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**House finch song on Cape Cod: Cultural evolution in a colonizing
bird species**

Burchsted, Albert Ernest, Ph.D.

City University of New York, 1994

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A

HOUSE FINCH SONG

ON CAPE COD:

CULTURAL EVOLUTION IN A COLONIZING BIRD SPECIES.

by

ALBERT BURCHSTED

**A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the
requirements for the degree of Doctor of Philosophy,
The City University of New York**

1994

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract**HOUSE FINCH SONG
ON CAPE COD:****CULTURAL EVOLUTION IN A COLONIZING BIRD SPECIES.**

by

Albert Burchsted

Adviser: Professor Paul C. Mundinger

The recent introduction of the House Finch into the north-east United States generated a natural experiment in the cultural evolution of bird song. Cape Cod was colonized by finches dispersing from a rich cultural heritage in metropolitan New York and coastal New England. Distributions of songs differed from those previously described for metropolitan New York. Some populations on the cape sang song patterns that were similar to those of several described institutions, while other populations sang song patterns that were unique or derived from alien songs. Song dialects were based on pronunciation and lexical variations. Some dialects were well defined with sharply demarcated boundaries while others were poorly defined with clinal changes in pronunciation. There were extensive regions of hybridization where songs of one tradition were included in repertoires containing songs of another tradition.

The migration routes that House Finches took during their recent colonization of Cape Cod were inferred from song patterns. The process of colonization was complex with multiple colonization events and modes. Colonies were formed (and expanded) by both diffusion (local dispersal) and jump dispersal. Four colonies were traced to

previously established populations at varying distances (15 to 250 km) from Cape Cod. Other colonies were satellites of recent, previously established Cape Cod colonies. Several colonies had more than one source.

Established Cape Cod colonies at either end of the cape founded secondary colonies located in the middle of the cape and along the outer arm. Some of these secondary colonies sang song patterns that resembled those of their source institutions, while others sang patterns that were unique, derived from alien songs, or were similar to song patterns sung by institutions that have not been described. There was evidence that several song traditions had been replaced by others in the twenty years since this species colonized Cape Cod.

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The College of Staten Island provided me a sabbatic leave during the spring semesters of 1992 and 1993 to work on this project. The CUNY Graduate School provided funding for this project. This research was also funded by a Chapman grant from the American Museum of Natural History and a Sigma Chi grant.

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INTRODUCTION

Animals communicate in many ways: chemical secretions and excreta, visual displays, physical contact or vibrations of the substrate, electrical discharges, and vocalizations. Bird song is the mode most similar to human communication. Marler (1956) and Thorpe (1958) proposed that bird song provides information transfer, although at a level of complexity far less than human speech conveys.

In many bird species, development of songs is a cultural phenomenon as young birds learn their songs by exposure to models (for reviews, see Marler and Mundinger 1971; Nottebohm 1972; Kroodsma 1978, 1982; Baker and Cunningham 1985). Related song patterns form cultural institutions (Mundinger 1982) which may be found over extensive geographic areas.

Variation in related populations within an institution is the basis by which song dialects are distinguished by field workers (Lemon 1975; Kroodsma 1978, 1982; Mundinger 1980; Baker and Cunningham 1985; Cunningham et. al. 1987). Dialect maps have been made for the White Crowned Sparrow, Zonotrichia leucophrys (Marler and Tamura 1964, Baptista 1975, Baptista and King 1980, Baker and Cunningham 1985, Cunningham et al. 1987). Baptista (1975) and Baker and Thompson (1985) proposed that dialect distributions of the White-crowned Sparrow are a result of historical dispersal events. Cunningham, et al. (1987) maintain that disjunct habitat distribution and historical processes, such as colonization, could result in variable distribution of song among populations.

The House Finch, Carpodacus mexicanus, was introduced to Long Island around 1940 (Elliott and Arbib 1953, Cant and Geiss 1961), and has become firmly established in the avian fauna of the eastern United States (Mundinger and Hope 1982). The release

and establishment of House Finches in the north eastern United States initiated a natural experiment in the cultural evolution of song. Baker and Thompson (1985) hypothesized that geographic variation in song dialects of the White-crowned Sparrow reflected recent dispersal movements. The arrival of the House Finch on Cape Cod is a very recent event. Analysis of song variation there can test Baker and Thompson's hypothesis. Also, a survey of the distribution of House Finch song institutions and dialects, and analysis of the similarities between them, may provide independent data with which to examine dispersal routes on Cape Cod.

I have several objectives in this thesis.

1. I describe the distribution of song patterns on Cape Cod, pointing out cultural relationships between populations.

2. I document phenomena that have influenced House Finch song on Cape Cod: (A) retention of ancestral song patterns, (B) apparent deletion of portions of the song repertoire upon dispersal, and (C) mimicking other species' songs.

3. By analyzing the geographic distribution pattern of dialects and institutions, I suggest possible dispersal routes onto and across the cape.

CHAPTER 1:

HOUSE FINCH COLONIES

ON CAPE COD:

HISTORY AND SIMILARITIES WITH LONG ISLAND

"By the rivers of Babylon we sat down and wept . . .

We hung our harps upon the willows . . .

For they . . . required of us a song . . .

How shall we sing the Lord's song in a strange land? . . ." (Psalm 137)

Establishment of the eastern House Finch population

House Finches were introduced from California to the metropolitan New York area in the early 1940's (Elliott and Arbib 1953, Cant and Geis 1961, Aldrich and Weske 1978). Since this successful introduction, eastern House Finches have expanded their breeding range along the eastern Seaboard from Maine to Georgia (Breckenridge 1981, Parrish 1993, Crawford 1993), west to the Mississippi River, and north to Minnesota and Ontario, Canada (Jackson 1981, Toupes and Hodges 1981, Graham 1988, USF&WS unpublished). Simultaneously the ancestral western population is expanding its range eastward and is breeding in Oklahoma, Texas, and Nebraska (Oliphant and Brown 1984, Taylor 1992, Helen Lapham, personal communication). Taylor (1992) suggested the eastern population of this species probably met with the western population in central Oklahoma about 1990.

The eastern population of House Finches has established distinct song dialect regions, and several song institutions (descriptively analogous to human languages)

developed in populations residing in Long Island, Westchester county, and along the Hudson River Valley in NY, and south western Connecticut (Mundinger 1975, 1980, 1982; Mundinger, Burchsted, and Gnam unpublished) (Figure 1).

In the early 1940's the first colonies of the disjunct eastern population of House Finches settled in western Long Island, New York : Hewlett, Babylon, Lawrence, and Westbury (Elliott and Arbib 1953). Mundinger (1975) examined the distribution of House Finch songs on Long Island and found three of the larger song institutions centered on these first colonies (institutions 1, 4, and 25, Figure 1). He postulated these institutions expanded as finches dispersed from the original colonies.

Expansion of the House Finch through the Eastern United States:

In their study of House Finch range expansion, Mundinger and Hope (1982) identified two patterns of spread through the northeast: diffusion and jump-dispersal. Pileou (1979) defined diffusion as the gradual moving of populations across hospitable terrain over a period of many generations; jump-dispersal is movement of individuals across great distances, usually to avoid inhospitable terrain. As used by Mundinger and Hope (1982), diffusion in the House Finch may occur over a period of just a few years; and jump-dispersal may occur over short or long distances (greater than 150 kilometers in some cases) over any terrain uninhabited by this species.

The post breeding dispersal pattern of this species is similar to incipient migration, especially when the finches disperse to the south or southwest and returned northward in the spring (Aldrich and Weske 1978, Cant and Geise 1961). Mundinger and Hope (1982) found groups of House Finches also dispersed to the north in winter. These winter dispersers often may have settled in their winter dispersal locales and established new

colonies. Many disjunct finch colonies were established in the period 1960 - 1970 (Mundinger and Hope 1982). It is probable some of these colonies were founded by post breeding adults, others by juveniles (Mundinger 1980).

Figure 2 (modified from Mundinger and Hope 1982) shows the expansion of the House Finch through New Jersey, eastern New York, Connecticut, Rhode Island, and Massachusetts over the period 1960 to 1968. The small circles represent Christmas Bird Count stations (CBCs) reporting in the years 1960 through 1968 (Figure 2). Open circles are CBCs that did not record House Finches during this period. Other circles are CBCs that began recording this species in 1960 and subsequent years: closed (●) = 1960, with asterisks (⊛) = 1962, with pluses (⊕) = 1964, with dashes (⊖) = 1966, and with dots (⊙) = 1968. By 1975, all CBCs on Figure 2, whether open or not, reported House Finches.

Lines forming irregular areas enclose CBCs that reported House Finches for the years indicated: solid () = 1960, with asterisks () = 1962, with crosses () = 1964, dashed () = 1966, and dotted () = 1968. These areas presumably represented this species' range for a given winter season. House Finches were first recorded at Chatham on Cape Cod in 1964 (and each subsequent year except 1967, Mundinger and Hope 1982). Chatham is the only portion of Cape Cod enclosed by the crossed line (which represents the 1964 winter range). This species was first recorded at Bourne in 1968, within the dotted line (which represents the 1968 winter range). From 1968 to present the entire cape has been included in this species' winter range.

