Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence

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Abstract. During the winter months, the acoustic structure of the 'chick-a-dee' call of black-capped chickadees, *Parus atricapillus*, is similar among flock members but varies significantly between different flocks. To investigate the process of within-flock convergence through which these differences arise, an experimental flock of birds previously unfamiliar with each other was established and maintained in captivity. The vocal behaviour of each individual was monitored over several weeks. Acoustic analyses revealed that significant vocal convergence occurred in less than 1 week after the birds were initially exposed to each other. No single individual appeared to provide a vocal model that other birds copied. Acoustic differences appeared in the spectral structure of the D-note of this complex call, especially in the frequency difference between adjacent overtones and in the bandwidth. Both of these acoustic features are attributable to specific physiological mechanisms of production. The significance of vocal plasticity in chickadees and its relationship to production and perception are discussed.

Most analyses of vocal plasticity in birds have focused on the ontogeny of oscine birdsong, a specialized learning process during which the young songbird acquires, practises and modifies the sounds that will ultimately crystallize into its adult song repertoire (Marler & Mundinger 1971; Kroodsma 1982; Marler 1984). By contrast, the phenomenon of plasticity in vocalizations other than song and the behavioural significance of this plasticity have received less attention. Beginning with Mundinger's (1970) work on cardueline finch calls, there is now increasing evidence that the acoustic structure of some non-song vocalizations remains plastic throughout adulthood, varying in accordance with an animal's social affiliations (Marler & Mundinger 1975; Mundinger 1979).

The 'chick-a-dee' call of the black-capped chickadee, *Parus atricapillus*, provides one such example of plasticity. During the winter months, chickadees form cohesive flocks (Odum 1942; Glase 1973; Smith 1984). At this time the acoustic structure of the 'chick-a-dee' call varies significantly from flock to flock (Mammen & Nowicki 1981), and field playback experiments show that these differences are perceived by the birds in the context of flock member recognition (Nowicki 1983). Flocks disband every spring, with membership often changing through subsequent years (Odum 1942; Smith 1967, 1984; Weise & Meyer 1979). There would be a selective advantage if

flock-specific features of the 'chick-a-dee' call remained plastic throughout a bird's lifetime, and within-flock similarities were learned through vocal imitation during the period of flock formation each fall. Preliminary data, obtained from manipulated flocks held in outdoor aviaries, support this hypothesis (Mammen & Nowicki 1981). In this report, I examine in detail changes that occurred in the vocal behaviour of a single experimental flock of chickadees in order to gain a better understanding of which acoustic features of the call are modified and to assess the timing of vocal convergence.

The 'chick-a-dee' call includes four types of notes (Fig. 1). Three of these note types ('A', 'B' and 'C' of Ficken et al. 1978; termed 'introductory notes' by Mammen & Nowicki 1981) are rapid FM sweeps. The fourth type, the 'dee' of the 'chick-a-dee' ('D' of Ficken et al. 1978), is a more complex, harmonic-like sound. A call may include a variable number and arrangement of these four note types. The sequence of note types within a call conforms statistically to combinatorial rules, suggesting that variation in note sequence contains information, such as that concerning an individual's locomotory tendencies (Hailman et al. 1985, 1987; Hailman & Ficken 1986). Acoustic differences in the 'chick-a-dee' call used in flock recognition were found primarily in the spectral structure of the D-note (Mammen & Nowicki 1981; Fig. 1), but the precise

acoustic bases for these differences and how they are perceived remained enigmatic. Recent work on vocal production, however, provides a better understanding of how birds might achieve control of the acoustic characteristics of this sound during vocal convergence (Nowicki & Capranica 1986a; Nowicki 1987).

