GEOGRAPHIC VARIATION IN BLACK-CAPPED CHICKADEE SONGS AND SINGING BEHAVIOR

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ABSTRACT.—Songbird species differ in how their songs vary geographically, and the vocal behavior of Black-capped Chickadees (*Poecile atricapillus*) exhibits an especially intriguing pattern of variation. Throughout most of their range (i.e. from Nova Scotia to British Columbia), males sing a simple two-tone "fee-bee-ee" (with the "fee" slightly higher in frequency than the "bee-ee" and an amplitude break between the "bee" and "ee"), and each male shifts the pitch of his single song type over a range of about 800 Hz. Birds sing differently, however, on the islands of Martha's Vineyard, Chappaquiddick, and Nantucket off Massachusetts. Island singing differs from mainland singing in four ways: (1) most island songs are monotonal, with the two whistles on the same frequency; (2) island songs exhibit much greater structural diversity than mainland songs; amplitude breaks may occur in the first, second, or both main whistles; (3) island males typically have repertoires of two or more different songs; and (4) song dialects occur both between and within the islands (even on Chappaquiddick, which is only 6 km wide). Song dialects and repertoires of different songs also occur in some Black-capped Chickadee populations in Oregon and Washington. The distinctive singing of birds on Massachusetts' offshore islands, and of birds in Oregon and Washington, may have arisen because these populations are sedentary and isolated. In mainland populations, young chickadees often migrate or irrupt, and the considerable movement of these young birds could promote uniform behavior from coast to coast among mixing populations. Geographic uniformity of song among mainland males is perhaps also maintained by young males learning an "average" song from their sound environment. In contrast, isolated groups of males (as has been shown for young birds of typical fee-bee-ee populations in the laboratory) may express divergent songs and singing behavior. *Received 16 January 1998, accepted 9 September 1998.*

AMONG SONGBIRDS, BLACK-CAPPED CHICKA-DEES (*Poecile atricapillus*) are especially fascinating singers. Although songs of many species vary geographically (e.g. Baker and Cunningham 1985), the fee-bee-ee song of Black-capped Chickadees is remarkably invariant across most of their range in North America (see Hailman 1989, Kroodsma et al. 1995). Among these

populations, males "pitch-shift" their simple song over a range of frequencies. Among all songbird species in North America, we know of no greater conformity to a single learned song type and singing style over such an extensive portion of the continent (see Byers 1996). This conformity is all the more exceptional given that males raised in the laboratory (1) do not readily learn the fee-bee-ee song, (2) acquire a great diversity of whistled songs, (3) have repertoires of two to four song types, and (4) show

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dialects from group to group (Shackleton and Ratcliffe 1993, Kroodsma et al. 1995). Hints of nonconformist singing behavior at the periphery of the range of Black-capped Chickadees (Jewett et al. 1953, Bagg 1958, Desfayes 1964, Hailman 1989) convinced us that a continent-wide description of male songs and singing behavior would be necessary before we could begin to understand the significance of these patterns.

To document chickadee singing patterns, we collected recordings of Black-capped Chickadees from throughout North America. We focused especially on the offshore islands of Massachusetts, including Martha's Vineyard, Chappaquiddick, and Nantucket. Good samples were also obtained from the chickadees in Oregon and Washington. For comparison, we analyzed recordings archived at Cornell University's Library of Natural Sounds, and we recorded chickadees from mainland North American sites, especially in Amherst, Massachusetts. Our analyses verify the great stereotypy of most mainland populations and the remarkably diverse array of songs and singing behavior among males at the extremes of the species' geographic range.

METHODS

Tape recordings used in these analyses were made by a number of recordists over several years and at many locations. Dolly Minis began recording on Martha's Vineyard in the 1970s and continued into the 1990s; her recordings, archived at Cornell University's Library of Natural Sounds (LNS), together with a report by Bagg (1958), prompted a scouting effort to the Vineyard by Kroodsma from 10 to 12 May 1994. A number of recordists then responded to the invitation to document Vineyard songs during 4 to 8 May 1995; those recordists included Byers, Bolsinger, Halkin, Houlihan, Kroodsma, Macaulay, Marantz, Minis, and Ortiz. Additional recordings were made on the Vineyard and Chappaquiddick by Halkin and Stoddard from 27 to 28 April 1996, and by Byers, Halkin, and Kroodsma from 10 to 13 May 1996. Marantz recorded on Nantucket during 19 to 21 May 1995, and Byers and Kroodsma returned to Nantucket from 10 to 12 June 1996.

Other recordists contributed to the sample elsewhere in North America. During 1995, chickadees in Amherst, Massachusetts, were recorded by Wilda, Dawson, Staples, and Kroodsma (see Acknowledgments). During 1996, Hill (5 to 16 April; Seattle and Everett) and Innes (28 April; Hoquiam) recorded in Washington, Keller (March to May; Coquille) in

Oregon, and Farrington (6 June and 1 July) at Falmouth, Massachusetts, a mainland site just opposite Martha's Vineyard. These recordings were supplemented with recordings from the collections of Innes and Kroodsma and with recordings in the archives of the LNS.

Recordists used their own recording systems. Tape recorders included the Marantz PMD222 and PMD430; Nagra IS-DT, IV-D, and IV-S; Panasonic DATR SV 255; and Sony TC-D5ProII, TC-D5M, TC-D10 PROII DAT, TCM-5000, and WM-D6 Professional Walkman. Parabolic reflectors were the Telinga ProII, Telinga DAT Pro III, Sony PBR-330, Dan Gibson, Roche 76 cm, and a metal 60-cm parabola. Microphones used were the Sennheiser ME-20, MKH 60, MKH 106, MKH 815, MKH 816, and MZW 60. Pitch pipes or tuning forks were used with many recordings, thus verifying consistent tape speed. In our analyses, we found no reason to believe that the variety of equipment used contributed to the variety in the songs and behavior we documented among the chickadees.

We used two basic approaches during our recording efforts. The first was to obtain a long sequence of songs from an individual during a dawn bout. For some males, we returned to the same territory on successive days or weeks; given our knowledge of the territory, the male's song perches, and the stability of the neighboring territories, we were fairly confident that the male was the same from visit to visit. Also, as we studied the songs recorded over several visits, we found no discontinuities in song types or behavior, again confirming that we could identify individuals on successive visits. We used a second approach to survey larger numbers of individuals in an area by recording just a few songs from a given male before quickly moving on to the next male.

All recordings used in this study will be archived at the LNS and therefore will be available for future reference. Most of them can be accessed by the following reference numbers in the Kroodsma tape collection: for 1994, tapes 3–4, 14–18, 24–28, 33, 36, 37, and 49; for 1995, tapes 6–14, 22–25, 28, 29, 32, 49–53, 55, and 59; for 1996, tapes 3–11, 13, 52, 53, 61–67, 112–119, and 121–130. The following tapes have already been archived at LNS: tapes 98–101 and 103–105 by Curtis A. Marantz for 1995; and tapes MV1-MV4 by Linda R. Macaulay for 1995.

