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Individual Differences and Within-Flock Convergence in Chickadee Calls

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Summary. A detailed sound analysis of the Chick-a-dee call of the black-capped chickadee (*Parus atricapillus*) was performed in order to determine a basis for individual recognition and for imitation within winter flocks. During the winter of 1978–1979 members of five free-living black-capped chickadee flocks were uniquely marked for individual identification, and their calls were recorded in the field. Nested analysis of variance of temporal call parameters measured from sonagrams and spectral parameters from frequency spectra showed that there were significant differences between individuals within flocks for every parameter measured. There were significant differences between flocks in the frequency ranges 800–2,200 Hz and 4,000–5,300 Hz, in the spectral parameters bandwidth and maximum frequency, and in the duration of the Dee syllable and total call duration.

Members of four of the five flocks were captured in December 1978 and held in aviaries segregated by original flock membership. In January 1979 the memberships of the three aviaries were rearranged to form experimental flocks. After one month, there were significant differences among the experimental flocks in the duration of the Dee syllable and total call duration. Convergence, as indicated by a significant decrease in variance among members (F-test), occurred in the experimental flock in Aviary 1 and was concentrated in the frequency ranges 1,300–1,800 and 6,200–6,900 Hz. The members of this experimental flock differed from each other in the number of 100 Hz frequency intervals within which each changed its own call.

The Chick-a-dee call contains sufficient information that it can potentially be used by black-capped chickadees for individual recognition. In addition, both field and aviary data suggest that flock members converge in some call characteristics. Possible explanations of the social significance of vocal convergence in chickadee flocks are discussed.

Introduction

Twenty years ago Marler (1960) suggested that individual-specific characteristics of birdsong may be used for individual recognition. This has since been demonstrated in many species, and individual vocal recognition is now considered a widespread phenomenon in avian social systems (Beer 1970a). Especially well-documented are cases of recognition between parents and young in colonial seabirds (Beer 1969, 1970b; Evans 1970; Stevenson et al. 1970), recognition between mated pairs (Watson 1969; Mundinger 1970; White 1971; Brooke 1978), and recognition among neighboring territorial males (Brooks and Falls 1975; Harris and Lemon 1976; see review in Kroodsma 1976).

In contrast, little work has been done on vocal recognition in flocks or large breeding groups. In the pinon jay (*Gymnorhinus cyanocephalus*), individual recognition may be facilitated by several call components that vary among individuals (Berger and Ligon 1977). Feekes (1977) reports colony-specific song in breeding caciques (*Cacicus cela*) and proposes that this helps prevent intrusion into the colony by alien males. Since colony-specific songs change over time, songs of individual males within each colony must converge through imitation.

Vocal imitation may also be a widespread phenomenon in avian social systems. Imitation is an integral part of song-learning in many passerines (Marler and Mundinger 1971), and in some species vocalizations do not crystallize but may change to match those of other conspecifics throughout an individual's lifetime. For example, mated pairs of several cardue-

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line species have closely matched flight calls through vocal imitation (Mundinger 1970; Marler and Mundinger 1975; Mundinger 1979). Male Indian hill mynahs (*Gracula religiosa*) imitate neighboring males, and females imitate neighboring females (Bertram 1970). In duetting species, imitation is exhibited in the similarity of notes between members of a mated pair (Grimes 1966; Wickler and Seibt 1980) or in the occasional completion of the full duet by one member (Thorpe and North 1965, 1966).

In this study, we demonstrate a basis for both individual recognition and imitation within flocks in a winter flocking passerine, the blackcapped chickadee (*Parus atricapillus*). We first analyse the spectral and temperal characteristics of Chick-a-dee calls given by free-living birds and show both inter-individual and inter-flock variability in the field. We then more closely examine vocal imitation and convergence among group members using data collected from captive experimental flocks.

Materials and Methods

Field Methods

We studied five black-capped chickadee (*Parus atricapillus*) flocks, each separated by at least 1.3 km, in the vicinity of Ithaca, New York. Number of birds per flock for Flocks 1–5, respectively, were 7, 16, 9, 6, and 9. Birds were marked with colored plastic leg bands, coding both flock and individual identity. Wing length of each bird to the nearest 1 mm was determined, and, where possible, degree of skull ossification was examined to determine sex and age (Glase 1973).