The spectrum of a D-note appears as a series of overtones, evenly spaced at roughly 400-Hz intervals (Fig. 1), suggestive of a harmonic series with its fundamental and first several harmonics missing (Greenewalt 1968). Physiological experimentation demonstrates that these regular spectral components are not harmonics, but instead are sidebands resulting from an interaction between signals originating from the two sides of the syrinx (Nowicki & Capranica 1986a, b). The first two components with significant amplitude, typically observed at approximately 1600 Hz and 2000 Hz (Fig. 1, components 1 and 2), are thought to represent the fundamental frequencies of signals from the two syringeal sources. The higher frequency components include the harmonics of these two fundamentals, as well as sum and difference frequencies resulting from cross-modulation between the two signals. The regular spacing observed among these frequency components is determined by the frequency difference between components 1 and 2 (Nowicki & Capranica 1986b). According to this interpretation, chickadees can vary the spectral structure of their D-notes by changing this interval, thus achieving a different spacing between all spectral components. Birds could also modify the D-note's spectrum by varying its bandwidth through changes in a vocal tract filter, analogous to the way the spectra of differing human vowel sounds are produced by changing the shape of the vocal tract (Fant 1970). The existence of such a vocal filter has recently been demonstrated in several species of songbirds, including chickadees (Nowicki 1987).

Another question concerns the rate at which vocal convergence occurs. Vocal changes have been observed in a captive group over a period of 1 month (Mammen & Nowicki 1981), but casual field observations suggest that convergence may occur more rapidly (Nowicki, unpublished observations). The rate of convergence not only provides insight into the mechanisms controlling vocal plasticity in chickadees, but it is also important for assessing the social significance of this plasticity. In the present study, each bird's calls were recorded

on a weekly basis, to permit a more accurate determination of the time course of vocal convergence.

METHODS

Animals, Housing and Behavioural Observations

In mid-October 1983, I captured five black-capped chickadees, *Parus atricapillus*, from different field sites near Ithaca, New York. Each site was separated by at least 1·5 km. Birds were aged by examining the degree of skull ossification, sexed according to wing chord length (Glase 1973), and marked individually with coloured leg bands. Sex was confirmed later by laparotomy. An adult male, WH, was captured first and allowed to remain in the experimental aviary for 12 days. I then added four other birds, one per day, to the aviary (Table I). Male WH was allowed prior residence in the enclosure in the hope that he would establish a dominant status in the experimental flock.

The experimental enclosure was an indoor free-flight aviary (roughly a 3·7 m cube) illuminated both with natural light from a ceiling sky light, and incandescent lights on an automatic timer/fader. Temperature was automatically controlled to produce normal daily variations. There was natural vegetation in the aviary, including a tree 3·5 m in height, for cover and perches. A central pool provided a constant supply of water. The birds were fed unlimited sunflower seeds, supplemented with a vitamin-rich artificial diet mixture and mealworms.

I recorded dominance interactions weekly, measured in terms of displacement behaviours at a feeder in the aviary, and a dominance hierarchy was constructed from these data (Brown 1975). At the same time, I noted other relevant behavioural observations, such as where birds were perching, the number of times each bird vocalized, and any significant interactions away from the feeder, on an ad libitum basis.