Rationale for studying Cape Cod

Cape Cod resembles Long Island in many respects. Both are about 170 kilometers long from the mainland to the tip. Each has a mixture of towns, forests, and agricultural areas, and is surrounded by water on three sides. In other features the cape has its own characteristics. Over most of its length, it is less than one half as wide as Long Island. In 1985 and 1986, towns were more widely spaced along the distal third of the cape than they were in the 1970's on Long Island, and the forests had until the middle 1970's been less disturbed than on Long Island. The total numbers and variety of bird species are greater on Long Island (Bull 1975) than on Cape Cod (Hill 1965).

Although geographically Cape Cod is similar to Long Island, a major change in the cultural heritage of the House Finch occurred between the colonization of western Long Island and the colonization of both eastern Long Island and Cape Cod: the number of sources of dispersants increased. This event increased both the frequency of dispersal and number of cultural lineages from which dispersants could have originated. These changes affected the establishment of new song institutions.

Mundinger (1975) found several large song institutions in the western and central regions of Long Island, and many smaller ones in the northern and eastern regions of the island (Figure 1). He postulated the differences were a result of historical and competitive events. First, western populations of finches were established in extensive suburban neighborhoods in the two decades following the release of finches in New York. These original populations experienced rapid radial expansion without cultural competition from other populations because there were only a few colonies from which dispersants could originate. In contrast, the outer (eastern) portions of Long Island were not colonized until the second two decades after this species became established in the east (Figure 2).

Range expansion was explosive during the 1960's and early 1970's (Mundinger and Hope 1982). Thus neighboring areas in eastern Long Island may have been (nearly) simultaneously settled by populations derived from different institutions. As postulated, as these later colonies subsequently dispersed, they would often confront other populations near where they settled. This may have limited further local expansion and may also have affected song learning in these locales.

The spread of House Finches on Cape Cod (reviewed in Mundinger and Hope 1982) is not as well documented as was the initial expansion on Long Island (Elliott and Arbib 1953). With the exception of 1967, this species has been recorded at Chatham, near the "elbow" of the cape, in winter every year since 1964 (Hill 1965, Mundinger and Hope 1982, Figure 2). Wintering House Finches were not recorded in the western end, near the base of the cape, until 1968 (Figure 2). When I visited the cape seventeen years later in 1985 and 1986, I found this species in every town and almost every village. The exceptions were three small settlements of bungalows along the eastern barrier dunes of the outer cape (Figure 3). These settlements had fewer than 40 houses each and were located in areas dominated by either dense pitch pine, Pinus sp., and scrub oaks, Quercus spp., stands or were treeless areas directly on the windward barrier dunes. Mundinger and Hope (1982) noted pine-oak forest also restricted House Finches from colonizing the Pine Barrens of New Jersey until 1976, several years after the surrounding areas had been occupied by this species (see Figure 2).

Song distribution patterns on Cape Cod

Figure 4 is a "global" view of song variation on Cape Cod in the mid 1980's. Seven populations, each singing a shared song repertoire, were identified on Cape Cod and are mapped on Figure 4. On Cape Cod there were several moderate to large sized

institutions interspersed with smaller (some restricted to a single small population) institutions. Song distribution patterns on Cape Cod more closely resemble those of western Long Island which had seven large institutions (institutions 1 through 7, 25, and 24 in Figure 1) than they do those of eastern Long Island which had 17 small institutions and one large one (institutions 6 through 23 in Figure 1).¹

Data from the USF&WS (unpublished), the Manomet Observatory (unpublished), and bird banders (Helen Latham personal communication, Blair Nicula personal communication) indicate juvenile House Finches disperse from their natal territories. Most adult finches are site faithful, being repeatedly observed at the same banding stations (USF&WS data, unpublished; Munding, personal communication). A few mature individuals disperse after one or more breeding seasons (USF&WS data, unpublished; Helen Latham, personal communication). House Finch song distribution patterns on Cape Cod may contribute to an understanding of the processes which affect the learning of song repertoires when this species disperses into regions without conspecifics to serve as song models.

Adult dispersers

When adult Carolina Wrens, Thryothorus ludovicianus, disperse to a new breeding area, they retain their learned song (Morton 1987). White-crowned Sparrows, also do not alter their songs when they relocate (Baptista and Morton 1988), nor do their repertoires change to the local song tradition if they accidentally misimprint on wintering migrants (Baptista 1974, 1977). Alternatively, adult Brown-headed Cowbirds, Moluthrus ater,

¹Several very small institutions were found among the larger institutions in this study but not in Munding's (1975) study. Munding (personal communication) attributed this a more fine grained coverage of Cape Cod (more stops per kilometer) when compared with a more coarse grained coverage of Long Island.

(Rothstein and Fleischer 1987 a) adopt local songs when dispersing from one dialect to another.

Indirect evidence suggests Sage Sparrows, Amphispiza belli, retain their own dialects after dispersal (Weins 1982). No studies have yet addressed the question of whether adult House Finches retain their learned songs after dispersal. Banded House Finches have been known to disperse after one or more breeding seasons into areas where the residents have a different song tradition from the population from which the dispersing bird originated (USF&WS data, Helen Latham personal communication). Unfortunately, the songs of these individuals remain unknown.

Isolation repertoires

As cohorts of juvenile House Finches moved by jump-dispersal from settled areas they presumably entered regions uninhabited by conspecifics. Although the congeneric Purple Finch, C. purpurea, resides in these cape regions, the microhabitats of the two species differ such that there was and continues to be little social contact between them (Bent 1968). Populations established on Eastern Long Island (Mundinger 1975, 1980) and Cape Cod frequently developed unique repertoires which differ from established song institutions (Mundinger 1975).

I assume these unique isolation repertoires were developed de novo by dispersing finches with or without previously learned traditions. In this study I found unusual song patterns with no relationships to other patterns. I also found examples of House Finch songs derived from songs of alien species.

Juvenile dispersers

Juvenile House Finches learn their songs from one or more models (Mundinger 1975, 1980, 1982). In other species, the adult song is not learned until after the young

have dispersed from the natal area (various species, Lemon 1975; Indigo Bunting, Payne 1981; Chaffinch, Slater and Ince 1982; Carolina Wren, Morton 1987; Brown-headed Cowbirds, Rothstein and Fleischer 1987 a,b; White-crowned Sparrows, Baptista and Morton 1988; Song Sparrow, Beecher et al. 1994). In these species the juveniles appear to match the songs of adjacent territory holders. Song matching is a form of social adaptation by which males benefit socially by copying the songs of neighboring established males (Payne 1981, 1982; Morton 1987; McGregor and Krebs 1984; Rothstein and Fleischer 1987 a; Lemon et al. 1994). Colonies founded by juvenile House Finches that did not learn their songs before dispersal would probably have developed isolation repertoires because there would be no conspecifics to serve as models.

CHAPTER 2:

METHODS

SONG RECORDING

Singing male House Finches were recorded in 1985 using a Nagra II reel-to-reel recorder in the FM record mode with a Sennheiser shotgun or Dan Gibson Model 650 parabolic reflector microphone. Inspection of sonograms of the 1985 recordings showed that House Finch syllables were sung with few if any harmonics. As it was not necessary to use FM recording to obtain harmonics, in 1986 I recorded on either the Nagra recorder or an AM recording SONY WMD-6C Professional Walkman cassette recorder and used the Dan Gibson microphone.

Birds were selected by driving or walking along roads and listening. When I heard a House Finch singing, I located the bird and recorded as much material as possible before moving on. At most locations I recorded several birds. A few locations are represented by only one bird.

I did not control for environmental degradation of song resulting from distance from the bird, extraneous noise, or echoes off buildings and foliage. Control for these factors was not deemed necessary for this study as I was examining the form of the information being transferred, not how much information was being obtained by recipient birds. Quite often auditory analysis of a song would allow me to identify that a song pattern sung by a distant bird was or was not similar to a near bird even if the sonogram of the distant song was severely degraded.

Field tapes were dubbed and sonograms were initially made on a Unigon II spectrograph Model 4500 using the Hanning window for Fourier transform. Sonograms were printed by sending the spectrograph image to a Tektronix Model 604 line oscilloscope and photographing the image on 35mm Kodak Linograph paper using a Nihon Kohden Kogyo continuous recording strip camera, Model PC2A, at a film speed of 10 mm/sec or 20 mm/sec. Song syntax and syllable structure were determined visually from the hard copy.

Publication quality Sonograms for this thesis were remade on a Uniscan II spectrograph, Model 4600 using the Hanning window for Fourier transform. Hard copy of these sonograms was produced by a SONY CRT printer Model UP 870 MD.