Most chickadee songs are relatively simple, and we classified them first by ear and later by eye (with sonagrams) according to their basic temporal and frequency variables (Fig. 1). Our initial classification of the songs was based on the number of consistent amplitude breaks in the two main whistles. In high quality, reverberation-free recordings, these amplitude "dips" are recognizable and consistently present or absent from the songs in a given sequence. Some songs had no breaks in the two whistles (song formula 1-1, indicating two uninterrupted whistles);
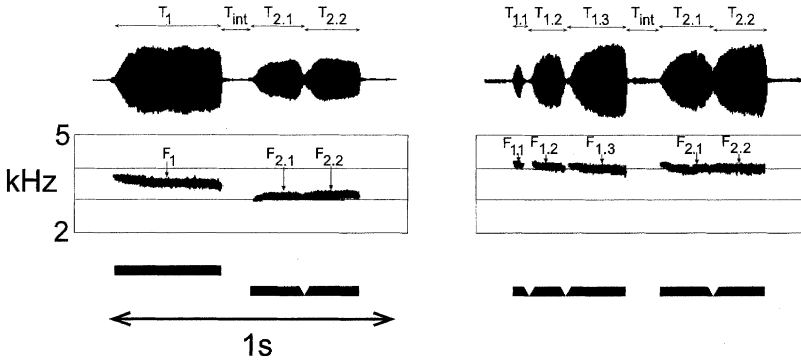
FIG. 1.   Amplitude (above) and frequency (middle) display of two Black-capped Chickadee songs, one from mainland North America (left; the well-known "fee-bee-ee," ["hey-sweetie"]) and one from Edgartown, Martha's Vineyard, Massachusetts (right; "sosweetie-sweetie"), showing the standard temporal (T) and frequency (F) measurements that we made on whistled songs. Songs typically consisted of two main whistles, each with one to three subcomponents separated by amplitude breaks. Hence, T_1 is the duration of the entire first whistle if it has no amplitude break, $T_{1.2}$ is the duration of the second subcomponent of the first whistle, etc. For all frequency measures, we used the "power spectrum" mode on a Kay Elemetrics DSP-5500 Sona-Graph (effective filter bandwidth, 29 Hz), taking one frequency measurement for each continuous whistle; for temporal measures, the spectrographic and waveform modes were used (bandwidth, 300 Hz). Below each sonagram is our short-hand notation for each song; these diagrams incorporate information on frequency, duration, and amplitude breaks.

some had an amplitude break only in the second whistle (such as the familiar fee-bee-ee; song formula 1-2; Fig. 1, left panel); and the song formulas of the other four groups were 2-1, 2-2, 3-1, and 3-2 (Fig. 1, right panel). Then, using the relative and absolute frequencies of the two main whistles, we identified several subgroups of songs. Because most chickadee songs consist of only two main whistles, we used the characteristics of the first two whistles even for songs that consisted of three or more main whistles, because the third and successive whistles were usually identical to the second.

Five song types, and usually several renditions of these types from different males, did not fall into these simple song formulas (see Table 1: column 21). Two Oregon songs consisted of more than two main whistles, and the third and successive whistles were different from the second whistle. One Massachusetts and two Washington songs included high-frequency "clicks" that made them unique.

We analyzed the tape recordings in two ways. First, for the males from which we recorded hundreds or even thousands of songs, we wanted to plot the changes in song frequency over successive renditions (cf. Horn et al. 1992). We therefore chose one particular whistled component for each song type and measured the frequency of that component for all songs of that type from that male. In our second analysis, we wanted to explore more quantitatively the variation in our recorded songs. We therefore measured relevant frequency and temporal variables (see Fig. 1) for a total of 900 songs. Our criteria for

choosing songs were simple: the recording had to be of high quality and it had to be typical of a series of such songs from a given male. Some males were represented several times in this sample, for the following three reasons. First, some males clearly had a repertoire of different song types, so we included one of each type in the sample. Second, if a male "pitch-shifted" a given song type, we wanted to examine the full range of frequency variation in the sample, so we included three to five of those songs from the same male, spaced at intervals of about 200 Hz. Third, we wanted to determine if a clustering algorithm would classify songs the way we did, so we intentionally included two or more renditions of what seemed to us to be the same song type from the same male.

We then submitted our temporal and frequency measurements from the 900 songs to a k-means cluster analysis (Wilkinson 1996). We chose to use a clustering procedure in an exploratory fashion, as a kind of mechanical check on the reliability of our aural and visual classification. We essentially "asked" the clustering algorithm to classify songs into types, based on variables that corresponded to the acoustic features that we had used in our aural and visual classification.

No numerical clustering or classification method can determine the optimal number of groups into which objects will be sorted (Everitt 1993), and the k-means clustering method requires that the investigator specify the number of groups. We initially directed the clustering algorithm to sort the 900 songs

TABLE 1. Classification by cluster analysis of Black-capped Chickadee songs from North America (columns 1 to 20), showing that chickadees from most of mainland North America (and eastern Nantucket) have similar songs (clusters 1 to 3), but that many songs from Massachusetts' offshore islands (Chappaquiddick, Martha's Vineyard, and Nantucket), Oregon, and Washington are different (clusters 4 to 20). The mnemonic aids for each group of songs are provided in the top row. The collection of unique songs in column 21 was not included in the analysis (the cluster analysis had been based on a total of 900 songs, but for this table we eliminated 205 songs so that each male could be represented only once in each cluster).

Site	Hey-sweetie					Sweetie-hey		Sosweetie-sweetie			Sweetie-sweetie					Hey-hey		Miscellaneous[a]				Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
Chappaquiddick	2	2		17	30			2		1	4	1	6	1	12							78
Martha's Vineyard					3	154	36	12	4	75	19	14	69	83		7						471
Nantucket	6	7	8								4	1			20		1	1				54
Nashawena Island	1	1	1																	1		3
Nova Scotia	1	1																				2
Maine		1																				1
Massachusetts	5	9	16									1									1	32
New Jersey		1																				1
New York	4	4																				9
Ontario	1	5													1							7
Pennsylvania			1																			1
Michigan	1	2	2																			5
Minnesota		1																				1
Montana	3	3	2	1							1											10
Utah	1	1	2																			4
Alberta	2	1													2							5
British Columbia	1																					1
Washington				2				1			3	1							1		2[b]	10
Oregon		1		1									1						1	1	2[b]	5
Total	28	40	33	21	33	154	36	15	4	76	31	18	76	84	35	7	1	1	1	1	5	700

[a] Cluster 18 was sosweetie-hey, 19 sweetie-sweetie, 20 sosweetie-sweetie, and 21 a variety of unique songs. They are placed together in the miscellaneous category because they are rare and only a side story (18 to 20) or because we chose not to use the cluster analysis to classify songs that were so obviously unique (21).

[b] Several males sang each of these unique songs types from Oregon and Washington, but we indicate only the number of different song types that we identified, regardless of how many males sang each type. Hence, category 21 actually represents five different clusters, each unique so that it was unnecessary to use the cluster program to classify them (see Methods).

in our sample into 15 clusters, in accordance with our initial classification. This procedure, however, grouped some markedly different songs together, so we repeated the analysis iteratively, increasing the number of clusters by one at each iteration. At 20 clusters, we reached a point of diminishing returns, beyond which adding additional clusters served only to subdivide groups of songs that we thought were highly similar. Our analysis is therefore based on the 20-cluster classification. Among these 20 clusters, the program always placed together those songs that we thought were essentially identical renditions of the same song type from the same male; furthermore, in almost all cases the classification matched our visual classification of songs, thereby giving us confidence in this approach. In presenting the results of this analysis (Table 1), we avoid pseudoreplication by presenting the classification of only 695 songs, so that each male is represented only once in a given cluster.

To test whether *P. atricapillus* from Martha's Vineyard were genetically different from elsewhere, Gill collected six birds and used a restriction-fragment analysis to compare their mitochondrial DNA (mtDNA) with that of a geographically diverse sample of chickadees examined in the same fashion by Gill et al. (1993; see their methods). *Poecile atricapillus* throughout North America exhibit a remarkably uniform mtDNA haplotype, with the single exception of the island population on Newfoundland, which has a distinctive haplotype.

With apologies to tradition and anguished colleagues, we use "hey-sweetie" instead of the favored "fee-bee-ee" to represent the familiar chickadee song throughout the rest of this paper. By using "hey-sweetie," we can more easily generate mnemonics that enable one to compare the familiar, widespread chickadee song with the unusual songs that occur on the offshore islands of Massachusetts.

RESULTS

First, we describe variation in song from throughout the geographic range of the Black-capped Chickadee. Next, we focus on individual variation, including song repertoires and pitch-shifting. Last, we review whether Martha's Vineyard birds are genetically different from birds elsewhere.

