomfield et al. found that the order of the chick-a-dee call note types of the mountain chickadee can be best described as $A \rightarrow (A/B \leftarrow ? B) \rightarrow C \rightarrow Dh ? D$. In other words, note Types A/B and B were often interchangeable within calls.

In the wild, birds must be able to discriminate among conspecific and heterospecific vocalizations. This perceptual ability is important because the signaler and receiver are often out of sight of one another as a result of natural barriers such as vegetation and geological obstructions. Thus, species-specific characteristics must be present and distinguishable in birds' acoustic signals. This is particularly important for black-capped and mountain chickadees because, in some regions, the two species live sympatrically and engage in interspecific activities such as foraging (Hill & Lein, 1989b) and interbreeding (Howe, 1985; Martin & Martin, 1996). Indeed, Hill and Lein (1989a) found that both species of chickadees responded weakly to playback of heterospecific song within

their (sympatric) territory, indicating that the songs of both black-capped and mountain chickadees contain information specific to each species. Moreover, sympatric black-capped and mountain chickadees in our study area, adjacent to that of Hill and Lein, although observed foraging in the area surrounding winter feeders, tend to arrive and depart in same-species flocks and to segregate by species to different feeder stations when possible (C. Sturdy and L. Bloomfield, personal observation). However, the species-specific features in the vocal repertoire of chickadees, including the chick-a-dee call, are not completely understood (but see Charrier & Sturdy, 2005). Taken together, it is reasonable to suppose that black-capped and mountain chickadees have species-specific characters in both their songs and chick-a-dee calls and that they attend to and use these in the wild to avoid heterospecific interactions.

One possibility is that species-specific features—in particular, features capable of discriminating black-capped from mountain chickadees—are present in the D notes of the chick-a-dee call. For instance, among black-capped chickadees, the D note contains frequency information specific to flock membership (Mammen & Nowicki, 1981), and birds respond differently depending on the presence or absence of this signature (Nowicki, 1983). In mountain chickadees, D notes were present in every one of the 200 calls sampled by Bloomfield et al. (2004), who hypothesized that, as in black-capped chickadees, they could contain cues for reliably identifying the signaler.

A second possibility is that non-D notes (i.e., black-capped chickadee A, B, and C notes and mountain chickadee A, A/B, B, and C notes) can also be used for species identification. The reason for this possibility is that such notes are short and occur early in the call, which would permit rapid species identification early in the temporal sequence of a call. This second possibility is not mutually exclusive of the first. The purpose of the current study is to explore the feasibility of both possibilities: whether either non-D or D notes are capable of mediating species identification.

To examine these two possibilities, we took a large number of non-D and D notes from the calls of both black-capped and mountain chickadees. We then summarized the spectrogram of each note in terms of either nine (non-D notes) or four (D notes) different spectrogram features, using a similar approach to that originally described by Nowicki and Nelson (1990). We then combined, separately for each non-D and D note, the data for each species into one set and normalized each of the measured features. Previous research has shown that when data for notes from one species are treated in this fashion, both traditional statistics and artificial neural networks are capable of using the normalized features to successfully classify the different notes into different types (Dawson, Charrier, & Sturdy, in press). The question of interest in the current study was whether such data could also be used to classify the species of chickadee regardless of the particular type of non-D note (Study 1) or using D notes (Study 2).

Study 1

Method

Subject description, recording procedure, and acoustic analyses have been published previously (Charrier, Bloomfield, & Sturdy, 2004; Bloomfield et al., 2004) and are outlined only briefly here.

Subjects. Six male and 4 female adult black-capped chickadees (*Poecile atricapillus*) and 11 male and 9 female mountain chickadees (*Poecile gambeli*) were captured during the winters of 2002 and 2003 from two locations in Alberta. Birds were housed in individual cages and had ad-lib access to food and were maintained on natural day–night cycle typical for the season in Edmonton and at approximately 20 °C.