Field recordings were made between 8 November and 16 December 1978. We used feeders to concentrate a flock in one area, but these were filled for only 1–2 days to minimize immigration of neighboring flocks. Our recordings were made at 730–790 or 1,400–1,600 EST from a distance of 5–7 m. We rotated recording sessions among the 5 flocks, recording each flock on average every 2 weeks.

Between 13–18 December we recaptured most members of 4 flocks (Flocks 1, 3, 4, and 5) and housed them, segregated by original flock membership, in outdoor aviaries spaced at least 1.4 km apart. On 2 January 1979 Flocks 3, 4, and 5 were mixed to form 3 experimental flocks, each composed of 1–3 members of each of the original 3 flocks. Flock 1 remained unchanged. We made recordings of the unaltered flocks in each aviary twice before 2 January; after that date we recorded experimental flocks (Aviaries 1–3) every 6–7 days (on average) and unchanged Flock (Aviary 4) on 2 occasions. In March 1979 all birds were released at their original sites of capture.

Sound Recording and Analysis

We recorded calls belonging to the Chick-a-dee call complex (Ficken et al. 1978). Of the 4 notes associated with this complex, the 3 "chick-a" (Ck) notes (Fig. 1A, B, C) are characterized by rapid frequency sweeps, resulting in a harsh or slurred quality (Emlen 1972). The "dee" (Dee) note possesses energy at a series of equally-spaced frequencies (Fig. 1c, D; Fig. 2). Calls may consist of various numbers and combinations of Ck and Dee notes; however, we only considered calls in which at least one Dee note was present.

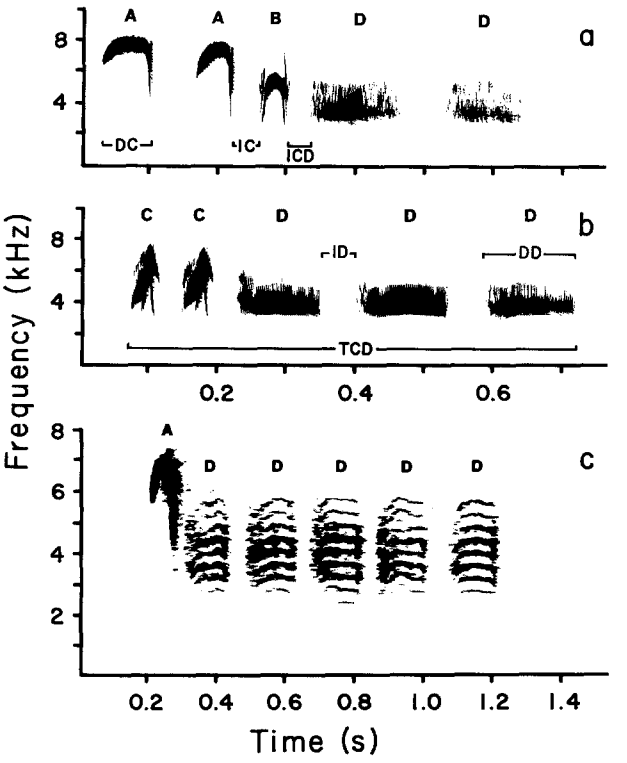

Fig. 1. Wide (600 Hz) band (top, middle) and narrow (90 Hz) band (bottom) sonagrams of Chick-a-dee calls. Abbreviations: *DC* duration of Ck; *IC* interval between Ck's; *ICD* interval between last Ck and first Dee; *DD* duration of Dee; *ID* interval between Dee's; *TCD* total call duration; *A, B, C,* Ck syllable types; *D* Dee syllable

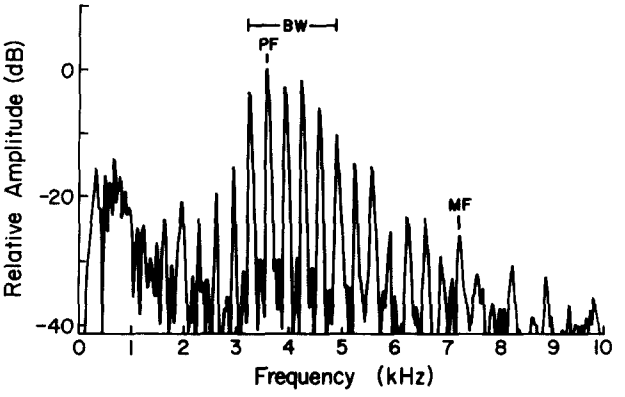

Fig. 2. Typical power spectrum of Dee note. Most of the energy below about 1,000 Hz is due to noise. Abbreviations: *PF* peak frequency (=reference component, relative amplitude 0 dB); *MF* maximum frequency; *BW* bandwidth