GEOGRAPHIC VARIATION IN SONG TYPES

Throughout most of their range in mainland North America, i.e. from Nova Scotia to British Columbia, the predominant Black-capped Chickadee song is the familiar, two-tone "hey-sweetie" (Fig. 1, Table 1). This song typically consists of two whistles, each about 0.4 s duration (Fig 1). The first whistle is slurred downward about 200 Hz from start to end; the second begins about 400 Hz below the end of the first, but the ratio of the frequency of the two whistles is more consistent than is the frequency difference (Weisman et al. 1990). An amplitude dip typically appears near the midpoint of the second whistle. These features of the song have been described or illustrated for Massachusetts, Pennsylvania, New York, Ontario, Missouri, Wisconsin, Alberta, Utah, British Columbia, Washington, and California (see Dixon and Stefanski 1970, Ficken et al. 1978, Hailman 1989, Kroodsma et al. 1995).

From "mainland" North America, a term we use to include the above geographic distribution (but not certain locations in Oregon, Washington, and Alaska; see below) and Nashawena Island (the distal island in the Elizabethan Island chain near Martha's Vineyard), 75 of 82 chickadee songs we analyzed were this typical two-tone hey-sweetie (Table 1). All 75 songs were of the 1-2 song formula, with a $F_1/F_{2.1}$ frequency ratio of 1.10 to 1.30 (see Fig. 1, Table 2), indicating a substantial drop in frequency from the first to the second whistle. The cluster analysis placed these 75 songs into three different clusters (1, 2, and 3) that differed in frequency, with a cluster of low, medium, and high-frequency songs (Table 2). Frequency ranges of these three clusters were broadly overlapping, however, and with no obvious trimodal distribution. Especially important here is that the three clusters did not segregate geographically; rather, because each male chickadee sings his hey-sweetie over a continuous range of frequencies, each individual for which we had lengthy recordings had a representative song in each cluster. We also emphasize that these three clusters do not identify three "song types" for the birds; for each individual chickadee, for example, the cluster analysis has simply taken a continuous frequency distribution and parsed it into three groups based on the level of splitting that we dictated when we chose a total of 20 clusters for the entire 900-song sample.

The seven songs from mainland North America that were not placed in clusters 1, 2, or 3 also sounded superficially like the standard hey-sweetie. One song from Montana had a relatively small frequency ratio ($F_1/F_{2.1}$ = 1.10),

TABLE 2. Frequency characteristics of songs in clusters 1 to 15, showing how the song clusters differed in absolute (median frequency) and relative (frequency ratio) frequencies of the whistled song components. Ranges are in parentheses.

Cluster	Median frequency of $F_{2,1}$	Frequency ratio[a]
Hey sweetie		
1	3.06 (2.74–3.34)	1.12 (1.10–1.30)
2	3.25 (3.00–3.46)	1.17 (1.10–1.30)
3	3.53 (3.32–3.70)	1.16 (1.11–1.25)
4	3.56 (3.42–3.72)	1.01 (0.99–1.10)[b]
5	3.89 (3.70–4.18)	1.02 (0.99–1.05)
Sweetie-hey		
6	3.63 (3.00–3.90)	1.01 (0.98–1.05)
7	4.16 (3.87–4.36)	1.02 (0.99–1.05)
Sosweetie-sweetie		
8	3.56 (3.44–3.63)	1.01 (0.98–1.05)
9	3.75 (3.66–3.92)	1.01 (1.03–1.07)
10	4.18 (3.98–4.52)	1.01 (1.00–1.07)
Sweetie-sweetie		
11	3.57 (3.30–3.98)	1.00 (0.95–1.16)
12	3.71 (3.30–3.86)	1.02 (0.99–1.16)
13	4.02 (3.90–4.18)	1.01 (0.99–1.03)
14	4.24 (4.12–4.51)	1.01 (1.00–1.05)
15	3.02 (2.78–3.26)	1.16 (1.09–1.25)

[a] The ratio of two frequencies, the frequency of the last (or only) whistled subcomponent of the first main whistle divided by the frequency of the first (or only) whistled subcomponent of the second main whistle (see Fig. 1). Thus, for hey-sweetie songs, the ratio is $F_1/F_{2,1}$, for sosweetie-sweetie songs, $F_{1,3}/F_{2,1}$, and so on.

[b] Includes an outlying value (1.10) from Montana; otherwise, range was from 0.99 to 1.06.

and it was classified with a group of monotone hey-sweetie songs (1-2 song formula) from Chappaquiddick that had frequency ratios of ≤1.06 (cluster 4; Tables 1 and 2). Five songs (two from Alberta, one from Montana, one from Massachusetts, one from New York) all sounded like typical hey-sweeties, but closer analysis showed a consistent extra amplitude break in the first whistle (2-2 song formula; sweetie-sweetie), so these songs were classified with clusters 11 through 15. The seventh song, from Falmouth, Massachusetts, contained some non-whistled "click" components; although it, too, sounded superficially like a hey-sweetie, the clicks made it unique (Table 1: column 21). Our hunch is that most of these seven songs represent unique individuals from populations of typical hey-sweetie singers (see Smith 1991), although it is possible that some undetected, unique song populations of this chickadee occur across North America.

Songs of Oregon and Washington birds clearly differed from those of the rest of North America (see also Hammond 1993). Four song types were so different that we did not include them in the clustering program (Table 1: column 21). Two of these songs were from Washington, and both contained clicks; one Oregon song consisted of a series of whistles that dropped in frequency as they increased in duration, and the other consisted of two high and several low whistles. Of the 11 Oregon and Washington songs that we included in the cluster analysis, only one song was classified in clusters 1 through 3, the typical hey-sweetie songs. Nine songs were classified with songs from other locations, and one was placed in a cluster by itself.

A great variety of songs occurred on the islands of Martha's Vineyard, Chappaquiddick, and Nantucket. Although the basic two-tone hey-sweetie (clusters 1, 2, and 3) was heard and recorded from several chickadees on eastern (but not central or western) Nantucket and from four males on Chappaquiddick (Table 1), other song types predominated on these islands, and the two-tone hey-sweetie songs were absent in our sample of 446 songs from Martha's Vineyard.

Perhaps most similar to the mainland hey-sweetie song was the commonest song throughout Chappaquiddick, a monotonal (i.e. $F_1/F_{2,1}$ ca. 1.0) hey-sweetie (clusters 4 and 5; Tables 1 and 2, Fig. 2). Each male shifted this song in frequency, and our cluster analysis partitioned the songs into one low-frequency and one high-frequency cluster (even though the frequency of songs appeared continuous to us). Although common on Chappaquiddick (47 of 78 songs in our sample, or 60%), this song was rare on Martha's Vineyard (only 3 of 471 songs, or <1 %).