Recording procedure, signal acquisition, and analysis. Each bird was recorded until we had a sample of at least 20 calls for each bird. Recordings (effective frequency range: 90–12,000 Hz) were digitized at 44,100 Hz, 16-bit samples/s using a 16-bit DartDisk Direct-to-Disk recorder (Engineering Design, Belmont, MA). Calls were analyzed using SIGNAL version 4.0 (Beeman, 2002).

We measured 100 calls from black-capped chickadees and 200 calls from mountain chickadees (i.e., 10 calls from each bird from each species). To standardize our analyses, each individual call note was saved as a separate file with a duration of 300 ms, which was accomplished by adding leading and trailing silence of equal duration to each individual note file. For A, B, and C notes for black-capped chickadees and A, A/B, B, and C notes for mountain chickadees, nine acoustic features, partially based on the methods described in Nowicki and Nelson (1990), were measured, including start frequency (SF), peak frequency (PF), end frequency (EF), all of which were measured in hertz on a digital spectrogram (window size = 1,024 points, frequency precision = 43 Hz) using a cutoff amplitude of –35 dB relative to the peak amplitude in the note. We also measured the loudest frequency (Fmax; in hertz) using a power spectrum (average window size = 4,096 points, frequency precision = 11 Hz). The duration measurements included were ascending duration (AD), descending duration (DD), and total duration (TD) and were measured in milliseconds on a digital spectrogram (window size = 256 points, temporal precision = 5.8 ms).

Two other measurements of frequency modulation were also made: the slope of the ascending frequency modulation (FMasc; in hertz/milliseconds) following the formula $(PF-SF)/AD$, and the slope of the descending frequency modulation (FMdesc; in hertz per milliseconds) following the formula $(EF - PF)/DD$.

Data preprocessing. The signal analysis described previously produced a raw data set that was composed of 840 different notes. This training set consisted of 370 notes from the call of the black-capped chickadee (205 A notes, 134 B notes, and 31 C notes). The training set also included 470 notes from the call of the mountain chickadee (150 A notes, 178 A/B notes, 93 B notes, and 58 C notes). Each of these notes was represented as a vector of nine different spectrogram features.

In our previous research (Dawson et al., in press), we had taken a set of notes represented by these features and had normalized the feature representation. This was accomplished by converting each feature into a z score. We found that this preprocessing of data permitted both traditional and nontraditional statistical analysis to classify different note types with a high degree of accuracy. Because of this previous success, we normalized the 840 notes in the current data set in the same way. All of the data were normalized together. That is, we did not perform separate normalizations for notes obtained from different species of birds.

Logic of using discriminant analysis for classification. When researchers are faced with data cases that can be assigned to a set of predefined classes, they often classify the data using discriminant analysis. Discriminant analysis is similar in many ways to multiple regression. Discriminant analysis determines a set of discriminant functions that can be used to categorize each instance. Each discriminant function has the form of a regression equation, $L = b_1x_1 + b_2x_2 + \dots + b_nx_n + c$, where L is the value of the function, each b_i is a discriminant coefficient, each x_i is a predictor variable, and c is a constant. If there are k different classes to which cases can be assigned, then discriminant analysis will compute a set of k different discriminant functions. The coefficients of these functions are selected to minimize classification errors. A case is classified by providing its input features as the predictors for each of the discriminant functions.

The case is assigned to the class whose discriminant function generates the maximum value.

Results

We used discriminant analysis to classify the 840 notes into bird species. That is, we asked discriminant analysis to classify which species produced each note in the data set regardless of type of note. If it is possible for non-D notes to be used for species identification, then discriminant analysis should be capable of classifying species with a high degree of accuracy. If such notes cannot be used for this task, then the performance of discriminant analysis in this particular analysis should be very poor. The discriminant analysis indicated quite clearly that non-D notes are sufficient for species identification, because it classified species with 100% accuracy. It was able to use spectrogram features to correctly identify the species that generated every single note in the data set. The discriminant functions that were generated by this analysis are provided in Table 1. One should use caution when interpreting the relative contribution of the particular acoustic features to the species classification presented in Table 1, because the p values may be inflated as a result of the large number of degrees of freedom in the analysis.