The Dee syllable has been described variously as being composed of a series of harmonics (Greenewalt 1968) or as being an amplitude modulated signal (Latimer 1977). The question of how the note is produced is not simple, since amplitude modulation can give rise to sideband frequencies difficult to distinguish from harmonic structures on sonagrams, power spectra, and oscilloscope (Watkins 1966). A detailed analysis of oscillograms (unpubl. data)

reveals the underlying signal to be sinusoidal with complex amplitude fluctuations. Thus we feel that the Dee syllable is produced neither as a harmonic series nor through simple amplitude modulation. The mechanism by which this signal is produced will be discussed in a subsequent paper.

Field recordings were made using a Nagra IV-D tape-recorder at 3.75 ips and a Sennheiser MKH 815T "shotgun" condensor microphone and windscreen. The same system, but with a Sennheiser MKH 415T condenser microphone and windscreen, was used for aviary recordings. Calling individuals were identified by their leg bands.

We made wide-band sonagrams of 396 calls from 35 individuals recorded in the field ($\bar{X}=11.0$, range=2 to 30) and 96 calls from 11 chickadees recorded in aviaries ($\bar{X}=8.7$, range= 4 to 10) on a Kay Electric Co. Sona-graph (Model 7029A) at the 160–16,000 Hz setting to obtain maximum time resolution. We measured the duration of each syllable and interval between successive syllables on the sonagrams to the nearest 3.8 m/s (=1 mm) using a Summagraphics ID Data Tablet/Digitizer directly interfaced with an IBM 370/168 computer. The gross temporal parameters measured are shown in Fig. 1. The numbers of Ck syllables and Dee syllables for each call were also noted.

Using an FFT spectrum analyser (Nicolet Scientific Corp. 444A Mini-Ubiquitous; resolution 25 Hz for the frequency range 0–10,000 Hz; coupled with Tektronix digital plotter), we plotted a power spectrum (Fig. 2) for each Dee note in 303 calls by 35 birds (1424 Dees; $\bar{X}=40.7$, range=10 to 78) recorded in the field and 96 calls by 11 birds (400 Dees; $\bar{X}=36.4$, range=12 to 61) recorded in aviaries. Sections of duration 0.08 msec were taken from the middle portion of Dee notes. To allow more precise triggering of the analyser we re-recorded the original tapes, using two Nagra recorders, at 7.5 ips and played them back at 3.75 ips (half-speed; flat response ± 1 dB to -3 at 6.7 kHz). The spectral component of maximum amplitude was assigned a value of 0 dB; all other components were specified in dB relative to this reference. The frequency and amplitude of all components of amplitude $\geqq -30$ dB were entered into the computer, using reference coordinates to convert digitized x,y-coordinate pairs in mm to frequency and amplitude.

For spectral analysis we divided the frequency range 500–7,000 Hz into sixty-five 100-Hz intervals. For each Dee note, we assigned to each frequency interval a value equal to the maximum amplitude in that interval. Intervals that contained no component $\geqq -30$ dB were assigned -30 dB. The 65 intervals were then treated as separate variables. We also determined the highest frequency with amplitude > -30 dB ("maximum frequency"), the frequency component with maximum (0 dB) amplitude ("peak frequency"), and the width of the band of frequencies around the peak with relative amplitude $\geqq -10$ dB ("bandwidth"; Fig. 2).