On Martha's Vineyard, adjacent to Chappaquiddick, the most common song (190 of 471, or 40%) was a monotonal "sweetie-hey" (clusters 6 and 7; Tables 1 and 2, Fig. 2), with an amplitude break in the first, not the second whistle. In the field, we recognized a low and a high-frequency form of this song (see bimodal distribution in Fig. 3), and the cluster analysis largely agreed with our aural classification (186 of 190 songs, or 98%). In our sample of Black-capped Chickadee songs from throughout North America, we found this sweetie-hey song only on Martha's Vineyard.
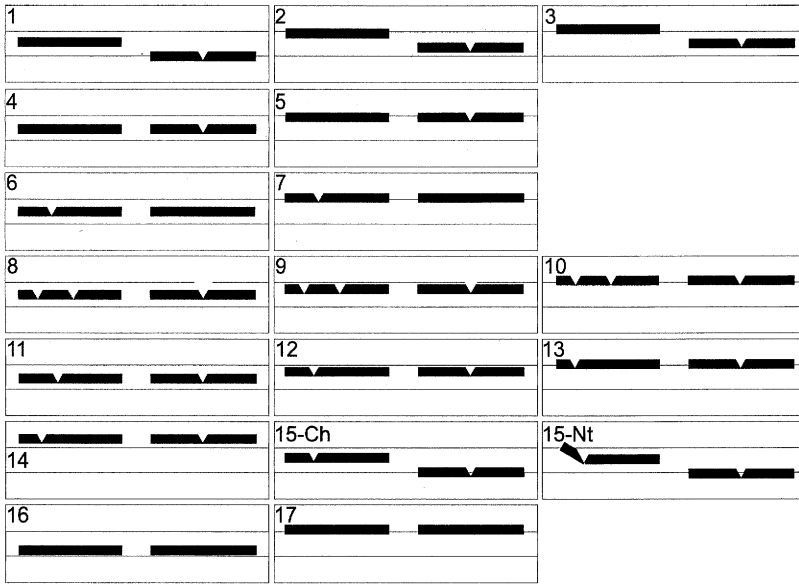
FIG. 2.   Diagrams (see Fig. 1) of songs representing 17 groups from our cluster analysis (see Table 1), showing the relative uniformity of Black-capped Chickadee songs throughout mainland North America (clusters 1 to 3) and the great diversity of songs on the offshore islands of Massachusetts (clusters 4 to 17). Frequency markers are 2 to 5 kHz, and the duration of each diagram is about one second, as in Figure 1; frequency and temporal characteristics for each diagram are based on average values for each cluster. Clusters 1 to 3 are low-, medium-, and high-frequency two-tone hey-sweetie songs (i.e. fee-bee-ee) from throughout North America; clusters 4 and 5 the low- and high-frequency monotonal hey-sweetie songs, mostly from Chappaquiddick; clusters 6 and 7 the low- and high-frequency sweetie-hey songs exclusively from Martha's Vineyard; clusters 8 to 10 the low-, medium-, and high-frequency sosweetie-sweetie songs found mostly on eastern Martha's Vineyard; clusters 11 to 14 the low to high monotonal sweetie-sweetie songs (Martha's Vineyard and Chappaquiddick); cluster 15 is the two-tone sweetie-sweetie song (Chappaquiddick and Nantucket); and clusters 16 and 17 the monotonal hey-hey, found mostly on Nantucket. We illustrate two diagrams for cluster 15 because songs from Chappaquiddick (Ch) and Nantucket (Nt) were separable by our ears and by sonagrams, even though they were combined by the cluster analysis.

Like other songs on the Vineyard, these two sweetie-hey clusters were not distributed at random (Fig. 4). The 36 high-frequency songs (cluster 7) occurred almost exclusively on the western edge of the Vineyard. The low-frequency song, in contrast, was distributed far more widely. It was the predominant low-frequency song over roughly the western 90% of the Vineyard and was replaced only on the eastern Vineyard, around Edgartown, by two other, more geographically restricted low-frequency forms (clusters 8 and 9, 11 and 12). For the 19 males in our sample that sang both a high-frequency sweetie-hey (cluster 7) and a low-frequency song, the low-frequency song was always a sweetie-hey (cluster 6).

Another monotonal song form, with two amplitude breaks in the first and one in the second whistle ("sosweetie-sweetie"; clusters 8, 9, 10),

was concentrated on the eastern Vineyard, near Edgartown (Figs. 1, 3, 4). In the field, we had recognized a high- and low-frequency version of this distinctive song, but our analysis allotted three clusters for these songs, with non-overlapping frequency distributions (Table 2, Fig. 3). The two lower frequency versions of these songs (clusters 8 and especially 9) were relatively rare, but examples of the highest-frequency version (cluster 10) were common in and around Edgartown.

The other common group of songs on the Vineyard and Chappaquiddick had one amplitude break in each of the two main whistles (i.e. "sweetie-sweetie"; clusters 11–15 in Tables 1 and 2; see Figs. 2, 3). Four clusters (11 to 14) contained monotonal songs. The 185 Vineyard songs in these four clusters segregated on the basis of frequency; clusters 11 through 14 con-
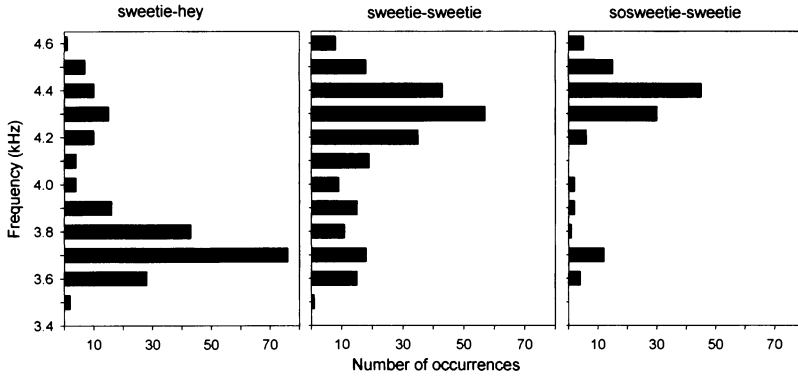
FIG. 3. Histograms of song frequency for the three main song types that occurred on Martha's Vineyard, showing that each type tended to occur in a high- and low-frequency form. All frequency measurements were made on F_2 or $F_{2,1}$ (see Fig. 1). Each bar represents the total number of songs within a given frequency range of 100 Hz. Left (clusters 6 and 7), center (11 to 14), and right (8 to 10) columns tend to represent west, central, and eastern Vineyard (see Fig. 4), respectively, except that low-frequency sweetie-hey songs (cluster 6) had a wider distribution, occurring over most of the island. Although Martha's Vineyard was not sampled uniformly, the relative abundance of each song type as illustrated in this figure is a rough index of how common that song type is on the island.

tained Vineyard songs with $F_{2,1}$ of 3.42 to 3.63, 3.62 to 3.84, 3.90 to 4.03, and 4.12 to 4.51 kHz, respectively. These sweetie-sweetie songs were concentrated primarily on the eastern and central Vineyard, with the two high-frequency clusters more common and distributed more widely than the two low-frequency clusters (Fig. 4). A noticeable gap in the distribution of high-frequency songs occurred in the east-central Vineyard, where high-frequency soswee-

tie-sweetie songs of cluster 10 predominated. Songs in these four clusters were much rarer on Chappaquiddick (12 of 78, or 15%) than on the Vineyard (185/471, or 39%; see Table 1). The fifth sweetie-sweetie cluster (15) contained two-tone songs from Nantucket and Chappaquiddick (Fig. 2, Table 2); by ear, however, based on the initial subwhistle, we could easily distinguish the songs from Nantucket and Chappaquiddick (see Fig. 2).
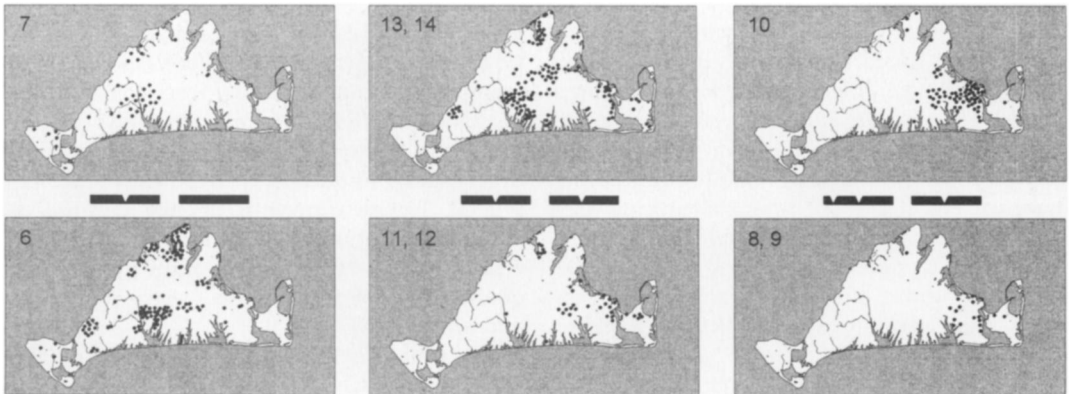

FIG. 4. Distribution of common Black-capped Chickadee song types on Martha's Vineyard, showing a separate system of dialects for high-frequency (upper maps) and low-frequency (lower maps) songs on this small island. Each map is labeled with the appropriate song diagram (Fig. 2) and the cluster number(s) to which the cluster analysis assigned those songs (Table 1); the six maps thus correspond to the six histogram peaks in Figure 3. Certain clusters are mapped together because songs within those pairs of clusters were highly similar (see Table 2) and because their geographic distributions were largely overlapping.