In this discriminant analysis, not all of the input features are equally important contributors to the discriminant functions. Table 1 also provides the F test of the contribution of each predictor variable to the set of discriminant functions. As can be seen, six of the nine note features were statistically significant predictors.

How is it possible for this discriminant function to use these non-D notes to perfectly classify chickadee species? Figure 1 presents the average z scores for a note from the black-capped chickadee (averaging over A, B, and C note types) as well as the average z scores for a note from the mountain chickadee (averaging over A, A/B, B, and C note types). It can be seen that the average note from a mountain chickadee exhibits a near mirror-image profile in comparison to the average note from a black-

Table 1
Discriminant Coefficients, With Tests of Statistical Significance of Each Predictor, for the Two Discriminant Functions Used to Classify the Non-D Notes as Being Generated by One of Two Species on the Basis of the Nine Predictor Features

Variable	Discriminant functions		F^a	p
	Black-Capped	Mountain		
Constant	–59.348	–37.044		
TD	0.926	–0.729	2.47	.1160
AD	–2.376	1.870	25.15	.0001
DD	0.863	–0.679	2.29	.1310
SF	–19.528	15.373	10.25	.0010
PF	107.752	–84.826	0.99	.3200
EF	1.718	–1.352	124.78	.0001
FMasc	3.638	–2.864	225.51	.0001
FMdesc	–22.121	17.414	678.41	.0001
Fmax	–5.130	4.038	12.99	.0003

Note. TD = total duration; AD = ascending duration; DD = descending duration; SF = start frequency; PF = peak frequency; EF = end frequency; FMasc = ascending frequency modulation; FMdesc = descending frequency modulation; Fmax = loudest frequency.

^a $df = 1, 838$.

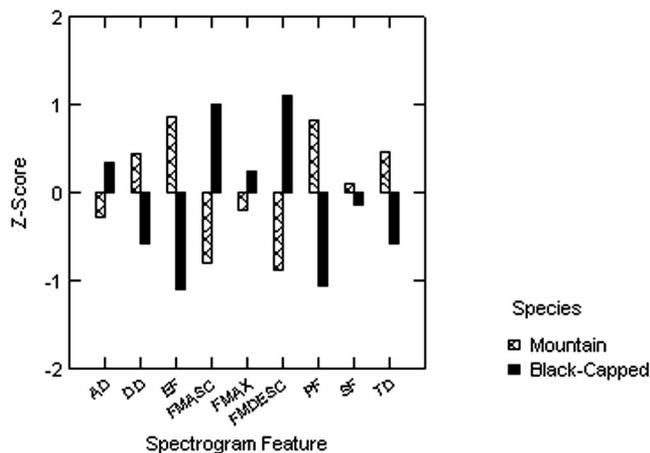


Figure 1. The average z score of each spectrogram feature for the notes from the two species of chickadees. The black-capped average is taken over all 370 A, B, and C notes, and the mountain average is taken over all 470 A, B, C, and A/B notes. AD = ascending duration; DD = descending duration; EF = end frequency; FMASC = ascending frequency modulation; FMAX = loudest frequency; FMDESC = descending frequency modulation; PF = peak frequency; SF = start frequency; TD = total duration.

capped chickadee. (This relationship between the two notes is also exploited by discriminant analysis, as can be seen in the near mirror reflection of the two sets of discriminant coefficients in Table 2.) On average, a note from a mountain chickadee has a longer total and descending duration and a higher starting, peak, and ending frequency than does a black-capped note. As well, a note from a mountain chickadee has a shorter ascending duration, shallower ascending and descending slope, and a lower frequency at maximum amplitude (Fmax).