STUDY AREA

Songs were recorded in all villages and towns on Cape Cod that I was permitted to enter. I was excluded from several private communities and the military reservations in central Sandwich. I divided the cape into three regions (inner, middle, and outer cape - Figure 5) which differ in vegetation, human and House Finch density, and song institution characteristics. Each region was further subdivided into sectors approximately 1 kilometer square by printing a grid on top of a map of the cape. Each sector was identified with a 4 digit number which represents its horizontal and vertical displacement from the southwestern corner of the map. E.g. 1201 is the sector coordinate for Woods Hole (12 km east and 1 km north of the sw corner), 6570 for Provincetown (65 km east and 70 km north of the sw corner), and 9324 for Chatham (93 km east and 24 km north of the sw corner). In the treatment below I refer to these regions and sectors repeatedly.

Inner Cape:

The inner cape includes the townships of Wareham, Bourne, Sandwich, Falmouth, Mashpee, and Barnstable (Figure 5). Much of this region is composed of forest with residential areas along the coastline and surrounding lakes in the interior. Camp Edwards and Otis Air Force Base occupy a large portion of this area. I was requested not to record in these reservations and so the song repertoires of finches in that part of the region are unknown.

Middle Cape:

The middle cape includes Yarmouth, Dennis, Harwich, Brewster, Chatham, and Orleans townships (Figure 5). This region was the least forested and most heavily populated area of my study. I found many males singing in residential developments still under construction. This suggests the birds may have only recently moved into some of these sample sites. Although they were absent from densely wooded regions, House Finches were observed in all areas of the inner and middle cape with human settlements.

Outer Cape:

The outer cape includes Eastham, Wellfleet, Truro, and Provincetown townships (Figure 5). This region contains the most sparsely settled and widely scattered human populations on Cape Cod. House Finch populations were correspondingly more scattered here than in the other regions. Although I searched for upwards of one half hour per site, House Finches were neither seen nor heard in several residential areas on the Atlantic Ocean side of the outer cape, notably LeCount Hollow Beach in Eastham, Newcomb Hollow in Wellfleet, and Hillside Heights in Truro (see Figure 3).

SONG STRUCTURE

Sonograms of most songs were made with a 0 to 5 kHz frequency bandwidth to enhance details of syllable structure. Portions of some syllables were sung at a frequency higher than 5 kHz. To obtain measurements of song structure, I recorded representative songs of each community with a 0 to 10 kHz frequency bandwidth. Sonograms of sixty songs from different populations were selected to determine the structure of House Finch songs.

I used ten song parameters to describe House Finch song structure. Two describe song complexity: number of notes per syllable and number of syllables per song segment. The others describe the amount of energy a finch uses to produce its song: syllable duration, song segment (introduction, core, or ending) duration, total song duration, syllable frequency sweep, median syllable frequency, median syllable frequency band width, and amplitude rank. These parameters were used primarily for analysis of cultural relationships rather than for macrogeographic and microgeographic distributions.

1. Number of notes per syllable:

The number of notes sung in each syllable was counted for each of the three song segments in the population sample of 60 songs.

2. Number of syllables per song segment:

The number of syllables sung in each song segment was counted for each of 60 songs.

3. Syllable duration:

To determine the syllable duration, I used a vernier caliper (Brown and Sharpe model 599-571-3) to measure the horizontal length of each syllable (l_v), in mm (Figure 6), as recorded on the sonogram. This caliper was connected to an IBM AT compatible

computer and the value input directly using the LesSoft software (Marcus 1989). Since the sonograms were recorded on photographic film at 20 mm per second, one mm on the sonogram represents 5 ms. I defined the time constant (k_t) as 0.005 sec/mm. I converted syllable length (l_y) to syllable duration (d_y) using formula 1.

$$\text{Formula 1: } l_y \cdot k_t = d_y$$

4. Routine duration:

A routine is a sequence of syllables repeatedly sung together in the songs of a population.

The length of each routine on the sonogram was determined as (l_r). This was converted to time by multiplying l_r by the time constant k_t using formula 1. Routine duration (d_r) was determined by multiplying l_r by the time constant.

$$\text{Formula 2: } l_r \cdot k_t = d_r$$

5. Segment duration:

There were three segments in the songs: introduction, core, and ending, and the duration of each segment was measured. Segment duration was determined in the same fashion except the linear measurement (Figure 6) that I converted to segment duration (d_g) was the length of the segment (l_g). The conversion was made using formula 1.

$$\text{Formula 3: } l_g \cdot k_t = d_g$$

6. Total song duration:

The total song duration (d_s) was determined using formula 4 after measuring the length of the entire song (l_s) from the sonogram.

$$\text{Formula 4: } l_s \cdot k_t = d_s$$

7. Syllable frequency sweep:

The syllable frequency sweep is the mean value of the range through which the frequency is modulated. To make this calculation, I first determined the distance from the base of the sonogram (0 kHz) to the top of the syllable (h_t), and the distance from the base of the sonogram (0 kHz) to the bottom frequency of the syllable (h_b) (Figure 6). The distance between these values is the syllable height (h_s). Frequency is a function of the vertical height on the sonogram: The original sonogram is 26 mm in height. This height represents 10,000 Hz. The frequency constant (k_f) is calculated as 10,000 Hz / 26 mm. Thus $k_f = 385$ Hz/mm. Determination of the frequency range (F_r) from vertical measurements was calculated using formula 5.

$$\text{Formula 5: } (h_t - h_b) \cdot k_f = F_r$$

8. Median frequency of the syllable:

The median frequency (F_m) is the center frequency between the syllable's top and bottom frequencies (Figure 6). To determine this, I used formula 6 which adds $\frac{1}{2}$ the frequency range (F_r) to the bottom frequency of the syllable.

$$\text{Formula 6: } h_b \cdot k_f + (F_r/2) = F_m$$

9. Band width of the syllable:

Band width (w_m) measures the purity of tone (range of frequencies in the syllable) at a given point in time. This measure provides a numerical method to differentiate between the buzzy and pure tone syllables. To determine this value, the heights of the upper edge of the syllable trace (t_u) and the lower edge of the syllable trace (t_l) were

measured at the point of the syllable's greatest amplitude (Figure 6). Band width (w_m) at the greatest amplitude was determined by multiplying the difference between the upper and lower edges of the syllable by the frequency constant (k_f) using formula 7.

$$\text{Formula 7: } (t_u - t_l) \cdot k_f = w_m$$

10. Amplitude rank:

The intensity of the sonogram trace (level of darkness) is a relative measure of the amplitude of the sound producing it. I ranked the density of the song segments on a scale of 1 to 3, 1 being the lightest, 3 the darkest. This ranking was applied to each of the three segments of a song: introduction, core, and ending. In the case of ties, I summed the ranks and divided by the number of segments in the tie. For example, if I felt the introduction and core were equally lighter than the ending, the ending was ranked 3, the introduction and core were each ranked 1.5 $((1 + 2)/2)$. If the core and ending were equally darker than the introduction, the introduction was ranked 1, the core and ending were each ranked 2.5 $((2+3)/2)$.

A wide variety of mensural parameters have been used by others (Martin 1979, Martindale 1980, Baptista and Morton 1982, Trainer 1983, Baker and Jenkins 1987, Cunningham, et. al. 1987) to quantitatively cluster song dialect populations of species that sing simple songs. These authors sometimes also used syllable morphology in their studies. The parameters used by these authors describe both song complexity and the relative amount of energy a bird uses to produce each song segment, but provide little information on the song's cultural derivation.

I found analysis of this type to work well on a local scale with 20 to 40 individuals, but that mensural variation within populations was so great that rather than reducing my data, cluster analysis of these parameters on a regional scale resulted in fractionizing

populations. For this reason, I used isogloss analysis exclusively for the purpose of determining cultural relatedness between populations.

Syllable pronunciation cannot presently be mathematically described. Yet this feature of the syllable most clearly indicates cultural relatedness. Thus when identifying institutions or inferring dispersal routes I followed the lead of many students of bird song (Mundinger 1975, 1982; Baptista 1977; Weins, 1982; Marler and Pickert 1984; Baker and Thompson 1985; Cunningham, et. al. 1987; Rothstein and Fleischer 1987 a; Bitterbaum and Baptista 1979) and use predominately qualitative features of the syllables and their alleles for my comparisons.

COMPARING REPERTOIRES

Determining the repertoire:

All syllables sung by each bird were identified to basic syllable categories which were later used for macrogeographic analysis. Syllable alleles within a category were identified for microgeographic analysis. Each syllable and its alleles was given a unique numerical descriptor, e.g. syllable 34 composed of alleles 34.1, 34.2, . . . , 34.9. To avoid confusing them with syllables, routines were given alphabetical designations, e.g. A, B, . . . , Z, AA, AB, . . . , ZZ, and themes were given alphanumeric descriptors, e.g. F1, F2, B1, B2, etc. These descriptors are used for statistical and isogloss analyses of population repertoires.