Our sample of 700 chickadee songs (Table 1) contained four additional clusters. Two clusters contained relatively simple songs, rendered "hey-hey" and with no amplitude breaks in either of the two whistles (clusters 16 and 17; see Fig. 2); these songs were either monotonal or distinctly two-toned and occurred over a range of frequencies. Two other clusters (18 and 19; 20 was discussed above) each contained only one exemplar.

INDIVIDUAL VARIATION IN SONGS AND SINGING BEHAVIOR

"Mainland" North America.—Although mainland Black-capped Chickadees tend to use only one song type, the hey-sweetie, each male pitch-shifts, singing that one type over a range of frequencies (see Ratcliffe and Weisman 1985, Hill and Lein 1987, Weisman et al. 1990, Horn et al. 1992). In our survey, we verified this pitch shifting by a number of males. In Amherst, Massachusetts, we sampled three males intensively; two that we sampled over a period of several weeks (one banded, his neighbor not) clearly used their songs over a broad range of frequencies (MA-1 and MA-2; Fig. 5). Even the single male recorded on Nashawena Island, just west of Martha's Vineyard, pitch-shifted his normal hey-sweetie song (see Table 1). Our cluster analysis recognized this pitch shifting by spreading the hey-sweetie songs of each male over three clusters (1, 2, and 3), apparently based largely on the frequency of the song (Table 2).

Only one male in our "mainland" samples clearly sang two different song types (MA-3; Fig. 5). He was from Falmouth, Massachusetts, on the mainland near the offshore islands. One type was a typical mainland hey-sweetie that he sang over a range of frequencies, in clusters 1 to 3, just like other mainland chickadees. His other type was used over a narrower frequency range.

Martha's Vineyard.—On the Vineyard, unlike the mainland, we found no evidence of pitch shifting over a continuous range of frequencies (Fig. 5). During a dawn chorus, one male in Chilmark (MV-1; Fig. 5) alternated between a sweetie-hey on a low frequency (122 songs of cluster 6; range 3.58 to 3.70 kHz) and a sweetie-hey on a high frequency (98 songs of cluster 7; range 4.14 to 4.24 kHz). Thus, each song was
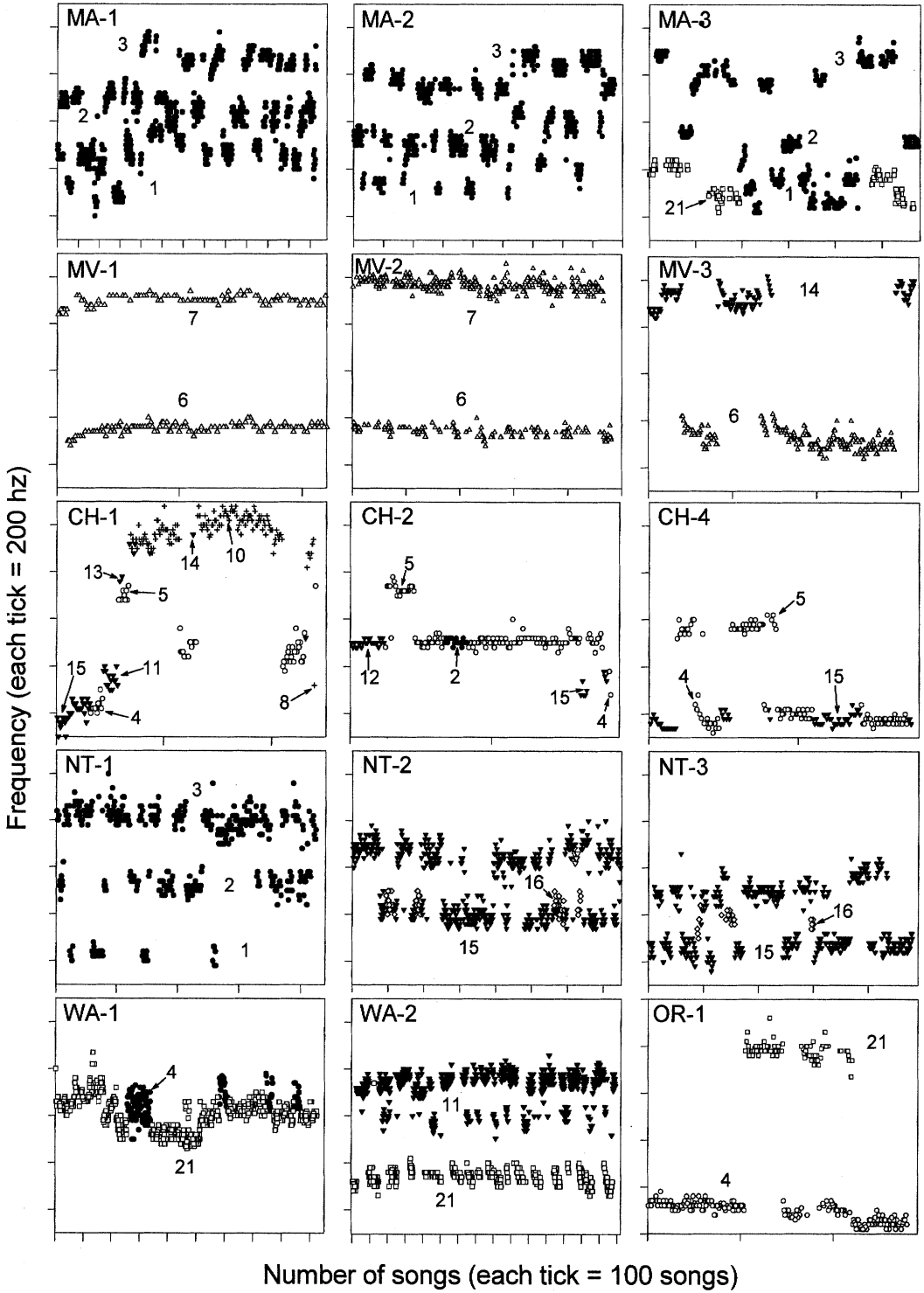
sung within a range of 120 Hz, with a gap of >400 Hz between the low and the high songs. On a second visit, this male sang within the same two frequency ranges.

A more extensive dawn chorus from an individual in West Tisbury gave similar results (MV-2; Fig. 5). He sang 149 songs of cluster 6 (range 3.58 to 3.70 kHz) and 331 songs of cluster 7 (range 4.18 to 4.36 kHz). The low-frequency range of this male was identical to that of the first male recorded, but both the frequency range and the absolute frequencies of the high-frequency songs were slightly greater than for the Chilmark male. The gap between low and high songs was again >400 Hz.

Another Chilmark male, recorded several times during dawn and daytime song bouts, behaved similarly (MV-3; Fig. 5). He sang a low-frequency (3.54 to 3.72 kHz) and a high-frequency (4.14 to 4.32 kHz) song over a narrow frequency range, with no songs in the intervening 400 Hz. Like most Vineyard males, he had a different song type on the high frequency (sweetie-sweetie; cluster 14) than on the low frequency (the widespread sweetie-hey; cluster 6), and he typically produced a series of songs of one type before switching to the other. This style of "eventual variety" (Hartshorne 1956) was especially typical of daytime singing, and rapid alternating of types occurred only during occasional dawn periods of intense singing.

The behavior of a fourth male, on the western edge of Edgartown, was consistent with that of other birds recorded on the Vineyard. He used a high- and low-frequency song, with about 400 Hz between the songs. The high-frequency song was the sosweetie-sweetie of cluster 10, and the low-frequency song the only example in cluster 17. The frequency range was 100 Hz for the low song and 140 Hz for the high song. During the dawn bout and later daytime singing this male repeated one of his song types several times before switching to the other.