Although these differences will vary from note to note, the successful discriminant function analysis demonstrates that, by considering several features at the same time (i.e., the six significant predictors in Table 2), one can still correctly identify species on the basis of note properties.

The results reported previously indicate that this particular set of notes can be used to discriminate the two species of chickadee. Another important issue is the extent to which discriminant functions based on these notes can be applied to new notes. To test the ability of the linear discriminant analysis (LDA) to generalize, we conducted a cross-validation test by conducting a new analysis of these notes. In this new analysis, 25% of the notes were randomly withheld from the discriminant analysis; the resulting discriminant functions were derived the remaining 75% of the notes. Species classification based on this subset of notes was accomplished with 100% accuracy. Generalization was then tested by observing the ability of these functions to classify the 25% remaining notes that had been withheld. It was found that these new notes were also classified perfectly. This provides solid evidence that the solution the LDA was using was indeed general in nature and not specific to the cases used to generate it.

Study 2

Study 1 demonstrated that non-D note types could be used to discriminate between black-capped and mountain chickadees.

Study 2 was aimed at determining whether D notes, involved in flock recognition in black-capped chickadees, could be used to discriminate between black-capped and mountain chickadees, using virtually identical methods as in Study 1.

Method

The description of subjects, recording procedure, and acoustic analyses have been published previously (Charrier et al., 2004; Bloomfield et al., 2004) and are similar to those used in Study 1. Because of this, only those methods that differ from Study 1 are outlined here.

Recording procedure, signal acquisition, and analysis. To standardize our analyses, each individual call note was saved as a separate file with a duration of 300 ms for black-capped chickadee notes and 500 ms for mountain chickadee notes, which was accomplished by adding leading and trailing silence of equal duration to each individual note file. For D notes for black-capped and mountain chickadees, four acoustic features, partially based on the methods described in Nowicki and Nelson (1990), were measured. Each D note was analyzed using a power spectrum (average window size: D notes = 16,384 points, frequency precision = 2.7 Hz) to obtain the frequency (kilohertz) of the first visible harmonic, note peak frequency, and loudest frequency (Fmax). TD (in milliseconds) of each note was measured in a digital spectrogram.

Data preprocessing. The signal analysis described previously produced a raw data set that was composed of 553 different notes. This training set consisted of 341 D notes from the call of the black-capped chickadee and 212 D notes from the call of the mountain chickadee. Each of these notes was represented as a vector of four different spectrogram features. We normalized the 553 notes in the current data set in the same way as in Study 1.

Results

As in Study 1, we used discriminant analysis to classify the 553 notes into bird species. The discriminant analysis indicated clearly that D notes are sufficient for species identification, because it classified species with an average accuracy of 94%. That is, it was able to use spectrogram features to correctly identify the species that generated 85% of mountain D notes and 99% of black-capped D notes in the data set. The discriminant functions that were generated by this analysis are provided in Table 2. In this discriminant analysis, not all of the input features are equally important contributors to the discriminant functions. Table 2 also provides the *F* test of the contribution of each predictor variable to the set

Table 2
Discriminant Coefficients, With Tests of Statistical Significance of Each Predictor, for the Two Discriminant Functions Used to Classify the D Notes as Being Generated by One of Two Species on the Basis of the Four Predictor Features

Variable	Discriminant functions		<i>F</i> ^a	<i>p</i>
	Black-Capped	Mountain		
Constant	-1.473	-2.721		
TD	-1.666	2.681	586.45	.0001
<i>f</i> ₀	-0.288	0.462	17.21	.0004
Fmax	-0.954	1.547	167.67	.0001
NPF	-0.121	0.187	3.36	.0673

Note. TD = total duration; *f*₀ = first visible harmonic; Fmax = loudest frequency; NPF = note peak frequency.

^a *df* = 1, 551.

of discriminant functions. As can be seen from that table, three of the four note features were statistically significant predictors. As with Study 1, one should use caution when interpreting the relative contribution of the particular acoustic features to the species classification presented in Table 2, because the p values may be inflated as a result of the large number of degrees of freedom in the analysis.