Routines were determined by examining the songs of several neighboring males in well sampled populations to determine the way in which they grouped syllables. These groups of syllables were designated as tentative routines. Other dialect populations were then examined to see if the tentative routines were sung consistently in the institution. If the original group of syllables was too inclusive, or was incomplete, I subtracted or added

syllables from or to the routine to make it more general. These idealized routines became the song routines.

My criterion for including a song routine in a male's repertoire was that it was included if 50% or more of its idealized syllable group were sung by the male and rejected if 49% or fewer syllables were sung. Thus a song routine of 4 syllables was included if 2 to 4 of the syllables were sung and excluded if only 1 of the syllables was sung. Ending routines composed of two buzzy syllables were included only if both syllables were sung. I treated ending routines differently because one ending syllable was often paired with different syllables in different routines.

A repertoire was produced for each male by determining the routines and syllable alleles he sang. In order to determine how many songs a male must sing to provide me with a reasonable representation of his repertoire, I plotted the mean cumulative number of both syllables and routines as a function of the number of songs for 19 birds for which I had recorded at least 42 songs (Figure 7). This plot indicated that a minimum number of 10 to 12 songs includes approximately 80% of the routines a male sings, and 15 to 18 songs includes 80% of the syllables. Both parameters reached an asymptote at about 40 songs. As a result of this plot, unless an individual's repertoire matched that of a well-sampled male, I excluded individuals (and populations) from which I recorded less than 10 songs when an analysis required examination of a relatively complete repertoire. To see if the asymptote described a male's complete repertoire, I extended this analysis for two males that provided me more than 60 songs (Figure 8). Males continued to add routines after 50, and syllables after even 60 songs are sung.

A local repertoire for each kilometer² sector was determined by summing unique routines in the repertoires sung by all the birds in that sector. These local repertoires were used for preliminary macrogeographic analysis.

Analysis of repertoires:

Isogloss plots were used to map and identify boundaries of song institutions and dialects. Isogloss plots were so named by linguists because each line (an isogloss) plots the geographic distribution of a shared vocal element (in this case a song routine sequence, routine, or syllable shared between populations of finches). Isogloss plots provide visual synopses of cultural sharing between populations. Map coordinates were determined for every sector in which songs were recorded. I examined each sector separately for which elements were sung in it. All sectors in which a given song element was sung were connected by a line, one line for each element shared. The number of lines enclosing two areas indicated their cultural relationship. Populations sharing many lines exclusively or nearly so were closely related (Figure 9), while those sharing fewer lines were less strongly related. Isogloss analysis of routine distributions determined the preliminary boundaries of song institutions.

By convention, microgeographic analysis of bird song dialects is based on sharing syllables and their alleles. Visual examination of my data indicated three features of House Finch song routines which led me to treat songs in a different manner than previously done.

1. Routines are more readily identified than syllables within a geographic area because routines have a syntax that characterizes them even though individual syllables in that syntax may be altered in different populations.

2. Routines are more stable than syllables. A given individual may substitute, delete, or insert syllables and syllable alleles in different articulations of the same routine.

3. Core and ending routines appeared to exhibit less geographic variability and endemism than routines in introductions.

Because of these features, I considered song routines instead of their component syllables when determining cultural affinities.

COMPUTER VIDEO STORAGE-RETRIEVAL PROGRAM

I found early in this project that it is difficult to return (for purpose of analysis) to a specific sonogram stored linearly on a reel of 35 mm Linograph paper. In order to facilitate review of sonograms, I wrote a computer program allowing the use of a camcorder or VCR to capture a video image of a specific sonogram and store it in computer memory. This program allows me to enhance the image, select a field to be stored, and retrieve images when desired. Minimum hardware requirements to use the program are an IBM AT, or compatible, with 640 K memory, both floppy and hard drives, a Genstar real time Video Capture board, and a multisync VGA video monitor.

There are two alternative video sources. First: the Uniscan II Model 4500 spectroanalyzer has a video port which allows direct output of the sonograms to a VCR. The VCR images can be input to the computer and frames captured directly through the Genstar Video Capture board. Second: a video camcorder can be used to input a printed sonogram to the computer. The VCR transfer provides more uniform images, while use of a video camera allows published sonograms to be saved in computer memory.

This program provides for manipulation and enhancement of captured sonograms in many ways. (1) The sonograms can be squeezed or stretched in both the X and Y axes so that sonograms originally produced with different time and frequency parameters can be displayed in similar time or frequency units. (2) Sonogram traces with poor contrast from the background can be enhanced. (3) False color can be added to an image to enhance amplitude differences. (4) One syllable or routine can be isolated from the song, manipulated, enhanced, and stored either separately or on a composite image with other syllables. (5) The order of syllables and routines can be rearranged.

CHAPTER 3

HOUSE FINCH SONG STRUCTURE

House Finch songs have structure at two levels: morphological and grammar.

MORPHOLOGICAL STRUCTURE:

The songs of House Finches can be divided into three segments: introduction, core, and ending. Each segment of the song is usually composed of one to three routines sung in a prescribed order. A complete song takes 2 to 4 seconds to be sung (average 2.2 sec) (Table 1). Each finch sings 1 to 5 (most commonly 2 or 3) distinct song patterns which differ lexically and syntactically and are considered here to be themes.

Six syllable parameters exhibit consistent differences between the three song segments: syllable duration, number of notes per syllable, mean frequency, frequency sweep, bandwidth, and amplitude. In addition, the number of syllables in and duration of the segments vary (Table 1).

Figures 10 and 11 show representative Cape Cod House Finch songs. The introduction of the song is usually a high pitched, softly sung sequence of syllables. The core is a louder sequence with more widely modulated frequencies. The endings are composed of either a loud, wideband, buzzy flourish (sonograms A, B, and the last syllable of sonogram D, Figure 10; sonogram A and last syllable of sonograms B and C, Figure 11) or rapidly

descending, narrow band syllables (sonograms C and D, Figure 10; sonograms B and D, Figure 11).

House Finch songs on Cape Cod often include introductory, core, subterminal, or ending routines in which one or more syllables are repeated several times as trills (Figure 11). Mundinger (1975) described the song of eastern House Finches as not including trills. This feature of House Finch song also was not described by Bitterbaum and Baptista (1979).

Introductory syllables:

Introductory syllables typically had short durations (109 msec), a low number of notes (mean 1.7), mean frequencies greater than 4050 Hz, frequency sweeps of less than 1100 Hz, bandwidths about 280 Hz, and the lowest relative amplitudes (1.08) of the three song segments. They are sometimes sung so quietly that it is hard to distinguish them from background noise (sonogram B, Figure 10b). Syllables in this part of the song varied within and between males (Table 2) and did not reliably reflect dialect and institution boundaries. Thus I only used introductory syllables to look at neighborhood relationships once institution and dialect boundaries were established.

Core syllables:

Core syllables also had short durations (110 ms). They had the most variable number of elements in the song (mean 2.2 ± 1.09). These syllables differed from introductory syllables by having lower mean frequencies (3550 Hz), wider frequency sweeps (1600 Hz), wider average bandwidths (450 Hz), and

greater relative amplitudes (2.29) (Table 1, Figures 10 and 11). They had more notes and were sung with less relative amplitude than buzzy ending syllables.

Ending syllables:

There were two types of ending syllables: (1) those composed of wide band, buzzy notes and (2) those composed of relatively narrow band notes. Ending syllables had the same mean frequencies and frequency sweeps as the core syllables, and the same numbers of notes as the introductory syllables (Table 1).

Wide band buzzy syllables:

Buzzy syllables had the greatest band-widths (880 Hz), durations (543 ms), and relative amplitudes of all syllables, (Table 1). They were readily distinguished on sonograms as bold traces which were wider than the traces of other syllables (compare ending syllables of sonograms A and B, Figure 10 and sonograms A and C, Figure 11 with introductory and core syllables of all sonograms in these figures). To the ear, they were buzzy, loud, and sung for a longer time than were the other syllables. I identified only eight basic buzzy ending syllable types, each having several alleles varying in frequency sweep and pitch, but these were arranged into a large number of routines. Individuals often sang the same pair of ending notes both separated as distinct syllables and joined, forming compound syllables (compare the last syllable of sonogram D with the last two syllables of sonogram B, Figure 10). Thus I identified buzzy terminal notes as individual syllables whether they were separate or joined.

Narrow band ending syllables:

The narrow band ending syllables resembled core syllables in mean durations (137 ms), mean frequencies (3840 Hz), frequency sweeps (1580 Hz), and numbers of notes per syllable (2.2). Although they were intermediate in relative amplitude (2.76) between the core and buzzy ending syllables, the higher frequency portions of these syllables were often sung so softly that they did not appear well on sonograms. In some populations narrow band ending syllables and buzzy syllables were similar in frequency slope and birds randomly interchanged them in songs.