Statistical Analysis

To examine which measured call characteristics provided evidence of a basis for individual recognition or convergence within flocks, we determined those call characteristics for which the variation among individuals was significantly greater than that within calls of single birds, and those call characteristics for which the variation among flocks was significantly greater than that among birds within flocks. The data are nested, the levels being *measurements* of calls by *birds* of known identity that were members of *flocks*, enabling us to eliminate the problem of variation among flocks when evaluating differences among individuals by means of nested analyses of variance (Snedecor and Cochran 1967). We used the Anova procedure of the Statistical Analysis System (SAS) on an IBM 370/168 computer to perform separate nested analyses of variance for each of the 8 temporal parameters measured (Fig. 1), the sixty-five 100-Hz frequency intervals, and the 3 additional frequency parameters (Fig. 2).

Results

Differences Among Individuals Within Flocks

Significant differences among individuals within flocks occur in every 100-Hz interval between 500 and 7,000 Hz ($P<0.05$). Significant differences among individuals within flocks also exist in the 3 additional frequency parameters and in the 8 temporal components measured (Table 1). Although each individual does not necessarily differ significantly from all flock-

Table 1. Summary of nested Anova analyses on 3 spectral and 8 temporal parameters: F-statistics, degrees of freedom, and significance levels for differences among individuals within flocks, among flocks, and among aviaries

Parameter	Individual			Flock[a]		Aviary[b]	
	F	(v_1, v_2)	P	F	P	F	P
Peak frequency	6.31	(30, 1,389)	<0.0001	2.23	0.09	3.05	0.11
Maximum frequency	17.22	(30, 1,389)	<0.0001	3.98	0.01	1.06	0.43
Bandwidth	9.48	(30, 1,389)	<0.0001	2.76	0.05	3.18	0.11
Number of Ck	3.98	(30, 361)	<0.0001	1.29	0.30	1.06	0.43
Number of Dee	3.74	(30, 361)	<0.0001	2.25	0.09	1.77	0.25
Duration of Dk	3.68	(30, 667)	<0.0001	2.32	0.08	1.27	0.37
Interval between Ck	2.38	(26, 348)	<0.0001	0.02	0.99	5.80	0.03[c]
Interval Ck-Dee	3.11	(30, 288)	<0.0001	1.58	0.21	0.68	0.60
Duration of Dee	13.45	(30, 1,843)	<0.0001	6.34	0.001	8.02	0.02
Interval between Dee	6.94	(30, 1,446)	<0.0001	1.65	0.19	2.39	0.17
Duration of call	3.53	(30 361)	<0.0001	3.15	0.03	4.08	0.07

[a] Degrees of freedom $(v_1, v_2)=(4,30)$

[b] $(v_1, v_2)=(3,6)$

[c] This is not a change due to the aviary treatment, because significance also occurs when previously obtained field data for these 10 birds are used in the same Anova

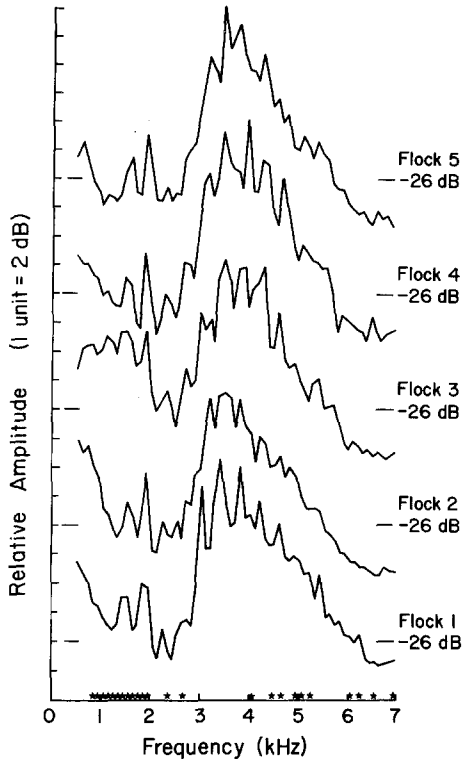

Fig. 3. Mean power spectrum of the Dee syllable for each of the five flocks, calculated by weighting flock members equally. Frequency intervals in which there are significant differences among flocks are indicated by a star above the abscissa. Sample sizes (number of calling flock members): Flock 1, $n=3$; Flock 2, $n=10$, Flock 3, $n=9$; Flock 4, $n=5$; Flock 5, $n=8$