How is it possible for this discriminant function to use these D notes to classify chickadee species? When we examined the average z scores of the four features for a note from the black-capped chickadee D notes and the average z scores of the four features for a note from the mountain chickadee D notes, we found once again that the average note from a mountain chickadee exhibits a near mirror-image profile in comparison to the average note from a black-capped chickadee (i.e., in a fashion analogous to Figure 1). This relationship between the two notes is also exploited by discriminant analysis, as can be seen in the near mirror reflection of the two sets of discriminant coefficients that are provided in Table 2.

Finally, we examined the ability of discriminant functions based on the features of D notes to generalize to new notes. We used the same procedure that was earlier described in Study 1: We conducted a new LDA on 75% of the D notes, when these notes were selected randomly. This new analysis achieved a similar degree of success as the full analysis, because it correctly classified 93% of the notes (99% accuracy for the black-capped notes and 84% accuracy for the mountain notes). The performance of these equations on the remaining 25% of the notes was even better, providing a species-classification accuracy of 96% (100% for the black-capped notes and 90% for the mountain notes). In short, the discriminant functions that are being derived for these notes appear to generalize quite well to new instances.

Discussion

We report on the ability of LDA to classify chick-a-dee call note types based on whether the notes were produced by black-capped or mountain chickadees. We examined this in two main parts: The first looked at species classification using non-D notes and examined the question of generality in the LDA equation, whereas the second examined species classification using D notes. LDA was able to perfectly classify non-D notes by species and performed at an extremely high level when classifications were based on D notes.

The results of the LDA show conclusively that the acoustic features of the non-D notes in the chick-a-dee call are sufficient to discriminate black-capped chickadees from mountain chickadees. The fact that the LDA achieved 100% accuracy indicates that any of these non-D notes could be used for this classification task. This finding is important because, as was noted earlier, it has been hypothesized that the D notes of the chick-a-dee call are most likely to be used by chickadees for species identification. Although our results with non-D notes do not rule out this possibility (and see later discussion), they do indicate that non-D notes potentially play a role in species identification, and this possibility is worthy of further empirical study.

One must be aware that our results are based on a sample and may not totally reflect the full range of variation either (a) among individual birds in our particular geographic region (i.e., western Canada) or (b) among populations across geographical regions.

Geographic variation leading to regional specialization is known to exist for several behaviors, including black-capped chickadee gargle call production (Miyasato & Baker, 1999), Carolina chickadee (*Poecile carolinensis*) chick-a-dee call production (Freeberg, Lucas, & Clucas, 2003), and patterns of multiple paternity in common garter snakes (*Thamnophis sirtalis*; Garner et al., 2002), to name a few. To this end, our technique of using statistical techniques to classify vocalizations could, in future studies, be used to determine whether chick-a-dee calls, or other bird vocalizations for that matter, vary in any significant way according to geographic location and, in turn, could be discriminated accurately on this basis, in the way that other vocalizations and other behaviors are seen to vary from one region to the next.

To test the possibility that D notes, like non-D notes, also were sufficient for species identification, we conducted another LDA using the summary features for D notes from black-capped and mountain chickadees. In contrast to the results of the LDA for non-D notes, the results for D notes revealed a less than perfect identification of species. Accuracy was still quite high (combined accuracy = 94%). These results suggest that, although species identity can be determined by D notes, the ambiguity is greater than with non-D notes. This ambiguity could be driven by at least two factors. One is that the acoustic properties of D notes are less consistent within species than are those of non-D notes. Perhaps D notes have not become as acoustically specialized as non-D notes and, as such, are not as species specific. Another possibility is that D notes were not summarized as thoroughly as non-D notes, because D notes were reduced to only four acoustic features whereas non-D notes were described with nine features. It remains possible that were D notes described with more features, the results of the LDA would have been even higher and more in line with those from non-D notes. The fact that with only four summary features an LDA was able to accurately identify birds by species in 94% of the time on average is still quite impressive.