Recordings, Analyses and D-Note Structure

Sound recordings of each individual were made on the day of its capture, before the individual was first introduced into the experimental aviary. I made the initial recordings of WH just before introducing the second bird to the aviary. Thus, initial vocal recordings of each bird's 'chick-a-dee'
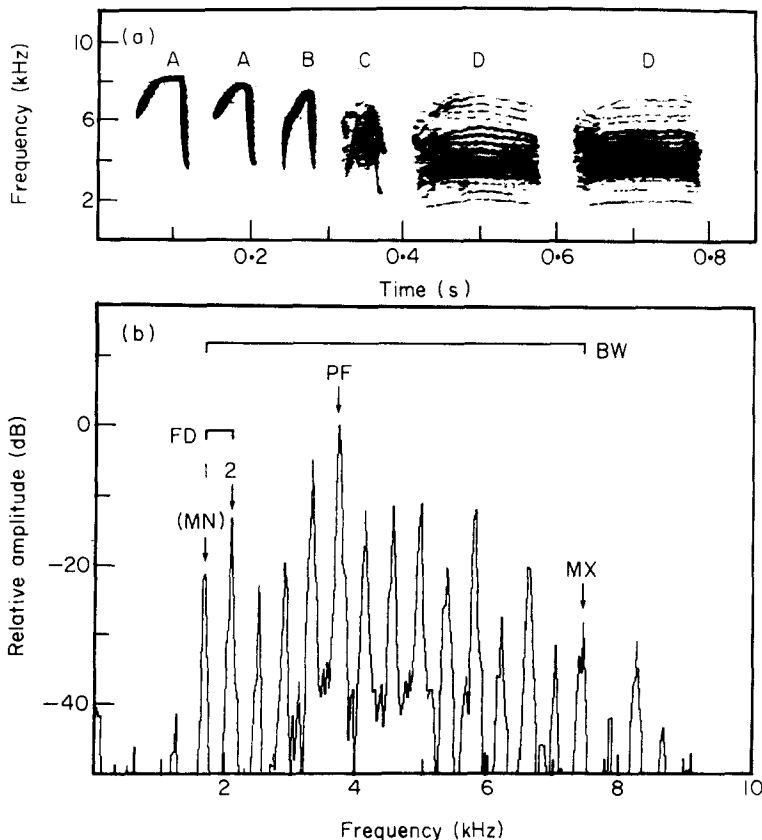
Figure 1. (a) Sonagram of a typical 'chick-a-dee' call, illustrating the four note types: A, B, C, D (Kay Digital Sonagraph model 7800, 16 kHz range, 90 Hz analysis filter bandwidth). (b) Digitally generated amplitude spectrum of a typical D-note. This spectrum is based on a 1024 pt FFT (about 41 ms) taken from the middle of the note, and is similar in its conception to the 'section' display of a conventional sonagraph. For each spectrum, measurements were taken of the peak amplitude frequency (PF), the minimum frequency (MN), the maximum frequency (MX), spectral component 1 (1) and spectral component 2 (2). From these were derived the frequency difference between components 1 and 2 (FD) and the bandwidth (BW). Note that MN and 1 represent the same spectral component in this case, as was true of most spectra. See text for further details of spectral analysis.

calls were made before it had the opportunity to hear any other experimental birds. Each bird was then recorded again individually once a week for 8 weeks. Birds were not recorded more often out of concern that the recording procedure itself might be disruptive to normal behaviour. An attempt was made to record at least 10 calls from every bird each week, although this proved to be impossible in many cases. The most complete recordings were obtained for weeks 0–3, and these recordings form the basis of the statistical analyses below. A preliminary analysis of the data (Nowicki 1985) suggested that the patterns apparent in week 3 remained the same at least until week 5. Insufficient recordings from later weeks precluded accurate

comparisons. One female, BL, ceased to call regularly after the initial recordings, and is excluded from the analysis. Sample sizes used in this analysis are given in Fig. 2.

I tape-recorded the birds in a large anechoic room, using a Nagra 4·2L tape-recorder (15 ips) and a Sennheiser ME20 condenser microphone. Sound spectrograms of each call were generated using a Spectral Dynamics Real Time Analyser (SD 301C-C; Hopkins et al. 1974); these spectrograms were used for temporal analyses (time resolution = 3·1 ms). For each call, I measured the durations of each note and intervals between notes, as well as the total numbers of each note type.