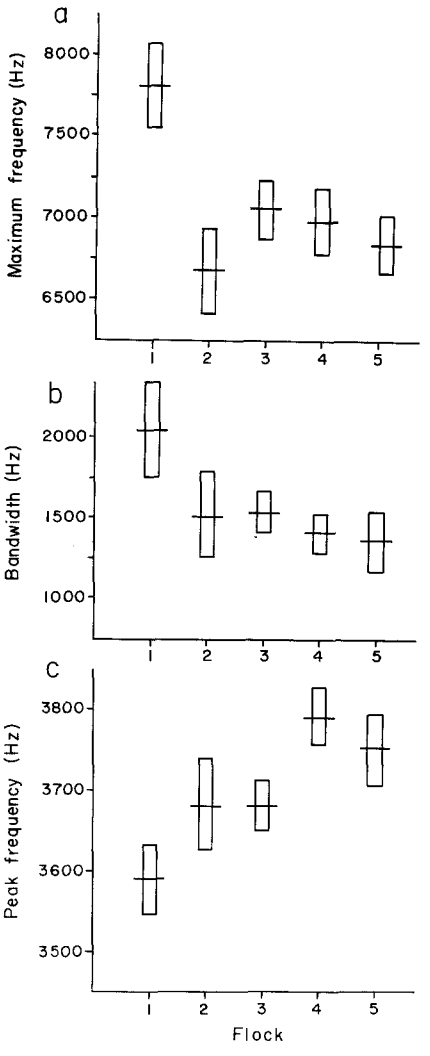

Fig. 4a–c. Mean values (± 1 standard error) for each flock of the frequency parameters for which significant differences among flocks are found. **a** Maximum frequency ($F_{(4,30)}=3.98$, $P=0.011$); **b** bandwidth ($F_{(4,30)}=2.76$, $P=0.046$); **c** peak frequency ($F_{(4,30)}=2.23$, $P=0.09$).

mates for each parameter (Mammen 1981), the nested Anova results show that the variation among individuals is significantly greater than the variation within individuals for every parameter studied.

Differences Among Flocks

Differences among flocks occur in several of the spectral and temporal parameters studied. Averaged power spectra for each flock are shown in Fig. 3. Nested Anova results show that significant differences among flocks exist for 24 of the sixty-five 100-Hz intervals ($P<0.05$, Fig. 3). Significantly greater variation among flocks than within flocks also occurs in the maximum frequency and in bandwidth ($P<0.05$, Fig. 4a, b); among-flock differences in peak frequency approach significance ($P=0.09$, Fig. 4c). Duration of the Dee syllable and total call duration are significantly different between flocks ($P<0.05$, Fig. 5a, b); differences in the duration of the Ck syllable and in the number of Dee syllables approach significance ($P<0.09$, Fig. 5c, d). There are no significant differences for the number of Ck syllables, the interval between Ck syllables, the interval between Dee syllables, or the interval between the last Ck syllable and the first Dee syllable. The results of the nested Anova tests are summarized in Table 1.

Although the nested Anova indicates significant inter-flock variability, each flock cannot necessarily be distinguished from the other four flocks on the basis of any one call characteristic alone (Figs. 3–5). If all significant characteristics are considered together, however, each of the five flocks can be distinguished from one another unambiguously (Table 2).

Convergence in the Aviaries

Ten birds, those for which there were at least 10 calls recorded in the field and 10 or more recordings