Following the initial classification of non-D notes, we conducted a cross-validation procedure (i.e., generalization test) aimed at uncovering whether the LDA equation obtained using 100% of the notes was general enough to classify any note to species or, alternatively, whether the initial LDA equation was specific to those patterns initially used in the analysis. The results of the cross-validation clearly showed that the LDA equation was general and capable of classifying novel notes to species with the same level of accuracy as the original equation that used 100% of the notes. When this procedure was repeated for D notes, we found highly convergent results, with the LDA equation generalizing well to novel notes. This is an important step in ensuring that the solution the LDA arrived at is, in fact, a general one that will work effectively with novel notes.

One problem in ethological research is a particular type of statistical or experimental design error, termed *pseudoreplication* (Hurlbert, 1984; Kroodsma, Byers, Goodale, Johnston, & Liu, 2001). This problem is caused by the inappropriate use of inferential statistics (e.g., analysis of variance) to test for effects in experiments in which treatments are not true replicates or in which there is a lack of independence in the data. Another problem in behavioral design and analysis has to do with what is known as the *pooling fallacy* (Machlis, Dodd, & Fentress, 1985). This can potentially be an issue when multiple behavioral observations are taken from a small number of individuals rather than collecting a smaller number of observations from a large number of individu-

als. Like pseudoreplication, inappropriate pooling, or use of multiple observations from relatively small numbers of subjects, can also lead to issues when interpreting results. Both of these problems should be minimized or avoided in the design and analysis of experiments when feasible.

Some may be concerned about the lack of independence in our analysis because each bird contributed more than one note to the total pool used for the LDA and our analysis may suffer from pseudoreplication or inappropriate pooling. Our logic to test for issues arising from pseudoreplication or pooling in our study is as follows: If something particular to the individual birds contributed to our results in a significant and meaningful way (i.e., we achieved near perfect species classification because of nonindependence in our sample), one would predict that an LDA aimed at classifying notes to singer, rather than to species, would be highly successful (i.e., the LDA should have high accuracy in determining which birds produced which notes).

Therefore, we conducted just such an LDA and asked the analysis to group notes according to singer. The results of this individual-based classification were far inferior to those of our species-classification LDA and not at all what one would predict if, in fact, the particular features of individual birds were contributing to our species classification. In contrast to our 97% classification accuracy (averaged across non-D and D notes) for the species classification, our individual classification returned a paltry 33% accuracy for individual birds. This suggests that using these acoustic features, normalized and pooled across species and individuals, results in lackluster individual recognition. If the repetition of individual birds contributed to our initial results, the impact was minimal at best.

Moreover, and perhaps even more telling, is an inspection of the errors of this bird-based LDA; out of all errors made in identifying the individual bird producing the call note, not once was an error made across the species boundary. Put another way, notes produced by a black-capped chickadee were mistakenly classified as being produced by a different black-capped chickadee but were never mistakenly classified as being produced by one of the mountain chickadees. The analogous pattern was observed for all of the mountain call notes. Taken together, our results suggest that the lack of independence in our analysis contributed, if at all, in a very minor way to our ultimate results.

To determine conclusively the role of non-D and D notes in species identification, empirical studies of bird behavior, including behavioral studies of bird responses to note playbacks in the field and operant studies of note discrimination in the lab, are required. The results presented previously have two main implications for these future studies. First, they motivate the need for detailed study of the chick-a-dee call notes for the function of species identification. If the LDA had not been able to categorize species, then there would be little motivation to study the extent to which chickadees themselves use these notes for species identification. Second, they provide specific information about particular acoustic features that may be relevant to the birds for this task and are thus particularly important for manipulation in laboratory studies (but see caveats in the Results section for Study 1 and Study 2 regarding interpretation of these results). For example, the results reported earlier in Table 1 indicate that the acoustic features of the ascending and descending slopes of the notes, and the ending frequency of the notes, are highly significant predictors of species. In contrast, the acoustic features of total duration, descending

duration, and peak frequency do not appear to carry species-specific information. Determining which features from which note types actually contribute to species discrimination will be answered only through careful field and laboratory studies of chickadee behavior.