VARIATION IN SONGS:

House Finches did not sing songs with rigid sequences. Variation occurred at three levels: the syllable, routine, and routine sequence. This variation was responsible for divergence of song themes into sub-themes.

The songs of thirteen males from four contiguous sectors in Truro serve as an example of variation in songs. These birds sang a total of 240 examples of Theme F1 which included at least part of the sequence of routines: I J K L M N Q (Figure 12, Table 3). Populations identified in the table are named from distinguishing landmarks or street names within the sector. Each column in the table lists the songs sung by one male House Finch of the identified local population. For example, there were three males recorded at Great Hollow. The rows indicate the number of times the finches sang the listed routine sequence. The row totals enumerate the number of times a particular routine variant

appeared in the total population sample. Sometimes ($n = 31$) a bird sang a theme unrelated to theme F1. Representative variations of Theme F1 are presented in Figure 12. In the following description, all songs referred to are found in Figure 12 unless otherwise stated.

Variation in syllables:

Syllables were usually pronounced with more than one microstructure within an institution. The different pronunciations are called alleles. Sonograms of several renditions of one song type sung in the outer cape demonstrate these pronunciation alleles (Figure 12). Although the songs in Figure 12 were not sung by the same bird, syllable and routine sequences in Figure 12 exhibited the typical range of variation when similar song patterns were repeatedly sung by one male. This group of populations was chosen because syllable pronunciations between individuals were nearly identical and would not interfere with observing changes in sequences. The most frequently used lexicon in these songs consisted of twenty one syllables of which four (106, 109, 919, and 920) had more than one form (Figure 12).

The several alleles of each syllable can be grouped into distinct allele complexes. The syllable alleles differed in frequency sweeps, complexity, and band width (Figure 12). Sometimes one syllable was substituted for another in the same position in a song. For example, both syllable 118 and 121 were sung before syllables 919 and 920 in different songs. Since syllable 118 appeared to

have a different origin from syllable 121, syllable 121 was treated as a distinct syllable type, not an allele of syllable 118.

Variation in routines:

Routines are composed of two or more syllables. Variation in routines is also seen in the songs presented in Figure 12. If more than one allele of the syllables were sung, or one or more syllables of a routine were substituted, the different variants of the routine were called routine alleles, and the group of alleles is called a routine allele complex. Three routines, K M N, comprise three routine allele complexes. Two of these routines (M and N) have syllable substitutions as well as alternate syllable alleles in some of their alternate forms.

Routine K had two routine alleles.

K (n = 84) composed of syllables 106a 106b 106c (Song B, Figure 12),

k (n = 58) composed of syllables 106.1a 106.1b 106.1c (Song C, Figure 12),

Routine M had four alleles:

M (n = 134) composed of syllables 125 109 117 (Song A, Figure 12),

M' (n = 32) composed of syllables 125.1 109 117 (not illustrated),

m (n = 69) composed of syllables 108 108 109.1 (Songs B and C, Figure 12),

m' (n = 5) composed of syllables 108 119.1 109.1 (not illustrated),

Routine N had three alleles:

N (n = 149) composed of syllables 121 919 920 (Song A, Figure 12),

n (n = 58) composed of syllables 118 919.1 920.1 (Songs B and C, Figure 12), and

n' (n = 5) composed of syllables 118.1 919.2 920.2 (not illustrated).

Variation in routine sequences:

The syllables of this population of songs were grouped into eight routines, and two variants of this theme were classified as sub-themes based on which routines were included. Three of thirty eight Cape Cod song themes were regularly sung as sub-themes (Chapter 5). The sequence of routines for sub-theme F1A was (I) J (K) L M N (O). Routines I, K, and O are enclosed in parentheses because individuals did not always include them in a vocalization. The presence or absence of routines I and O had no effect on the inclusion or exclusion of other routines or routine variants. Routine J was sung in this sub-theme, however, and always followed by routine allele K. In all instances of sub-theme F1B, routine J was absent and routine allele k was always sung.

In a sequence of songs consisting of repetitions of the same theme, an individual sometimes repeated syllable number 115, generating a trill (sonograms A and B, Figure 12), and sometimes not (sonogram D, Figure 12).

Four permutations of the basic routine sequence (I) J (K) L M N (O) were sung by the Truro population:

Theme	routine sequence	frequency sung	sonogram illustrated in Figure 12
F1A	<u>(I) J (K) L M N (O)</u>	(n = 23)	(Sonogram A),
F1A	<u>(I) J (K) L m n (O)</u>	(n = 159)	(Sonogram B),
F1B	<u>k L m n (O)</u>	(n = 51)	(Sonogram C),
F1B	<u>k L M N (O)</u>	(n = 7)	(not illustrated).

Since routines M', m', and n' were rarely sung, I grouped them here with their more common alternates (e.g. M' with M, m' with m, and n' with n).

GRAMMATICAL STRUCTURE

The morphological structure of song suggests a within-song grammar which may convey individual and species identification to the listener. The grammar of a language is correlated with a function. Date, et al. (1991) and Thompson and Baker (1993) found the introductory elements provide enough information for American Redstarts and White-crowned Sparrows to identify the species (Redstart) and dialect (Sparrow) of the singer. Date, et al. (1991) and Searcy (1990) suggest there is information in other parts of songs besides that found in the introduction.

This study was not designed to examine the function of the grammar, merely to record its possible existence. Thus the following is a description of grammar in House Finch song, but does not discuss grammatical function.

Core routines were usually composed of non-repeating syllables (i.e. not trilled), sung more loudly than, and having larger frequency sweeps than, introductory routines. There were, however, two types of trills included in the cores of some Cape Cod House Finch songs: those composed of repetitions of simple syllables and those composed of repetitions of complex syllables. Trills composed of simple syllables (having one or two notes) sung with short duration, when found, were always in the second half of Cape Cod songs, and subterminal (immediately preceding ending routines). When trills were followed by other core routines, the syllables were always complex with three or more notes per syllable,

and each syllable sung with durations longer than syllables of the subterminal trills.

The ending flourish syllables of Cape Cod songs were usually composed of one or two notes, buzzy, with a large frequency sweep, loud, and sung with long duration. When they were not as above, ending routine syllables were complex (composed of two or more notes), loud, with a large frequency sweep, and sung with short duration.

I found other levels of potential grammar in House Finch song. Individual finches sang, on average, three different song types called themes (Chapter 4). The inclusion of three themes in an individual's repertoire was rather constant with most birds singing three themes. It appeared the grammar of the repertoire was complete with three themes. Within most populations, two of the themes were often culturally related, while the third had usually evolved independently.

Individuals often sang one or more themes with two or more consistent variations. These variations were called sub-themes.

Stratification zones:

In some areas of Cape Cod individual song themes were sequentially replaced as song boundaries were crossed. Each population appeared to have a layered grammar which was complete when there were three themes (strata) in the song repertoire. As one population replaced another in these regions, one song theme replaced another in a non-random manner as if to complete each portion of the grammar. I call this pattern of replacement "stratification," and the

areas in which this replacement occurred "stratification zones" (see Chapter 6, boundary regions). Thus this term describes the layering of songs in a grammar much as a geologist uses stratification to describe the layering of rocks in a geological formation.

Individuals that sang themes from each of the bordering traditions comprised the majority of the populations in these stratification zones. Repertoires of birds located in stratification zones included themes commonly sung by populations on both sides of the zone (Figure 13), and sometimes unique themes sung only within the zone. Within these zones, each song of the new repertoire was taken from an adjacent institution in toto. There was no blending of syllables or routines of the two institutions into a single hybrid theme. Rather there was an abrupt, stepwise replacement of themes at the boundaries of the stratification zone.

CHAPTER 4

MACROGEOGRAPHIC VARIATION OF

SONG ON CAPE COD:

SONG THEMES AND INSTITUTIONS

This chapter is divided into sub-sections, each addressing one of the main objectives: **(1)** differentiate between themes and institutions, and **(2)** identify themes and institutions and describe their macrogeographic distributions on Cape Cod.

1 - DIFFERENTIATION BETWEEN THEMES AND INSTITUTIONS

House Finch songs differ in syllable structure, syntax, and ending syllables such that in any one neighborhood the birds each sing several song types, called themes (Mundinger 1975). Neighborhood males tend to sing the same basic theme patterns and one to six themes were sung as song complexes by local Cape Cod finch populations. The vocabularies (syllables) that make up themes differ from locale to locale. Different populations that share the same basic vocabulary are said to be members of the same song institution (Mundinger 1975). The word institution is used as song institutions are considered to be avian cultural institutions, i.e. culturally inherited, functional traditions (Mundinger 1980). Song institutions are often regional in distribution and may be composed of

several local song dialects which utilize the same basic vocabulary (lexicon). Thus song institutions sung in a given region differ from the institutions sung in other regions. The vocabularies differ in different regions, but the birds organize these vocabularies into themes at every locale. By analogy, German and English are two cultural institutions but people organize their different vocabularies into sentences in locales where both languages are spoken.