Our briefer recordings from other Vineyard chickadees were largely consistent with what we found among these four more intensively recorded males. The frequency of the monotonal Vineyard songs was distinctly bimodal, with one peak at 3.7 kHz and another at 4.2 to 4.4 kHz (Fig. 3), a difference of 500 to 700 Hz. This bimodal distribution of song frequency was generated largely by each individual singing a

high- and a low-frequency form, with no songs at intervening frequencies. For 72 males, for example, we recorded a high- and low-frequency song, with a median difference of 540 Hz between the two songs. Also, some males near Edgartown seemed to have larger repertoires, with songs in three or even four clusters (e.g. clusters 6, 10, 11; 10, 12, 13; or 8, 10, 13); from these males we typically recorded one or two low-frequency and one or two high-frequency songs. Song repertoires of Chappaquiddick males, just beyond Edgartown, were also large (see below).

Chappaquiddick.—On Chappaquiddick Island, just a few hundred meters from Martha's Vineyard, we found not only different songs (see above; Fig. 2), but also some large song repertoires and some apparent pitch shifting. Our largest recorded samples were from three neighbors on Chappaquiddick Road, about 2.75 km east of the ferry (257 songs from male 1, 172 from male 2, 100 from male 3). Overall, these three birds used an impressive variety of songs. The three males all used the three most common Chappaquiddick songs (clusters 4, 5, and 15; Table 1; males CH-1 and CH-2 in Fig. 5). The monotone hey-sweetie songs of clusters 4 and 5 were pitch-shifted over a semicontinuous frequency range of 540, 500, and 520 Hz by the three males; larger recorded samples would be needed to understand more thoroughly the extent of this pitch shifting. Each male also had monotone sweetie-sweetie songs. Altogether, male CH-1 had songs distributed among eight clusters, and CH-2 and

CH-3 used songs from five clusters apiece. Nowhere else in North America did we encounter such variety.

The behavior of another group of three males, which occurred only 1.25 km to the south, was simpler. At this location we recorded 175 songs from male 4 (see Fig. 5), 92 from male 5, and 37 from male 6. Like other Chappaquiddick males, each of these males used songs of clusters 4 and 5, and the two males from which we had larger samples also sang songs of cluster 15. Neither here nor in our 14 recordings farther to the southeast did we find any songs of clusters 8 to 10 or 11 to 14, all of which are typical songs from Martha's Vineyard and all found among males 1 to 3, only 1 to 2 km to the north. Apparently, these typical "Vineyard" songs are used on Chappaquiddick only by males at the northwestern part of the island, nearer to the Vineyard. Thus, microgeographic differences in Black-capped Chickadee songs occur even on the small island of Chappaquiddick.

Nantucket.—Surprisingly, on the most isolated of the offshore islands, some males seemed to be singing typical mainland song types in pitch-shifting fashion. On the northeastern part of the island, one male shifted his two-tone hey-sweetie between 3.58 and 4.40 kHz (NT-1; Fig. 5). As expected, our cluster analysis placed his songs into the three mainland song clusters (1 to 3).

Elsewhere, however, Nantucket proved to be as idiosyncratic as Martha's Vineyard and Chappaquiddick. Nantucket males usually had

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FIG. 5.   Singing behavior of 15 Black-capped Chickadees from throughout North America, illustrating how males use their song types during extended song sequences. Data from mainland Massachusetts (MA), Martha's Vineyard (MV), Chappaquiddick (CH), Nantucket (NT), Washington (WA), and Oregon (OR). Sample sizes range from 200 (CH-2) to 1,500 (WA-2) songs for each male, with F_2 or $F_{2.1}$ measured on the songs. Frequency span is 1,000 Hz for each male, but the absolute scale varies from bird to bird (lowest tick mark for MA birds is 2.9 kHz; for MV and CH, 3.5 kHz; for NT-1, 3.6 kHz; for NT-2, NT-3, and WA, 3.1 kHz; for OR, 3.4 kHz). Frequency scales change to use space more efficiently, and we emphasize that frequency comparisons among and even within graphs must be made with care. "Homologous" whistles cannot be measured from drastically different song types, and the absolute frequency of songs therefore depends largely on which whistled components we chose to measure. Thus, absolute and relative frequency can be compared only for songs of related song clusters, which are represented and labeled in the figure by a common symbol (closed circles, clusters 1 to 3; open circles, 4 to 5; open triangle, 6 to 7; +, 8 to 10; closed triangle, 11 to 15; diamond, 16; square, 21; except for male WA-1, where the cluster 4 symbol has been filled in to contrast with the open symbol of cluster 21; also, the frequency of the unique songs of group 21 in Table 1 cannot be compared with each other). For all but three males, the illustrated sequence consists of one or more relatively long strings of recorded songs; for the three males from Chappaquiddick, however, each sequence represents a series of brief samples from an ongoing dawn bout.

repertoires of songs unique to that island, and song dialects also occurred. Like the males on Chappaquiddick and typical mainland North America, but apparently unlike the males on the Vineyard, individual Nantucket males sang their commonly used songs over a frequency range of 500 Hz or more.

Washington and Oregon.—Recordings from Washington revealed song dialects and repertoires much like what we found on the Massachusetts islands. Song dialects were evident over 46 km, and songs of Everett males clearly were geographic replacements of songs at Discovery Park in Seattle. Also, we recorded two other song types at Hoquiam 133 km southwest of Seattle, suggesting that different song dialects occur throughout western Washington. Three intensively recorded males had repertoires of two different song forms, which were shared with neighbors, and song forms were pitch-shifted over 120 to 360 Hz (Fig. 5). One song form from two males at Discovery Park was strange even by standards of island chickadees, consisting of four monotonal whistles with a brief high-frequency click preceding the first, third, and fourth whistles (Table 1).

Oregon males also showed song dialects and repertoires of at least two different song types. The dawn bout of nearly 300 songs from one male (OR-1; Fig. 5), for example, showed that the male used two different song types, sometimes alternating them, but during the sample each song was used over a relatively narrow frequency range.

GENETIC ANALYSES

The Vineyard chickadees exhibit no substantial, fixed genetic divergence from mainland populations, at the level that we examined them. Four of the six sampled individuals had the standard mainland mtDNA sequence. Two individuals exhibited a unique *Pvu* II restriction site. Such minority variants are also present locally in other populations of *P. atricapillus*. We conclude that mtDNA haplotypes of chickadees from Martha's Vineyard are not markedly divergent from those throughout most of the rest of North America.

DISCUSSION

Geographic patterns in behavior.—Our survey confirmed that Black-capped Chickadees from selected locations throughout mainland North America conform to a relatively simple singing style (see Ficken 1981, Ratcliffe and Weisman 1985, Hill and Lein 1987, Hailman 1989, Kroodsma et al. 1995). Males have a single song type, the two-tone hey-sweetie (i.e. fee-bee-ee; Fig. 1), that is remarkably invariant geographically and that shifts in frequency over a range of several hundred Hz (e.g. MA-1 and MA-2; Fig. 5). The song and singing behavior of the Black-capped Chickadee is thus especially stereotyped over much of the North American continent, from British Columbia to Nova Scotia.

Given this behavioral consistency over much of mainland North America, we were astonished at the variety of song types and singing behavior found among males on the islands offshore from Massachusetts. Only on northeastern Nantucket did we find males singing in ways that were indistinguishable from males of the mainland. Elsewhere on Nantucket, and throughout Martha's Vineyard and Chappaquiddick, males sang very differently. On the Vineyard, most songs were monotonal, as noted by Brewster in 1891 (*in* Griscom and Emerson 1959) and reported by Bagg (1958). We also discovered that males tended to have two songs in their repertoire, one delivered on a high and one on a low frequency; sometimes the high and low songs were of the same type (e.g. both sweetie-hey, as on the western Vineyard), but usually they were of different types, with patterns of amplitude breaks in the whistles largely defining the song types. Song dialects also were clearly audible on the Vineyard, with distributions of the high- and low-frequency songs of the same type largely independent of one another. Dialects occurred on both Chappaquiddick and Nantucket, too, over a distance as small as 1.25 km, and song repertoires for some males on Chappaquiddick were especially large. Furthermore, on Chappaquiddick and Nantucket, but not on the Vineyard, males pitch-shifted some of their songs. Compared with most of North America, the diversity of songs and behavior on these small islands is extraordinary.