References

- Beeman, K. (2002). *SIGNAL 4.0 reference guide*. Berkeley, CA: Engineering Design.
- Bloomfield, L. L., Charrier, I., & Sturdy, C. B. (2004). Note types and coding in parid vocalizations: II. The chick-a-dee call of the mountain chickadee (*Poecile gambeli*). *Canadian Journal of Zoology*, *82*, 780–793.
- Bloomfield, L. L., Sturdy, C. B., Phillmore, L. S., & Weisman, R. G. (2003). Open-ended categorization of chick-a-dee calls by black-capped chickadees (*Poecile atricapilla*). *Journal of Comparative Psychology*, *117*, 290–301.
- Catchpole, C. K., & Slater, P. J. B. (1995). *Bird song: Biological themes and variations*. Cambridge, UK: Cambridge University Press.
- Charrier, I., Bloomfield, L. L., & Sturdy, C. B. (2004). Note types and coding in Parid vocalizations: I. The chick-a-dee call of the black-capped chickadee (*Poecile atricapilla*). *Canadian Journal of Zoology*, *82*, 769–779.
- Charrier, I., & Sturdy, C. B. (2005). Call-based species recognition in black-capped chickadees. *Behavioural Processes*, *70*, 271–281.
- Dawson, M. R. W., Charrier, I., & Sturdy, C. B. (in press). Using an artificial neural network to classify black-capped chickadee (*Poecile atricapillus*) call note types. *Journal of the Acoustical Society of America*.
- Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: Common themes and mechanisms. *Annual Review of Neuroscience*, *22*, 567–631.
- Ficken, M. S., Hailman, E. D., & Hailman, J. P. (1994). The chick-a-dee call system of the Mexican chickadee. *Condor*, *96*, 70–82.
- Freeberg, T. M., Lucas, J. R., & Clucas, B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, *Poecile carolinensis*: Identity and redundancy within note types. *Journal of the Acoustical Society of America*, *113*, 2127–2136.
- Gaddis, P. K. (1985). Structure and variability in the vocal repertoire of the mountain chickadee. *Wilson Bulletin*, *97*, 30–46.
- Garner, T. W. J., Gregory, P. T., McCracken, G. F., Burghardt, G., M., Koop, B. F., McLain, S. E., & Nelson, R. J. (2002). Geographic variation of multiple paternity in the common garter snake (*Thamnophis sirtalis*). *Copeia*, *1*, 15–23.
- Gill, F. B., Mostrom, A. M., & Mack, A. L. (1993). Speciation in North American chickadees: 1. Patterns of mtDNA genetic divergence. *Evolution*, *47*, 195–212.
- Hailman, J. P., Ficken, M. S., & Ficken, R. W. (1985). The chick-a-dee calls of parus-atricapillus: A recombinant system of animal communication compared with written English. *Semiotica*, *56*, 191–224.
- Hill, B. G., & Lein, M. R. (1989a). Natural and simulated encounters between sympatric black-capped chickadees and mountain chickadees. *Auk*, *106*, 645–652.
- Hill, B. G., & Lein, M. R. (1989b). Territory overlap and habitat use of sympatric chickadees. *Auk*, *106*, 259–268.
- Howe, W. H. (1985). *Hybridization in black-capped (Parus atricapillus) and mountain (P. gambeli) chickadees in the Middle Rio Grande Valley of New Mexico*. Unpublished master's thesis, University of New Mexico, Albuquerque.
- Hughes, M. Nowicki, S., & Lohr, B. (1998). Call learning in black-capped chickadees (*Parus atricapillus*): The role of experience in the development of "chick-a-dee" calls. *Ethology*, *104*, 232–249.
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, *54*, 187–211.
- Kroodsm, D. E., Byers, B. E., Goodale, E., Johnson, S., & Liu, W. C.