A. Song themes

Themes are composed of distinct sequences of routines which distinguish one song from another. The repertoires of individual birds on Cape Cod include two to four themes. The sum of the themes sung by a group of populations of finches provide the vocabulary used. That vocabulary, in turn, identifies the song institution.

Here, I define the concept of the theme in a broad sense in order to facilitate description. I lump all songs that include variants of distinctive core routines as one theme and ignore differences in introductory and terminal routines as well as occasional minor core routine variants. Thus distinctive core routines in songs identify the themes the songs belong to. Core routines are the most conservative units of Cape Cod songs.

There were differences in the distribution of song vocabularies on Cape Cod as compared with the distribution of vocabularies on Long Island. These differences suggested a modification of the original concept of the song institution. In this thesis I identify institutions as groups of themes, rather than

using shared syllable groups to identify institutions (Mundinger 1975). Each group of themes included the basic vocabulary sung in a song institution. Since themes are identified by their core routines, song institutions on Cape Cod are identified here by several core routines traditionally sung in two or more differing themes. As seen in the discussion below, a given theme was not always restricted to a single song institution.

A few populations within several song institutions sang repertoires composed of two variants of a single theme. These populations were classified here as singing one theme. In one instance a small institution was identified on the basis of one shared theme. Thus the shared vocabulary of a song institution varied from a minimum of one theme to a maximum of six shared themes.

Variations in introductory and ending routines, which helped to identify institutional dialects, are not described in this chapter. They will be examined in the microgeographic analysis of songs in Chapter 5.

B. Song Institutions

The song institution, as defined by Mundinger (1975, 1980), is a common vocabulary shared by birds living within a geographic region. This term describes cultural features of the song and does not attempt to convey functional attributes to bird songs. Mundinger (1980) found House Finches singing the same institution have characteristic syllable patterns, and used the term institution to convey the idea of general sharing of a vocabulary within "(nearly) mutually exclusive" (Mundinger's parentheses) boundaries. Local variations within a song

institution make up song dialects. A large song institution may be made up of many culturally related dialects.

The House Finch was not found in eastern North America until about 1940, at which time captive birds were released on Long Island (Elliot and Arbib 1953). Munding (1975) found twenty nine song institutions that had become established on Long Island and in lower Westchester County, NY (see Figure 1). Divergence in song traditions thus coincided with the explosive geographic spread of the House Finch in the north east.

Geographic isolation of colonies favors the evolution of unique song institutions (unique syllable vocabularies) by the process of "allopatric cultural speciation" (Munding 1980). There are five previously described mechanisms that could have affected song differentiation: (1) song drift in satellite populations that retained a learned song after dispersal; (2) improvisation by partially tutored juveniles; (3) reticulate evolution, joining elements of two learned vocabularies (lexicons); (4) improvisation by untutored juveniles, and (5) adopting songs from another species. These mechanisms by which the songs of new populations diverge from established songs are described below.

Song Drift

Colonies established by adult birds or tutored juveniles may sing songs that resemble another population's patterns. Song drift occurs as copy errors are accumulated by subsequent generations (Thielke 1973, Munding 1980). Thus

the songs of a new colony may diverge from established traditions even if the founders retained components of the vocabulary of the parent population.

Improvisation by tutored juveniles

Colonies founded by juvenile birds which had incompletely learned the songs of their natal population prior to dispersal may develop parts of their songs by improvisation. Here the birds incorporate elements from their natal population in songs which also include new elements independently developed by the isolated population (Thielke 1973).

Reticulate Evolution

Colonies founded by juvenile birds which had incompletely learned the songs of their natal population prior to dispersal may learn their songs by the process of reticulate evolution (Mundinger 1980) if these birds are also tutored with songs from one or more other song institutions. They then incorporate portions of each tradition. These elements may then be modified or retained in the form presented by the model.

Improvisation by untutored juveniles

New colonies founded by untutored juveniles would presumably learn song after dispersal (Mundinger 1975), but would have no conspecifics to learn from. These colonies would be the natural equivalent of "group social isolates" used in studies of the ontogeny of bird song (Marler 1970, Marler and Mundinger 1971). Because of their geographic isolation, these birds would perforce learn song in acoustic isolation from conspecifics. The songs may be formed by improvisation

(the process most often observed in group social isolates - Marler 1970, Marler and Mundinger 1971).

Interspecific copying

Alternatively, House Finches could learn song by mimicking the songs of other bird species (Hartshorne 1973, Baptista 1977, Baylis 1982, Payne 1991), perhaps in conjunction with improvisation. Songs learned in this fashion would resemble the other species' song initially, but may be altered somewhat if song drift (Mundinger 1980) and/or species specific syllable and syntax preferences are manifested (Hartshorne 1973, Baylis 1982).

2 - GEOGRAPHIC DISTRIBUTION OF THEMES AND INSTITUTIONS DEFINED BY THEMES

Song themes were classified as regional, minor, or local depending upon how widely the themes were distributed. Since themes are the indicators of institutions, song institutions also exhibit regional, minor, and local distributions (see Figure 14).

REGIONAL THEMES (7 themes) - sung in at least 20 1-km² sectors dispersed within an area of at least 200 km²,

MINOR THEMES (twelve themes), sung in 5 to 10 1-km² sectors dispersed within a 60 to 100 km² area , and

LOCAL THEMES (eighteen themes), sung in 1 to 4 sectors dispersed within a 1 to 40 km² area.

A. Regional themes

The seven regional themes are sung in four partially distinct areas on Cape Cod (Figure 14). The distributions of six of these themes overlap such that there are three pairs of themes. One pair (F1 and F2, Figure A.1 in Appendix A¹) is sung on the western edge of the inner Cape (population 1, Figure 14) and birds singing them make up the Falmouth song institution. A second pair (B1 and B2, Figure A.2) is sung in the middle Cape. Populations singing these themes comprise the Barnstable institution (population 2, Figure 14). Two themes (C1 and C2, Figure A.3) form the third pair that is sung on the eastern edge of the middle Cape and extends along the southern half of the outer Cape. Birds singing these themes are in the Chatham Institution (populations 3, Figure 14). The seventh theme (M1, Figure A.4) is sung in the center of the inner Cape (population 4, Figure 14) and birds singing this theme are in the Mashpee institution.

1. Falmouth

This institution was characterized by themes F1 and F2 (Figure A.1). Theme F1 was sung in four forms depending on the number of core routines and trills in the song (see Sub-themes, Falmouth below). Birds singing this song institution were found in Falmouth, Bourne, west Sandwich, south Plymouth, south Mashpee (population 1, Figure 14), and Truro (population 1s, Figure 14).

¹Figures in the appendices are referred to using the letter of the appendix, point, and the number of the figure (e.g. Figure A.1 refers to the first figure in Appendix A).

2. Barnstable

This institution was characterized by the regional themes B1 and B2 (Figure A.2). Theme B1 was sung in three forms (see Sub-themes, Barnstable below). In parts of Dennis, Brewster, and Harwich, other themes were sung in place of one or more of these regional themes (this results in stratification of themes). Birds singing this song institution are found in Barnstable (except the southwest portion), Yarmouth, Dennis, west Brewster, Harwich, west Chatham, and south Orleans (population 2, Figure 14).

3. Chatham

This institution was characterized by themes C1 and C2 (Figure A.3). Theme C1 was sung with four pronunciation variants (see Sub-themes, Chatham below). Birds singing this song institution are found in Chatham, east Harwich, east Brewster, Orleans, Eastham, and south Wellfleet (population 3, Figure 14).

4. Mashpee This institution was characterized by theme M1 (Figure A.4). Three minor and several local themes were sung with theme M1 in various locations (see Minor themes below). Birds singing this song institution were found in Mashpee and southwest Barnstable (population 4, Figure 14).

Themes of each of the four regional institutions were sung by one or more satellite populations in addition to being sung in the areas described above. A satellite population is a disjunct, usually small, population of finches which sang the same song vocabulary of another, usually larger, population (population 1S in Figure 14 is a satellite of the Falmouth institution).

B. Minor themes

Twelve minor themes were sung in seven separate areas on Cape Cod (Figure 15). The distributions of six of these themes overlapped such that there were three pairs of minor themes. One pair (A1 and A2, Figure A.5) was sung in Wareham and Marion (Figure 15). A second pair (S1 and S2, Figure A.6) was sung in Sagamore and Sandwich (Figure 15). The third pair (W1 and W2, Figure A.7) was sung in Wellfleet and north Eastham (Figure 15). I distinguish these minor theme pairs as minor song institutions. These minor institutions were not sung by satellite populations as were the regional institutions.

5. Wareham

This institution was characterized by themes A1 and A2 (Figure A.5). Theme F1 was also sung in this institution. Birds singing this song institution were found in Wareham, Marion, and west Bourne (A1 + A2, Figure 15).