Increased diversity in singing behavior also occurs among males at the far western end of the North American range, in Washington and Oregon. There, song types often were unique, especially those with high-frequency clicks,

but some song types found on the Massachusetts islands recurred in the West (e.g. clusters 4, 8, 11, 12, and 13 in Table 1). Songs varied from place to place in dialectal fashion, too, just as they did among the island populations. Furthermore, Washington males appeared to shift the frequency of at least one song type. This behavioral diversity apparently also extends to parts of Alaska (Hailman 1989).

Processes that produce the geographic patterns.— Our working hypothesis is that rapid, postglacial range expansion (Gill et al. 1993), song-learning strategies, and current-day population movements, or lack thereof, are involved in producing these geographic patterns in songs and singing behavior. We first consider vocal development. Males from mainland North America clearly must learn their hey-sweetie song. In the laboratory, males usually develop highly abnormal song types (Shackleton and Ratcliffe 1993, Kroodsma et al. 1995). Furthermore, captive-reared males typically acquire repertoires of two or more abnormal songs that they do not pitch-shift, and males within groups learn from each other more readily than they do from tutor tapes, so that dialects of unique songs emerge in groups isolated from one another in the laboratory (Kroodsma et al. 1995). Perhaps some social forces, absent in the laboratory but present in nature, are responsible for guiding the learning of the stereotyped hey-sweetie song.

Perhaps the learning process that produces the uniformity in the North American hey-sweetie song also requires that a male learn an "average" song from within his social environment. Learning the song of only one particular male inevitably would lead to lineages of copy errors that eventually would destroy the standard hey-sweetie songs, and probably the pitch-shifting singing behavior, found throughout most of North America (Kroodsma 1996). In contrast, learning an average song guarantees an inertia in song change, so that vocal behavior can remain remarkably stable over considerable time and space. Abundant opportunities exist, too, for many young birds to hear songs of distant populations. Long-distance irruptions occur among young birds (<1 year old) every few years (Lawrence 1958, Hussell and Stamp 1965, Bagg 1969, Bock and Lepthien 1976, Smith 1991), so that dispersing young males (and females) have ample opportunities

to learn from adults of other populations during singing that occurs in late winter and early spring. Although many of these irrupting birds may perish, many undoubtedly survive, because banding recoveries show that winter-banded "visiting migrants" (Smith 1991) occasionally are found at distant sites during the next breeding season (Bagg 1969, Smith 1991, Loery et al. 1997). Population movements tend to be to the south or southwest during the fall and to the north or northeast in the spring, although at times the movements seem rather aimless (Smith 1993), so that population mixing would occur throughout much of mainland North America. Learning an average song, perhaps combined with strong social forces, such as females responding only to certain highly stereotyped male songs (e.g. West and King 1988), could thus guarantee stereotypy in songs and singing behavior over a large geographic range.

Just as isolated groups of chickadees in the laboratory develop unique song types, so too would one expect that isolated natural populations would develop unique songs. Chickadees seem reluctant to fly across water (e.g. Bagg 1969), and Hunn (1982) suggests that in Puget Sound, just 3 km of water is sufficient to slow the population expansion of Black-capped Chickadees. A few chickadees have been seen to leave Martha's Vineyard from Gay Head (V. Laux pers. comm.), but no evidence suggests that chickadees regularly migrate from mainland Massachusetts to offshore islands. Most likely, the songs and behavior of these island birds have evolved in isolation from mainland birds, probably since the colonization of the Vineyard after the last glaciers retreated. Some physically distinctive western populations, such as those in Oregon and Washington, may also be relatively isolated from the population movements over most of North America (Duvall 1945, Hammond 1993). We found no reports documenting the kinds of migratory movements or irruptions observed in other parts of North America, but good data on chickadee movements in Oregon and Washington are lacking (see Jewett et al. 1953).

Isolation of populations perhaps has also been responsible for the origin of microgeographic differences in songs within the small Massachusetts islands. Given the reluctance of chickadees to cross water, we can understand

why songs would differ among the islands, as they clearly do even between adjacent Martha's Vineyard and Chappaquiddick. But how dialects originated within each of these islands is puzzling. One possibility is that the resident status of the chickadee, together with the exceptionally high density of its population, led to selection for increased repertoire size with a continued premium on neighboring males being able to countersing with like songs; song differences might then have arisen over short distances in more or less continuous habitat, such as in the original forests that covered the Vineyard before European settlement.

Alternatively, today's song dialects could be a consequence of habitat fragmentation that occurred during European settlement. Although the Vineyard is once again heavily forested, for several hundred years the settling Europeans rendered the Vineyard mostly treeless (Dunwiddie 1994). Fires routinely swept the Great Plain from West Tisbury to Edgartown, and, where only trees are visible today in Gay Head, Koch in 1844 saw "a level, desolate moor, treeless, shrubless and barren of all vegetation, save coarse grass and weeds, and a profusion of stunted dogroses" (Dunwiddie 1994:16). Just a century ago, chickadee populations on the Vineyard were undoubtedly still isolated from one another in small forest refugia, and perhaps the song dialects arose in those isolated populations. It would seem most likely that songs of the same type but with different frequencies (e.g. clusters 6 and 7, the sweetie-hey) arose together in isolation; modern-day evidence for such a scenario can be found on Gay Head, where all males seem to have a high- and low-frequency sweetie-hey, or in Edgartown, where high- and low-frequency sosweetie-sweetie songs are clustered. As populations expanded during reforestation of the island, however, the fates of these high- and low-frequency song types were largely independent of one another. Thus, the low-frequency sweetie-hey songs (cluster 6) are now distributed widely over the Vineyard, whereas the related high-frequency songs (cluster 7) are confined to the western portion of the island (Fig. 4).

The island dialect of northeastern Nantucket, where males sing much like males of mainland North America, could have originated in several ways. Nantucket is the most isolated of the offshore islands, but it is possible that this

"normal" style of singing is a consequence of a relatively recent invasion of mainland chickadees. Alternatively, perhaps this behavior was simply maintained in a refugium on Nantucket since the earliest chickadees colonized the island. Another, albeit less likely, possibility is that the behavior of these chickadees independently converged on the mainland style.

The larger song repertoires of the island birds also require an explanation. Horn et al. (1992) speculated that the mainland behavior of using one song type over a range of frequencies might be an alternative to using different song types, and that these two strategies might be alternative singing styles to accomplish an equivalent diversity in a singing program. What Horn et al. (1992) did not realize, however, was that each mainland chickadee, depending on the quality of his experience, is capable of adopting either approach (Shackleton and Ratcliffe 1993, Kroodsma et al. 1995). Perhaps a major contributing factor on the offshore islands is the high population density of chickadees. Territories of chickadees are exceptionally small on these islands, as is typical of many island populations (e.g. Blondel et al. 1988), and within some species and among some species groups, density is correlated with repertoire size (e.g. *Acrocephalus* warblers and *Cistothorus* wrens; Catchpole 1980, Kroodsma 1996). Perhaps the larger repertoire sizes are a consequence, in part, of resident status and this high density (see also Wunderle et al. 1992), because males countersing at close range with their competitors.

As song repertoires increase in size, males often alternate song types, or sing with "immediate variety" (e.g. see Hartshorne 1956; Kroodsma 1990, 1999). The song sequences recorded from some males on the Vineyard (e.g. MV-1 and MV-2 in Fig. 5) are consistent with this trend, because some of these males rapidly alternated the song types in their song repertoire, more so than we have seen among chickadees elsewhere. Such alternations might also be more common when birds are highly motivated, as during the dawn chorus.