- (2001). Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour*, 61, 1029–1033.
- Machlis, L., Dodd, P. W. D., & Fentress, J. C. (1985). The pooling fallacy: Problems arising when individuals contribute more than one observation to a data set. *Zeitschrift Tierpsychology*, 68, 201–214.
- Mammen, D. L., & Nowicki, S. (1981). Individual-differences and within-flock convergence in chickadee calls. *Behavioral Ecology and Sociobiology*, 9, 179–186.
- Marler, P. (2004). Bird calls: Their potential for behavioral neurobiology. In H. P. Zeigler & P. Marler (Eds.), *Annals of the New York Academy of Sciences: Vol. 1016. Behavioral neurobiology of birdsong* (pp. 31–44). New York: New York Academy of Sciences.
- Martin, S. G., & Martin, K. A. (1996). Hybridization between a mountain chickadee and black-capped chickadee in Colorado. *Colorado Field Ornithology*, 30, 60–65.
- McCallum, D. A., Grundel, R., & Dahlsten, D. L. (1999). Mountain chickadee (*Poecile gambeli*). In A. Poole & F. B. Gill (Eds.), *The birds of North America* (Vol. 453, pp. 1–27.). Washington, DC: Academy of Natural Sciences and American Ornithologists' Union.
- Miyasato, L. E., & Baker, M. C. (1999). Black-capped chickadee call dialects along a continuous habitat corridor. *Animal Behaviour*, 75, 1311–1318.
- Nowicki, S. (1983). Flock-specific recognition of chickadee calls. *Behavioral Ecology And Sociobiology*, 12, 317–320.
- Nowicki, S., & Nelson, D. A. (1990). Defining natural categories in acoustic signals: Comparison of three methods applied to “chick-a-dee” call notes. *Ethology*, 86, 89–101.
- Slater, P. J. B. (2003). Fifty years of bird song research: A case study in animal behaviour. *Animal Behaviour*, 65, 633–639.
- Smith, S. M. (1993). Black-capped chickadee (*Poecile atricapilla*). In A. Poole, P. Stettenheim, & F. B. Gill (Eds.), *The birds of North America* (Vol. 39, pp. 1–19.). Washington, DC: Academy of Natural Sciences and American Ornithologists' Union.
- Vicario, D. S. (2004). Using learned calls to study sensory-motor integration in songbirds. In H. P. Zeigler & P. Marler (Eds.), *Annals of the New York Academy of Sciences: Vol. 1016. Behavioral neurobiology of birdsong* (pp. 246–262). New York: New York Academy of Sciences.

Received October 7, 2005

Revision received December 21, 2005

Accepted December 30, 2005 ■

Low Publication Prices for APA Members and Affiliates

Keeping you up-to-date. All APA Fellows, Members, Associates, and Student Affiliates receive—as part of their annual dues—subscriptions to the *American Psychologist* and *APA Monitor*. High School Teacher and International Affiliates receive subscriptions to the *APA Monitor*, and they may subscribe to the *American Psychologist* at a significantly reduced rate. In addition, all Members and Student Affiliates are eligible for savings of up to 60% (plus a journal credit) on all other APA journals, as well as significant discounts on subscriptions from cooperating societies and publishers (e.g., the American Association for Counseling and Development, Academic Press, and Human Sciences Press).

Essential resources. APA members and affiliates receive special rates for purchases of APA books, including the *Publication Manual of the American Psychological Association*, and on dozens of new topical books each year.

Other benefits of membership. Membership in APA also provides eligibility for competitive insurance plans, continuing education programs, reduced APA convention fees, and specialty divisions.

More information. Write to American Psychological Association, Membership Services, 750 First Street, NE, Washington, DC 20002-4242.