Detailed spectral analyses of D-notes were per-

Table I. Dominance relationships among flock members, based on numbers of displacement interactions between individuals at a feeder in the experimental aviary, and calculated as in Brown (1975)

Winner	Loser					Total wins	Total losses	% Wins	Sex	Age
	WH	OR	BL	RD	PU					
WH	—	25	13	13	13	64	0	100	Male	Adult
OR	0	—	9	3	6	18	27	67	Male	Juvenile
BL	0	1	—	5	6	6	27	18	Female	Juvenile
RD	0	0	4	—	0	4	22	15	Female	Adult
PU	0	1	1	1	—	3	19	14	Female	Adult

formed using a PDP-11/23 computer (Digital Equipment Corporation), with the 'SIGNAL' sound analysis software system developed by Kim Beeman (Engineering Design and The Rockefeller University). I sampled calls digitally with 12-bit precision at a rate of 25 000 Hz, yielding an effective digital Fourier transform (FFT) bandwidth of 10 000 Hz. Amplitude spectra were generated for the first D-note of each call recorded (Fig. 1B), using a 1024 pt FFT taken at the mid-point of the note. The FFT used 41 ms of the signal, representing about one-third of the duration of an average note, and yielded a frequency resolution of 25 Hz.

From each D-note's spectrum, I measured the frequencies of the following five identifiable spectral components (Fig. 1): (1) the component with the greatest amplitude ('peak amplitude frequency'), (2) the lowest frequency component with amplitude greater than −30 dB relative to the peak amplitude ('minimum frequency'), (3) the highest frequency component with amplitude greater than −30 dB ('maximum frequency'), (4) component 1 and (5) component 2. Note that the minimum frequency and component 1 were usually the same, differing in only seven cases (less than 5% of the total sample). In three of these cases, a component with amplitude greater than −30 dB occurred at a lower frequency than component 1 (this designation is always reserved for the component occurring in the range of 1600 Hz; Nowicki & Capranica 1986a). In the other four cases, component 1 itself was slightly lower in amplitude than −30 dB, and so the minimum frequency coincided with component 2. The frequency difference between components 1 and 2 was calculated, as was the bandwidth at −30 dB (the interval between the minimum and maximum frequencies).

Statistical Analyses

A two-way analysis of variance was used to test the significance of changes over time in the individual birds' means for each measurement. Convergence was considered to have occurred if (1) the plot of means revealed a decrease in the dispersal of those means over time, and (2) the analysis of variance revealed a significant bird-by-date interaction for that measurement. Levene's test for equality of variances (Sokal & Braumann 1980) was used to test the analysis of variance's assumption of equal group variances for each measurement. Spearman rank coefficients (Siegel 1956) were used to evaluate correlations among the measured parameters. In some cases, a one-way analysis of variance was used to test whether an individual bird's mean changed significantly between 2 weeks. Because of the post hoc nature of this last test, its value here is descriptive.

RESULTS

Dominance interactions are presented as a hierarchy in Table I. WH, the adult male first introduced to the aviary, strongly dominated the other four birds, while the juvenile male, OR, established a clear second position in the hierarchy. Although uniformly dominated by the males, a linear relationship was not established among the three females (BL, RD, PU) in the experimental flock. These dominance relationships became apparent in the first week of the experiment.