Unanswered questions.—We believe that our working hypotheses present the most likely scenarios for the origin and maintenance of the diversity of Black-capped Chickadee vocal behavior in North America. Without a firm understanding of the historical and ontogenetic

processes that produced the current geographic patterns, however, we are left with many unanswered questions. We list five of these questions below, hoping that they will stimulate further research on these common, but enigmatic, birds.

1. From whom, where, and how do young males learn their song (see Beecher 1996)? On the mainland, do they learn an average song from among those heard during migratory or irruptive movements, and do these processes ensure stereotyped singing behavior in much of North America? On islands, is the learning strategy identical, but dialects occur because the movement of individuals is more restricted? Do birds disperse into neighboring island dialects and learn those songs, as do resident populations of other species (e.g. Kroodsma 1974, Jenkins 1978)?

2. What is the fate of the diverse songs on the offshore islands? How dynamic are their distributions? Will some dialects become extinct and others succeed? By archiving our tape recordings at Cornell's Library of Natural Sounds, we hope that others will be able to study future changes in these island populations.

3. How isolated are birds of the offshore islands and of Washington and Oregon? We need additional genetic and banding studies to monitor population movements.

4. We are puzzled by the ultimate causation of these population differences. What benefits do mainland birds receive by conforming to the widespread song type and singing behavior, and why do peripheral birds not seem to benefit from such a conformist approach? Are population movements, or lack thereof, sufficient to explain the relative benefits of these behavioral outcomes?

5. Is the behavior of chickadees on the offshore islands of Massachusetts related to other aspects of island phenomena, such as the often high density of conspecifics and relative lack of competitors (e.g. Baker 1994)? The Tufted Titmouse (*Baeolophus bicolor*), for example, is absent from these islands, and chickadee densities seem especially high. Additional studies of avian vocal behavior on islands, such as that by Wunderle et al. (1992), are needed before this question can be answered.

LITERATURE CITED

BAGG, A. M. 1958. A variant form of the chickadee's "fee-bee" call. Bulletin of the Massachusetts Audubon Society 43:9.

BAGG, A. M. 1969. The changing seasons: A summary of the fall migration season 1968 with special attention to the movements of Black-capped Chickadees. Audubon Field Notes 23:4–12.

BAKER, M. C. 1994. Loss of function in territorial song: Comparison of island and mainland populations of the Singing Honeyeater (*Meliphaga virescens*). Auk 111:178–184.

BAKER, M. C., AND M. A. CUNNINGHAM. 1985. The biology of bird-song dialects. Behavioral and Brain Sciences 8:85–133.

BEECHER, M. D. 1996. Birdsong learning in the laboratory and field. Pages 61–78 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

BLONDEL, J., D. CHESSEL, AND B. FROCHOT. 1988. Bird species impoverishment, niche expansion, and density inflation in Mediterranean island habitats. Ecology 69:1899–1917.

BOCK, C. E., AND L. W. LEPTHIEN. 1976. Synchronous eruptions of boreal seed-eating birds. American Naturalist 110:559–571.

BYERS, B. E. 1996. Geographic variation of song form within and among Chestnut-sided Warbler populations. Auk 113:288–299.

CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex songs among European war-

blers of the genus *Acrocephalus*. Behaviour 74: 149–166.

DESFAYES, M. 1964. An observation on the song of the Black-capped Chickadee. Condor 66:438–439.

DIXON, K. L., AND R. A. STEFANSKI. 1970. An appraisal of the song of the Black-capped Chickadee. Wilson Bulletin 82:53–62.

DUNWIDDIE, P. W. 1994. Martha's Vineyard landscapes: The nature of change. The Vineyard Conservation Society and Peter W. Dunwiddie, Martha's Vineyard, Massachusetts.

DUVALL, A. J. 1945. Distribution and taxonomy of the Black-capped Chickadees of North America. Auk 62:49–69.

EVERITT, B. 1993. Cluster analysis, 3rd ed. Halsted Press, New York.

FICKEN, M. S. 1981. What is the song of the Black-capped Chickadee? Condor 83:384–386.

FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. Auk 95:34–48.

GILL, F. B., A. M. MOSTROM, AND A. K. MACK. 1993. Speciation in North American chickadees: I. Patterns of mtDNA genetic divergence. Evolution 47:195–212.

GRISCOM, L., AND G. EMERSON. 1959. Birds of Martha's Vineyard with an annotated check list. Massachusetts Audubon Society, Martha's Vineyard, Massachusetts.

HAILMAN, J. P. 1989. The organization of major vocalizations in the Paridae. Wilson Bulletin 101: 305–343.

HAMMOND, D. K. 1993. Geographic variation in the "fee-bee" song of Black-capped Chickadees, *Parus atricapillus*. Thesis, University of Puget Sound, Tacoma, Washington.

HARTSHORNE, C. 1956. The monotony-threshold in singing birds. Auk 73:176–192.

HILL, B. G., AND M. R. LEIN. 1987. Function of frequency-shifted songs of Black-capped Chickadees. Condor 89:914–915.

HORN, A. G., M. L. LEONARD, L. RATCLIFFE, S. A. SHACKLETON, AND R. G. WEISMAN. 1992. Frequency variation in the songs of Black-capped Chickadees (*Parus atricapillus*). Auk 109:847–852.

HUNN, E. 1982. Birding in Seattle and King County. Seattle Audubon Society, Seattle, Washington.

HUSSELL, D. J. T., AND R. W. STAMP. 1965. Movements of Black-capped Chickadees at Long Point, Ontario, during the spring of 1962. Bird-Banding 36:71–80.

JENKINS, P. F. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. Animal Behaviour 26:50–78.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, AND J. W.

ALDRICH. 1953. Birds of Washington State. University of Washington Press, Seattle.

KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. Zeitschrift für Tierpsychologie 35:352–380.

KROODSMA, D. E. 1990. Patterns in songbird singing behavior: Hartshorne vindicated. Animal Behaviour 39:994–996.

KROODSMA, D. E. 1996. Ecology of passerine song development. Pages 3–19 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

KROODSMA, D. E. 1999. Trying to make ecological sense of song development by "the bird." In press *in* Neural mechanisms of communication (M. Konishi and M. Hauser, Eds.). The MIT Press, Cambridge, Massachusetts.

KROODSMA, D. E., D. J. ALBANO, P. W. HOULIHAN, AND J. A. WELLS. 1995. Song development by Black-capped Chickadees (*Parus atricapillus*) and Carolina Chickadees (*P. carolinensis*). Auk 112: 29–43.

LAWRENCE, L. DE K. 1958. On regional movements and body weight of Black-capped Chickadees in winter. Auk 75:415–443.

LOERY, G., J. D. NICHOLS, AND J. E. HINES. 1997. Capture-recapture analysis of a wintering Black-capped Chickadee population in Connecticut, 1958–1993. Auk 114:431–442.

RATCLIFFE, L., AND R. G. WEISMAN. 1985. Frequency shift in the fee-bee song of the Black-capped Chickadee. Condor 87:555–556.

SHACKLETON, S. A., AND L. RATCLIFFE. 1993. Development of song in hand-reared Black-capped Chickadees. Wilson Bulletin 105:637–644.

SMITH, S. M. 1991. The Black-capped Chickadee: Behavioral ecology and natural history. Cornell University Press, Ithaca, New York.

SMITH, S. M. 1993. Black-capped Chickadee (*Parus atricapillus*). *In* The birds of North America, no. 39 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

WEISMAN, R., L. RATCLIFFE, I. JOHNSRUDE, AND T. A. HURLY. 1990. Absolute and relative pitch production in the song of the Black-capped Chickadee. Condor 92:118–124.

WEST, M. J., AND A. P. KING. 1988. Female visual displays affect the development of male song in the cowbird. Nature 334:244–246.

WILKINSON, L. 1996. SYSTAT 6.0 for Windows: Statistics. SPSS Inc., Chicago.

WUNDERLE, J. M. J., R. A. CORTES, AND W. CARROMERO. 1992. Song characteristics and variation in a population of Bananaquits on Puerto Rico. Condor 94:680–691.

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