6. Sandwich

This institution was characterized by themes S1 and S2 (Figure A.6). Themes F1 and F2 were also sung in this institution. Birds singing this song institution were found in north Bourne and north Sandwich (S1 + S2, Figure 15).

7. Wellfleet

This institution was characterized by themes W1 and W2 (Figure A.7). Birds singing this song institution were found in Wellfleet and north Eastham (W1 + W2, Figure 15).

Of the six other minor themes, three, M2, M3, and M4 (Figure A.8), were sung in portions of the Mashpee song institution (M2 + M3, and M4, Figure 15). Two others, the unpaired minor themes, D1 (sonogram A, Figure A.9) sung in Dennis and west Brewster (D1, Figure 15), and H1 (sonogram B, Figure A.9) sung in Harwich (H1, Figure 15), were separately sung with themes of the Barnstable song institution. The last minor theme, P1 (sonogram C, Figure A.9) was sung in Provincetown (P1, Figure 15).

C. Local themes

Most local themes were sung in small, disjunct areas on Cape Cod (Figure 16). In several populations, one or two local themes were sung along with themes of a regional or minor institution. In such instances, I considered the local themes as dialectical variants (see chapter 5) of the institution with which they are sung. In four areas, however, local themes were sung exclusively, and I considered the song traditions of these populations to be local song institutions.

8. Woods Hole

Birds singing this song institution were found just north and east of Woods Hole in Falmouth (WO, Figure 16). Two individuals east of Woods Hole sang both the Woods Hole theme WO1 (sonogram A, Figure A.10) and theme F1. The remainder sang only theme WO1.

9. Johns Pond

Six birds singing two unique themes were found on the east shore of Johns Pond in Mashpee (JP, Figure 16). The themes JP1 and JP2 (sonograms B and C, Figure A.10) were found nowhere else in this study.

10. Salt Marsh

Four birds singing this song institution were found on the barrier beach at the salt marsh east of the town of Sandwich (SM, Figure 16). Two birds found about 1/2 mile south-west of the marsh also sang this institution. The institution was characterized by themes SM1 and SM2 (sonograms A and B, Figure A.11).

11. Crosby Landing

A population of about twenty finches found at Crosby Landing in north Brewster (CL, Figure 16) sang an institution composed of two variants of theme CL1 (sonograms A and B, Figure A.12).

Other local themes were found at:

a. Herring Brook, a population found along a five mile transect in Dennis (HK, Figure 16) sang theme HK1, a variant of theme F1, plus theme B2 (sonogram C, Figure A.12);

b. Pimlico Pond, a colony of about three dozen individuals in Sandwich (PP, Figure 16) sang one unique theme (sonogram A, Figure A.13) plus portions of themes of the Mashpee and Falmouth institutions;

c. Spectacle Pond, a colony of several dozen finches in Sandwich (SP, Figure 16) sang themes of the three neighboring institutions plus two unique themes (sonograms B and C, Figure A.13);

d. Sandy Pond Camp, (SC, Figure 16; sonogram A, Figure A.14) in southern Plymouth;

e. Swallow Lane, (SW, Figure 16; sonogram B, Figure A.14) in Brewster;

f. Kompass Lane, (KM, Figure 16; sonogram C, Figure A.14) in Mashpee;

g. Phyllis Lane, (PL, Figure 16; sonogram A, Figure A.15);

h. Yarmouth, (YM, Figure 16; sonogram B, Figure A.15);

i. Marstons Lane, (ML, Figure 16; sonograms A and B, Figure A.16) in Brewster;

j. Long Pond, (LP, Figure 16; sonogram A, Figure A.17) in Harwich; and

k. Doane Road, (DR, Figure 16; sonogram B, Figure A.17) in Harwich.

A few other themes were sung by only one or two birds as ideolects. These themes are ignored here as they were not important features of the cultural traditions of Cape Cod.

D. Satellite Populations

The regional song themes had disjunct distributions in that some were sung both in the previously described (core) region and also by populations separated from the core region by at least five miles. Since these populations were detached from the main body of populations, and populations singing other regional themes were located between the core populations and the secondary populations, I consider the secondary populations to be satellites of the populations singing the regional themes. These satellite populations probably arose as a result of jump dispersal. Figure 17 shows the locations of these

populations and the regional institutions from which they seemed to have originated.

A satellite population which sang two versions of Falmouth theme F1 was found in Truro. This population included two versions of theme F1 in its repertoire.

A satellite population singing the Barnstable theme B1 was found at Spectacle Pond in Sandwich. Several finches in Provincetown included theme B2 in their repertoires.

Satellite populations which sang Mashpee themes were found in south Dennis, Harwich, and Eastham. The Dennis population sang theme M1, the others sang M2.

Satellite populations which sang both Chatham themes were found at the northern Sandwich/Barnstable border and in north Dennis.

The above populations were satellite populations singing regional themes. A population of birds in Osterville (OS, Figure 17), that otherwise sang Barnstable themes F1 and B2, sang theme SP1, a minor theme also sung by the colony at Spectacle Pond in central Sandwich. This population was considered to belong to the Barnstable institution, with cultural ties with Sandwich. This was the only case of a satellite involving a local institution.

Provincetown songs: a satellite with mixed heritage

The population in Provincetown, at the tip of the outer cape, sang a montage of songs which were sometimes entire themes or intergraded routines

from Falmouth themes F1A and F1B, Barnstable theme B2, Chatham theme C2, and Wellfleet theme W1. Thus, the Provincetown population was culturally related to four other institutions (Figure 4). In addition to patterns derived from other institutions, many individuals sang the reticulate theme P1 (sonogram C, Figure A.9) composed of syllables from themes W1 and W2 (or C1) plus several unique syllables.

E. Sub-themes

Although themes were distributed throughout large portions of an institution's range, one theme each of the Falmouth, Barnstable, and Chatham institutions was sung in two or more forms by many populations. In some local populations or dialects of each of these song institutions (e.g. the North Falmouth, Truro, and Buttermilk Bay dialects of the Falmouth institution) the sub-themes were treated by some finch populations as distinct themes, being alternately sung by the same individuals to the exclusion of other themes.

Falmouth

In southern Falmouth, Theme F1 diverged into sub-themes F1A and F1B, each of which (a) sometimes included a subterminal trill and (b) sometimes did not. A series of sonograms from a local population (Figure 18) shows how the core routines of the sub-themes culturally evolved independently within a local population once the sub-themes were established.

Two routines composed of syllables (a) 106 through 109 (core routine FA), and (b) 920 (ending routine E) were included in all variants of this theme sung by

the represented population (Figure 18). The inclusion of core routine FA in each of the variants designates them as variants of theme F1. One core routine, routine FC, composed of a trilled sequence of syllable 115 was found in variants F1Ba (sonograms C and E) and F1Bb (sonogram G, Figure 18). Finally, a core routine, FB, composed of a trilled sequence of syllable 110 plus syllable 111 was found in two minor variants of this theme: F1Aa (sonograms B and C) and F1Ba (sonograms D and E, Figure 18).

Sonograms B and D (Figure 18) show the transition of this theme into form F1A. Sonograms C and E show the transition of this theme into form F1B. The songs in sonograms B and C show the first indications of divergence: modifications of (1) syllable sequences and (2) altered pronunciations of syllables 106 and 107. Sonograms D and E show further modifications of sequences and syllable pronunciations to the lexical variants they were most often sung on Cape Cod. Sonograms F and G show variants of the sub-themes in which the trilled syllable 110 was absent.

In theme F1A (sonograms B, D, and F, Figure 18) syllable 105 was dropped and syllable 116 was inserted after syllable 106. In theme F1B (sonograms C, E, and G, Figure 18), syllable 105 was retained, syllable 115 was inserted between syllables 105 and 106, and syllable 115 was repeated as a trill (sonograms B, D, and F, Figure 18). Pronunciations of syllables 105, 106, 107, and 109 were modified from their original forms in sonogram A.

Subterminal trills were common in the Falmouth institution. Renditions of both sub-themes F1Aa and F1Ba included subterminal repetitions of syllable 110 (sonograms A through E, Figure 18). Sonograms F and G show variants F1Ab (sonogram F, Figure 18) and F1Bb (sonogram G, Figure 18) without this trill.

Several populations in Wareham, Bourne, and Truro omitted theme F2 and sang only variants of the themes F1A and F1B (Figure 19). Either or both sub-themes were sung with and without syllable 110 as a trill in these populations. In some populations, e.g. the satellite population in Truro, the sub-themes and the alleles of homologous syllables were quite similar to each other (sonograms A and B, Figure 19). In parts of Wareham and Bourne the pronunciation alleles of homologous syllables sung in the two sub-themes diverged (sonograms C and D, Figure 19). In addition to the sub-themes in Figure 19, the Truro population sang versions of these sub-themes that included the subterminal trill; and the Buttermilk Bay population sang sub-theme F1A with (usually) and without (rarely) the subterminal trill, but did not include the subterminal trill in sub-theme F1B.