The spectral data revealed a significant convergence in the frequency difference between components 1 and 2 of the D-note (Fig. 2; $P < 0.001$). A large decrease in the dispersal of bird means for this
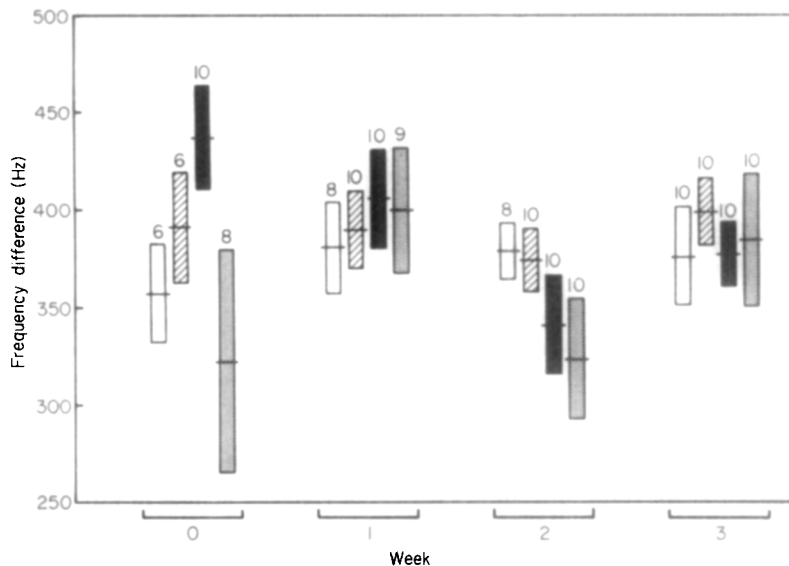
Figure 2. Frequency difference between components 1 and 2 for four individuals plotted as a function of time, illustrating a striking convergence within the first week of the experiment and a significant bird-by-date interaction ($F = 9.63$, $df = 9$, $P < 0.001$). Shown are means (horizontal centre lines), SD (vertical bars) and number of calls sampled. Key: □, ♂WH (dominant); ▨, ♀ RD; ■, ♂ OR; ▥, ♀ PU. 'Week 0' recordings were made before the individuals had any social contact with each other. See text for further details of analysis.

measure occurred within the first week of the experiment. The means diverged slightly in week 2, but were tightly clustered again in week 3. It was not obvious that any single individual served as a model for other birds to copy. Individuals OR and PU, whose initial means (week 0) were furthest from the centre, changed their means significantly between week 0 and week 1 ($P < 0.02$ and $P < 0.01$, respectively). WH, the dominant male, and RD, a female, both showed no significant change in means between weeks 0 and 1, with RD's mean remaining virtually unchanged. These two birds' means at week 0, however, were already close to the arithmetic average of the group.

The data did not reveal consistent trends in the absolute values of components 1 and 2 themselves. The means for these components displayed some convergence between weeks 0 and 1, especially for component 2, but this trend was obscured by significant heterogeneity among the variances (Levene's test, $P < 0.01$ for both). Not surprisingly, the values of components 1 and 2 were highly correlated with each other ($r = 0.69$, $P < 0.001$), and each was also independently correlated with the value of the frequency difference between them

($r = -0.29$ for component 1, $r = 0.42$ for component 2, $P < 0.001$ for both).

Convergence was also observed in the D-note's bandwidth (Fig. 3). In this case, some decrease in the dispersal of the means was evident after 1 week, but the means were not highly convergent until week 3 of the experiment. A two-way analysis of variance failed to find significance for this trend over all four dates ($P = 0.10$), possibly due to large variances, especially in weeks 1 and 2 (Fig. 3). A post hoc two-way analysis of variance comparing weeks 0 and 3 only, however, was highly significant ($P < 0.001$).

The trends observed in the absolute value of the maximum frequency component almost exactly paralleled those observed for the bandwidth. This was expected, given that the maximum frequency is highly correlated with the value of the bandwidth ($r = 0.98$, $P < 0.001$). The minimum frequency (usually equivalent to component 1) did not correlate at all with the bandwidth ($r = -0.06$, $P = 0.51$). No consistent trends were observed for the peak amplitude frequency.