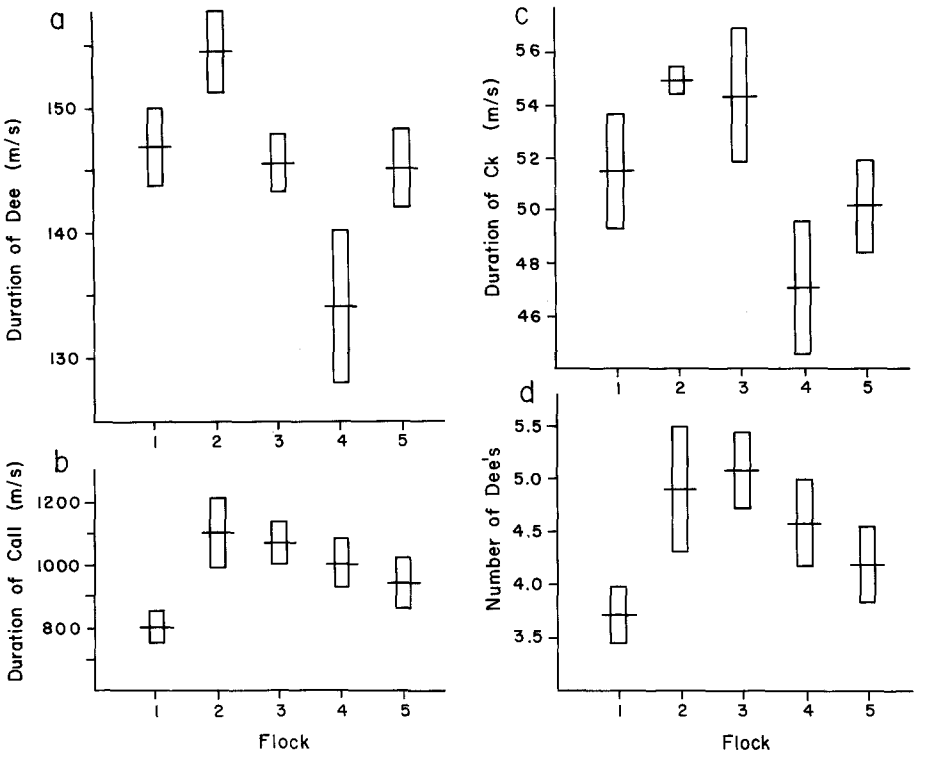

Fig. 5a–d. Mean values (±1 standard error) for each flock of the temporal parameters for which significant differences between flocks are found.
a Duration of Dee ($F_{(4,30)}=6.34$, $P=0.001$);
b duration of call ($F_{(4,30)}=3.15$, $P=0.028$);
c duration of Ck ($F_{(4,30)}=2.32$, $P=0.08$);
d number of Dee's ($F_{(4,30)}=2.25$, $P=0.087$)

Table 2. Call characteristics for which the means ±1 standard error of pairwise comparisons of flocks do not overlap, based on the data presented in Figs. 3, 4, and 5

		Flock			
		2	3	4	5
Flock	1	Maximum frequency Duration of Ck Duration of Dee Number of Dee Duration of call	Maximum frequency Bandwidth Peak frequency Number of Dee Duration of call	Maximum frequency Bandwidth Peak frequency Duration of Dee Number of Dee Duration of call	Maximum frequency Bandwidth Peak frequency
	2		Duration of Dee	Peak frequency Duration of Ck Duration of Dee	Duration of Ck Duration of Dee
	3			Peak frequency Duration of Ck Duration of Dee	Duration of Ck Number of Dee
	4				Duration of Dee

in the aviaries at least one month after the experimental flocks were formed, were used in this analysis. To test the hypothesis that these individuals' calls converged in the experimental flocks (thus establishing new flock differences among the aviary "flocks"), we performed a nested Anova on each parameter using the aviary recordings, grouping the 10 birds by aviary. After at least one month, no differences were apparent in the power spectra or the other 3 frequency parameters. Duration of the Dee syllable was significantly different among the experimental flocks ($P<0.02$, Fig. 6b; closed bars), and differences in total call duration were nearly significant ($P<0.07$, Fig. 6a; closed bars). The nested Anova results for all 8 temporal components and the 3 frequency parameters for these aviary data are also summarized in Table 1. A nested Anova using previously obtained field recordings, but still grouping the birds by aviaries, shows no significant differences in these parameters (Fig. 6a, b; open bars), demonstrating that differ-