There were no significant trends in any of the temporal measures analysed, including the
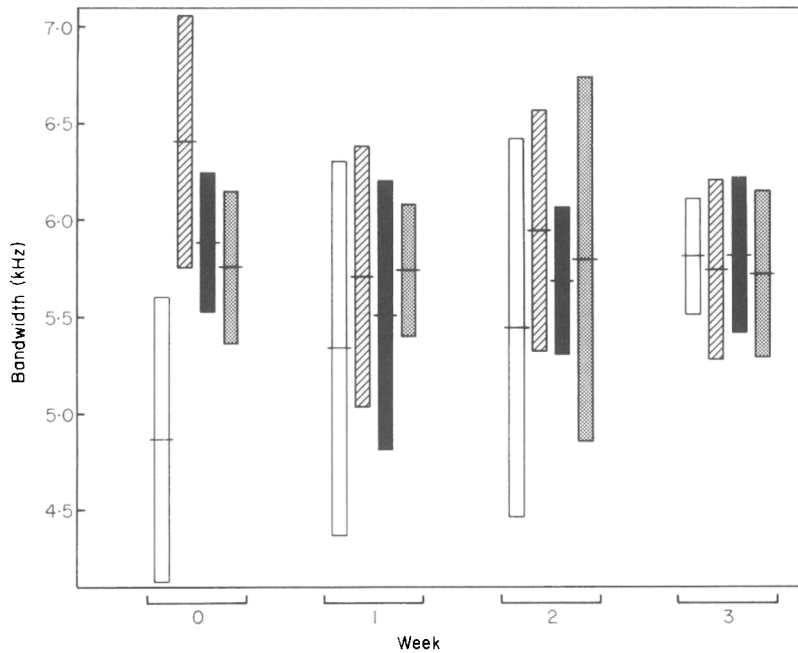
Figure 3. Bandwidth measured at -30 dB below the peak frequency for four individuals plotted as a function of time, illustrating a gradual convergence over the 3 weeks of the experiment. This convergence is not significant if all four dates are considered ($F = 1.67$, $df = 9$, $P = 0.10$), but a test comparing weeks 0 and 3 alone is highly significant ($F = 8.27$, $df = 3$, $P < 0.001$). Shown are means (horizontal centre lines) and SD (vertical bars). See Fig. 2 for key to individuals and number of calls per sample. See text for further details of analysis.
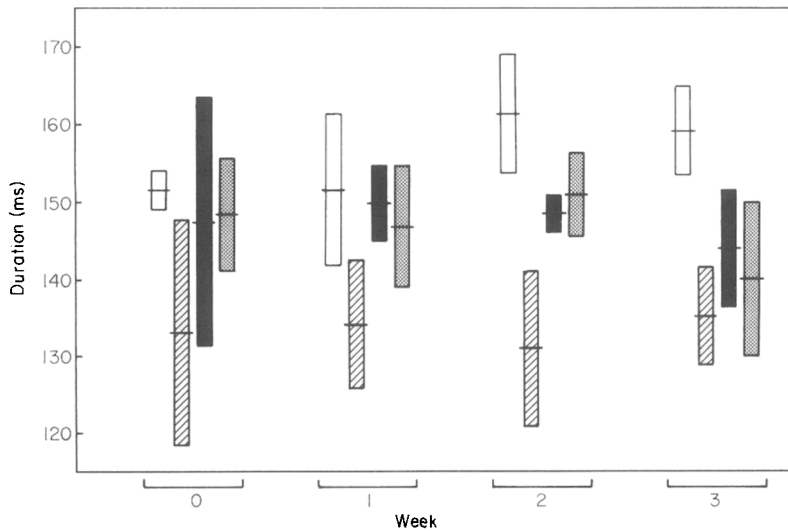
Figure 4. Duration of D-notes for four individuals plotted as a function of time, illustrating a lack of convergence over the course of the experiment. Shown are means (horizontal centre lines) and SD (vertical bars). See Fig. 2 for key to individuals and number of calls per sample. See text for further details of analysis.

durations of the introductory notes and the internote intervals. Of special interest here is the duration of the D-note, since significant flock differences were found for this measure in the field (Mammen & Nowicki 1981). In the present case, there was no convergent trend in the dispersal of the means (Fig. 4). The two-way analysis of variance revealed a marginally significant bird-by-date interaction ($P = 0.05$), possibly reflecting a slight divergence over the four dates, but this result is compromised by highly significant unequal variances in the data (Levene's test, $P < 0.001$). No trends were apparent in the numbers or proportions of the four note types in the calls.

DISCUSSION

These results demonstrate that black-capped chickadees, when housed together in a captive flock, modify certain acoustic features of their 'chick-a-dee' calls so as to converge on a common mean. This finding supports the hypothesis that flock-specific call differences observed in the field arise through a process of mutual imitation during flock formation (Mammen & Nowicki 1981). It also shows that vocal plasticity and the ability to learn new vocal patterns are maintained in adult as well as juvenile chickadees.

Of those acoustic features measured, the one displaying the most pronounced convergence was the frequency difference between components 1 and 2 (Fig. 2). These two frequency components probably represent the fundamental frequencies of two syringeal oscillators which interact during production to create the complex spectrum of the D-note, and their difference determines the regular spacing of the entire spectrum (Nowicki & Capranica 1986a, b). In theory, then, a chickadee can exert control over this spacing simply by varying the relative tuning of the two syringeal sides. There are some constraints on tuning, since the most orderly D-note spectra result if the absolute values of components 1 and 2 are evenly divisible by their frequency difference (Nowicki & Capranica 1986b). Nonetheless, the mechanism provides a simple way for a bird to vary this acoustic feature of its 'chick-a-dee' call.

How might a bird perceive the evenly spaced spectral components of the D-note? Recently, Cynx & Shapiro (1986) demonstrated that starlings, *Sturnus vulgaris*, can distinguish between complex frequency spectra on the basis of periodicity pitch perception. In other words, given only the upper overtones of a harmonic series, starlings perceive a sound as the pitch corresponding to the missing fundamental frequency. This 'missing fundamental' is equal to the frequency difference between adjacent upper harmonics. Although the D-note is not produced as a harmonic series, its spectral structure is virtually identical to those used by Cynx & Shapiro (1986). It seems likely that, like starlings, chickadees might perceive the complex spectrum of a D-note as a derived periodicity pitch, this pitch corresponding to the interval between adjacent frequency components of the spectrum. If such is the case, then the frequency interval between spectral peaks (Fig. 2) is more than just a convenient measure of acoustic differences between calls; it is in fact a direct measure of how the sound is perceived.

Because the frequency difference between components 1 and 2 is reflected in the spacing of all higher frequency components, this single interval itself does not necessarily play any special role in the perception of differences in the D-note. The same information can be obtained from the spacing of frequency components across a broad spectrum of the bird's hearing range. This fact suggests that the information content of the D-note is uniquely immune to problems of frequency-dependent environmental attenuation that are thought to constrain the physical structure of many birdsongs (Morton 1975; Wiley & Richards 1982; Brenowitz 1986).

The bandwidth of D-notes also converged, although with greater overall variability and at a slower rate (Fig. 3). The correlations between the bandwidth and the maximum and minimum frequencies indicate that variations in bandwidth are almost entirely determined by changing the upper frequency limit while the lower limit stays roughly the same. This arangement can be understood in the light of signal production. Since the minimum frequency is usually the same as component 1, its value and that of component 2 determine the frequency difference between spectral components, as discussed above. Thus, variations must remain relatively small, on the order of 10–100 Hz. The value of the maximum frequency is under no such constraint, however, and can vary as much as 1000 Hz or more.

The discovery that vocal tract resonances play an important role in songbird phonation (Nowicki

1987) suggests that a chickadee might control bandwidth through variations in the tuning of its vocal tract filter. Chickadees vocalizing in helium show an upward shift in the amplitude distribution of their D-note spectra, as predicted by this model (Nowicki 1987). The perceptual significance of the D-note's bandwidth is not as clear. If such differences are perceived by the birds, they might be analogized to the timbres of different musical instruments (Seashore 1938; Marler 1969), or to the differences between vowel sounds in human speech (Fant 1970). It is also unclear whether the slower rate of convergence in bandwidth is significant. Given the generally high variances for this measure, it is conceivable that the bird simply has less control over the D-note's bandwidth than over the tuning between components 1 and 2.