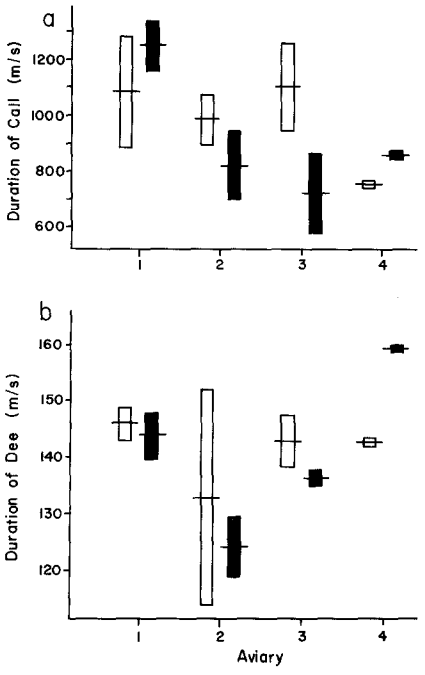

Fig. 6a, b. Mean duration of call (±1 standard error; (**a**)) and mean duration of Dee (**b**) of the flocks formed experimentally in the aviaries, using calls recorded in the field before exposure to each other (open bars) and calls recorded after at least 1 month following formation of the experimental flocks (closed bars). Number of birds calling in Aviaries 1, 2, 3, and 4, were, respectively, 5, 2, 2, and 1. F-statistics and significance levels. **a** open bars $F_{(3,6)}=2.04$, $P=0.209$; closed bars $F_{(3,6)}=4{,}08$, $P=0.067$; **b** open bars $F_{(3,6)}=1.17$, $P=0.396$; closed bars $F_{(3,6)}=8.02$, $P=0.016$

ences among the experimental flocks were due to convergence after the birds were regrouped.

Some degree of convergence in other call characteristics may have occurred even though not detected by the nested Anova. To examine this possibility, we compared the within-group variance in the call characteristics of one aviary group at the time of their field recordings with recordings made at least one month after the experimental flocks were formed. The 5 birds of Aviary 1, for each of which we had recorded at least 10 calls both in the field and in the aviary, were used for this analysis. A significantly decreased variance, indicating convergence, occurred in 16 of sixty-five 100-Hz frequency intervals (F-test; Sokal and Rohlf 1969, $P<0.05$), concentrated in the 600–1,800 Hz and 6,200–6,900 Hz ranges. The call of the known adult male in Aviary 1 changed more than did those of the two known females (ten 100-Hz intervals versus 5 and 6). The other 2 birds in Aviary 1, of unknown sex and age, changed their calls to a degree comparable to the adult male (9 intervals each).

Discussion

Black-capped chickadees form stable winter foraging flocks that defend flock territories from early fall until early spring. Flock size is small, averaging 6–7 birds (as many as fifteen have been recorded (Odum 1942)). Flocks consists of the pair that bred in the flock territory the preceding season, one or more non-breeding adults, and several juveniles that are not the offspring of the mated pair (Glase 1973). Group territories contain winter food resources and encompass the breeding sites of 1–3 pairs from the flock in spring. The over-winter stability of flock membership and of dominance relationships (Glase 1973, pers. obs.) suggests that individual recognition plays a significant role in chickadee social organization.

Use of auditory cues for contact and individual recognition seems especially likely for chickadees. Since they are extremely invariant in plumage, recognition using morphological cues may be difficult. In addition, use of visual cues may be impractical because flock members are often out of sight of each other. Even when in a fairly tight group, birds can not easily maintain visual contact while foraging in dense cover.

The contexts in which the Chick-a-dee call is used suggest that it may play a role in recognition of individuals and in flock cohesiveness. Black-capped chickadees of both sexes give the call (1) as a contact note between foraging flock members and during group movements (Ficken et al. 1978); (2) when separated from the flock (Odum 1942; Glase 1973); (3) while "scolding" or mobbing predators (Odum 1942; Ficken and Witkin 1977); and (4) during flock encounters at group territory boundaries (Glase 1973, pers. obs.).

Our results show significant differences among individuals within flocks for every spectral and temporal parameter examined; the numbers and durations of notes, intervals between notes, distribution of spectral energy in the Dee note, peak and maximum frequencies, and bandwidth. The great potential for individual recognition found in this study is not surprising. The coding of individual identity need not be restricted to a small number of characteristics; several variable parameters may provide additional information, especially when the variability in each characteristic is great. Considerable redundancy may exit, and only a subset of the characteristics may be important, as Emlen (1972) has shown for the indigo bunting (*Passerina cyanea*).

Fewer call characteristics are significantly different among flocks (Figs. 3, 4, and 5). All of these characteristics, potentially involved in flock discrimination, are also potentially used for individual recognition;

however, segregation of different functions to different components of song has been found for nearly every species studied (see Emlen 1972). If within-flock similarities are coding for flock identity, there may be some conflict in coding both levels in one call: flock recognition is facilitated by stereotypy of some components with the flock, while individual recognition requires considerable variability among individuals. Flocks cannot usually be distinguished from one another on the basis of a single parameter. Nonetheless, all of the flocks we studied can be unambiguously identified if several parameters are considered in concert (Table 2). Marler (1960) observed a similar phenomenon (at the individual level) in chaffinches: a particular combination of song-types allowed for identification of a bird although each of the song-types was shared with other individuals. The set of parameters that distinguishes any 2 flocks is a subset of a group of parameters potentially available; this flexibility itself increases the potential for flock discrimination.

The particular characteristics of a song or call that code identity will depend on the birds' physiological capabilities to produce and detect variability, the physical constraints of the environment, and on other selective pressures affecting the structure of a call (e.g., predation). Significant individual differences in the Chick-a-dee call occur in every 100-Hz interval between 500 and 7,000 Hz, while flock-specific differences are concentrated in two frequency ranges, 800–2,000 Hz and 4,000–5,300 Hz (Fig. 3). Passerines have maximum sensitivity in frequency resolving power between 500 and 4,000 Hz and in absolute threshold between 2,000 and 4,000 Hz (Dooling 1980). The lower frequency range of flock differences falls within this region of maximum resolving power; however, flock differences lie on either side of this band of maximum sensitivity. High frequency resolving power may be more important for analyzing individual differences, in which a greater number of unique discriminations are required. Limits of avian temporal sensitivity are about 3 to 5 m/s (Dooling 1980). Significant differences among individuals in all temporal parameters and among flocks in syllable length and total call duration both in the field and the aviaries (Mammen 1981; Figs. 5 and 6) are well within the limits of avian temporal sensitivity and are probably easily distinguished by chickadees.

Because there is less attenuation with distance for lower frequencies than for higher frequencies (Wiley and Richards 1978; Roberts et al. 1979), concentration of some flock differences in a lower frequency region permits flock identity information to be propagated further than individual identity information. This idea is compatible with the use of the call in promoting flock cohesiveness while foraging or defending territorial boundaries. Convergence occurred in the lower frequency range (600–1,800 Hz) in the aviary experiment, suggesting the greater importance of this region over the higher frequency range where flock differences are also found. The wide band width of the Chick-a-dee call may be an adaptation to signalling to individuals at varying distances and heights (Roberts et al. 1979).

The convergence of calls that occurred in the experimental flocks (Fig. 6) suggests that convergence contributes to flock-specific differences observed in the field. The parameters that changed (duration of the Dee syllable, total call duration, and to a lesser extent the spectral distribution of energy in the Dee syllable) were a subset of the parameters that differed among flocks in the field. Since the aviary experiment was unlike natural flock formation in that the birds were regrouped in January, four months after flock formation normally occurs, one would not necessarily expect complete convergence in all of the flock-specific characteristics. The parameters that did change may be either the most fundamental to flock recognition or simply the most labile.

Vocal imitation in chickadee flocks may be adaptive for several reasons. Thorpe and North (1965) and Mundinger (1970) suggest that vocal imitation is sometimes used for recognition and maintaining contact with conspecifics. Since their flocks are small and there is much variability among individuals, it would appear that chickadees could distinguish and maintain contact with their flock-mates by recognizing the calls of the other members individually, without converging among the group. Convergence may result in more rapid discrimination of flock members. This is advantageous in encounters between neighboring flocks, and abbreviated social interactions might be less conspicuous to predators or allow more time for feeding and other activities.

Alternatively, imitation may serve as a mechanism of integration of new members into a flock. All chickadee species share the pattern of alternating periods of aggregation in flocks and breeding in territorial pairs (Brewer 1961; Dixon 1963, 1965; Glase 1973; McLaren 1975). During flock formation, imitation of flock members already present by new individuals may be a means of minimizing aggressive responses to a stranger. Members of closed groups or stable dominance hierarchies (such as chickadee flocks) are often very xenophobic (Wilson 1975, p 286). The aviary experiment provides preliminary evidence that convergence is asymmetric among flock members. The two known females made relatively few changes in their calls; since they are not a threat to territory ownership, females may have freer access into winter

flocks. More rigorous tests of the function of intra-flock imitation are needed.

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