The acoustic features of the 'chick-a-dee' call exhibiting flock-specificity in the field (Mammen & Nowicki 1981) were similar to the convergent features seen in the present study with captive birds, but some differences were found. In both studies, measures of bandwidth and maximum frequency showed significance. The frequency difference between spectral components was not measured in earlier work, but it is likely that the differences observed in the field in the distribution of energy between 1000 Hz and 2000 Hz are a consequence of the tuning of components 1 and 2 (Nowicki 1985). Mammen & Nowicki (1981) suggested that the peak amplitude frequency might be an important flock-specific feature, even though this measure was not quite significant ($P = 0.09$) in their study. The present results argue against that conclusion.

The greatest difference between the two studies occurred in temporal measures. In the field, Mammen & Nowicki (1981) found significant differences between flocks in both the duration of the D-note and the total call duration, the latter measure being correlated with the former. In the present study, no such convergent trends were observed (Fig. 4). Perhaps temporal features are less robust acoustic indicators of flock convergence or converge more slowly, and simply did not appear under laboratory conditions. Alternatively, different acoustic features may be used at different times or under different conditions to encode information redundantly (e.g. Emlen 1972). Out of five flocks studied in the field, three were indistinguishable on the basis of D-note duration alone (see Fig. 5a in Mammen & Nowicki 1981).

It seems likely that the frequency interval between spectral components of the D-note is the most reliable convergent feature of the 'chick-a-dee' call. The bandwidth or other cues might redundantly encode the same information, or possibly even more subtle information concerning flock affiliation. Confirmation of the perceptual and functional roles of any of these features awaits playback studies or psychoacoustical tests using controlled manipulations of natural signals.

Insight into the behavioural significance of vocal convergence and flock-specific acoustic markers for chickadee social behaviour (e.g. Mammen & Nowicki 1981; Hailman et al. 1987) must also await further field studies. The present data, however, raise two points. The first is that no particular individual or group, such as dominant flock members, appear to provide a model which other birds imitate. Instead, birds converge on a common mean. One could argue that the dominant bird in this study happened by chance to begin the experiment at the mean of the four individuals for the most significantly convergent measure (Fig. 2). It is of interest, though, that the two birds (WH and RD) which converged the least in the frequency difference between spectral components (Fig. 2) converged the most in bandwidth (Fig. 3).

A second point concerns the rate at which convergence occurs. Following proposals for vocal duetting (e.g. Wickler 1980), we previously suggested that vocal convergence may represent a type of investment, ensuring that an individual maintains allegiance to a particular flock (Mammen & Nowicki 1981; Nowicki 1983). The rapidity of convergence observed here (Fig. 2) dispels this notion. This is not surprising, given Smith's (1984) discovery that some chickadees switch regularly between two or more flocks over the course of the winter. The present results suggest that flock switchers might repeatedly modify their calls within a season in order to acquire an appropriate flock dialect.

Regardless of the significance of convergence, these results support the view that the D-note has special importance in encoding information in the 'chick-a-dee' call. Hailman et al. (1987) discovered that, although constraints operate to limit the length of 'chick-a-dee' calls in terms of the total numbers of notes included, there is a significant tendency always to include at least one or two D-notes in a string, regardless of its length. This finding is expected if the structure of D-notes

provides an acoustic 'flag' used in recognition (Mammen & Nowicki 1981; Nowicki 1983; Hailman et al. 1987), irrespective of information that might be encoded in the combination of note types (Hailman & Ficken 1986). Marler (1960) originally suggested that different kinds of information could be encoded in different features of a complex sound. The 'chick-a-dee' call provides a good illustration of this principle, with independent and qualitatively distinct acoustic features, the combination of note types and the spectral structure of one particular note, used to encode qualitatively different messages, both of which vary throughout the lifetime of an individual.

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