Barnstable

In the Barnstable song institution, both theme B1 and B2 diverged into sub-themes. Theme B1 sub-themes were primarily based on pronunciation variation, while theme B2 sub-themes were primarily based on lexical variation.

Theme B1 was sung as sub-themes B1A (sonograms A and C, Figure 20) and B1B (sonograms B and C, Figure 20) in Barnstable. Theme B1A was usually sung with one introductory routine (blA, sonogram A, Figure 20), and the core

contained three syllables in two routines (routines BA and BB, sonogram A, Figure 20). Theme B1B was usually sung with two introductory routines (bIB and bIA, sonogram B, Figure 20), and the core contained four syllables.

Theme B2 was sung in two lexical forms: (1) a short form, B2A, with five or six routines. Two of these were introductory (bIB and bIC, sonogram A, Figure 21), two were in the core (BL and BM, sonogram A, Figure 21), and one or two ending routines (bEL [always sung] and bEM [usually sung], sonogram A, Figure 21).

Sub-theme B2B was sung with up to eight routines. There were one or two introductory (bIB [not pictured in sonogram B] and bIC, sonogram B, Figure 21), a core routine (BO, sonogram B, Figure 21), a repeat of introductory routine bIC (sonogram B, Figure 21), two core routines (BL and BM, sonogram B, Figure 21), and one or two ending routines (bEL and bEM, sonogram B, Figure 21). Most populations sang both sub-themes of theme B2².

Birds singing the Barnstable institution often added a characteristic connecting routine (CA, sonogram C, Figure 20) to themes B2 or B1B which was usually followed by a partial rendition of theme B1A (rarely by a rendition of theme B1B). Theme B1A did not precede other themes. The Barnstable institution was the only institution in which characteristic connecting routines were found. When

²This was the only theme on Cape Cod in which an introductory routine followed a core routine. Some finches would repeat the sequence of routines BO bIC two or even three times with modifications. This would generate an extremely long song of up to 4.5 seconds in duration.

individuals of other song institutions sang two themes sequentially, they usually did not include a connecting routine (such as routine CA, sonogram C, Figure 20), but modified introductory syllables of the second theme when progressing to the second theme.

Local themes were substituted for one of the sub-themes of theme B1 or B2 by some populations (see Chapter 5, Barnstable well formed lexical dialects). This mode of theme replacement in dialects is unlike that found in the Falmouth institution in which some dialect populations sang two variants of theme F1 and omitted theme F2.

Chatham

Theme C1 was sung as sub-themes C1A (sonogram A, Figure 22) and C1B (sonogram B, Figure 22). Although these sub-themes are composed of pronunciation variants of the lexicon common to the core routines CA and CB, the birds differentiated between these sub-themes as they were both sung by most individuals. When sub-themes C1A and C1B were sung with the complex introduction clB (sonogram C, Figure 22), they were differentiated as sub-themes C1Ab and C1Bb. Introduction clB was atypical for House Finch songs on Cape Cod because it was longer than four syllables, the mean note frequencies were below 4.2 kHz, and many syllables were sung with harmonics (see Chapter 3).

Sub-themes C1A and C1Ba of the Chatham institution differed primarily in syllable pronunciation with few lexical differences (Figure 22). Lexical differences, when present, were usually in the introductions of Chatham themes. This was

unlike the Falmouth and Barnstable institutions where distinct lexical differences were found in theme cores.

F. Summary

Macrogeographic variation can be described at both the theme and institutional levels. I found seven major themes, twelve minor themes, and eighteen local themes. The seven major themes were distributed in four large regional song institutions, sung in areas of at least 200 Km². Six of the twelve minor themes made up three minor song institutions, sung in areas of between 50 and 200 Km². Five other minor themes were included in the Mashpee or Barnstable regional institutions. These minor song institutions were recorded from one to several bird populations. The minor theme P1 was sung in Provincetown where an intergraded mix of themes was sung.

The lexicons and pronunciations of song themes were often varied. Several themes were consistently sung with additional routines, and the pronunciations of syllables in these lexical variants were different. This was especially evident in the three regional song institutions where themes F1, B1, and C1 were subdivided into four, three, and four sub-themes respectively.

CHAPTER 5

MICROGEOGRAPHIC VARIATION

OF SONG ON CAPE COD:

DIALECTS

In this chapter I examine microgeographic (between population) variation in song themes (dialects). Here I treat dialects in a general manner, based on distributions of syllable alleles, syllables, and/or routines. Unusual boundary interactions are mentioned where they appear, but boundaries are examined in more detail in Chapter six.

Variation in song traditions was found in all Cape Cod song institutions. In general, most populations singing the same song institution sang one or more themes in common, but these themes were not sung with the same lexicon or pronunciation by all populations in a song institution. These variants constituted dialects as described below.

First, theme variation was intimately associated with dialect variation, and there were several ways themes varied. In three of the regional institutions (Chatham, Barnstable, Falmouth) one song theme differentiated into sub-themes. In some instances, local groups retained songs that appeared to be intermediate stages in the process of differentiation into sub-themes. In other populations variants of these sub-themes were sung as separate and distinct themes.

Second, in some regions, several populations sang a subset of the institutional themes (sometimes in conjunction with themes of another song institution), at other times with one or more unique themes. In still other regions, populations inserted, deleted, or substituted segments of a theme.

Finally, the songs of some House Finch populations contained routines which were derived copies of the songs of other species. These alien derived routines were usually sung by local populations and were not generally sung within a song institution.

A. DIALECTS

Historically there has been no universally accepted definition of dialect in bird song research. I use the term dialect to refer to populations that sing similar pronunciation (Baptista 1975, Baker 1975, Mundinger 1975). Here, I am also using lexical variants to describe dialects. Variants that differed by at least thirty percent of their lexicons or pronunciations were distinguished as dialects if the variants differed abruptly at a boundary (see Chapter six for boundary determinations). When variants gradually merged into each other, I did not distinguish dialects. Thus dissimilar song patterns were considered dialects when they varied discretely, but not when they varied continuously.

There was almost a continuum of modes of variation: well defined lexical dialects, well defined lexical and pronunciation dialects, well defined pronunciation dialects, poorly defined pronunciation dialects, non-dialects with pronunciation variants, and non-dialects with lexical variants. Examples of each of these modes

of variation were found in the regional and minor song institutions. Here I describe variation in five of these song institutions: Wellfleet (well defined lexical dialects), Barnstable (well defined lexical and pronunciation dialects), Falmouth (poorly defined pronunciation dialects), Chatham (non-dialects with pronunciation variants), and Mashpee (non-dialects with lexical variants).

The Wellfleet institution: Well defined, lexical and pronunciation dialects

Populations singing the Wellfleet institution were found on the outer cape in the townships of Wellfleet, south Truro, and north Eastham (Figure 23). The Wellfleet institution was characterized by themes W1 and W2. Wellfleet themes (Appendix A, Figure A.7) were distinct from themes of the neighboring institutions to the south (Chatham, Figure A.3) and north (Truro, Figure A.1).

An isogloss analysis (Figure 23) revealed there were two dialects in this song institution, one large one centered in the town of Wellfleet and a much smaller dialect in south Truro. These dialects were identified by both lexical and pronunciation variations of themes W1 and W2 (Figure 24). Populations that sang the Chatham institution (smaller, filled circles) are not included in this analysis and should be ignored at this time.

Wellfleet dialect

Individuals singing the dialect centered in Wellfleet and Eastham sang several introductions and two endings for theme W1. Since pronunciation and the lexicon of core routines remained constant, theme W1 did not diverge into sub-themes. The alternate introductions and endings constituted variants of the same theme.

Sonograms A, B, and C in Figure 25 depict three songs sung by one typical bird in Wellfleet. Each song begins with a different introduction, and there were two endings. In Eastham (sonogram D, Figure 25), only the introduction of sonogram C was sung and core syllables 504 and 505 were dropped from the song. Some renditions of theme W2 sung in Eastham were sung with identical pronunciations and lexicon as were found in the Wellfleet population's rendition, others varied slightly in the introduction (Figure 26). Since, in this thesis, dialects are defined by the cores of themes and not introductions, and the cores of the Eastham and Wellfleet populations did not differ by more than thirty percent, the Eastham populations did not constitute a separate dialect.

Eastham populations which sang the Wellfleet dialect were dispersed in a reticulate or interdigitating pattern with populations which sang the Chatham institution (Figure 23). In north Eastham, two populations of finches (O) sang only themes of the Wellfleet institution; individuals of three populations (⊗) included themes of both the Wellfleet and Chatham institutions in their repertoires; and seven populations (⊙) sang only Chatham institution themes. Populations that

included themes of both the Wellfleet and Chatham institutions in their repertoires sang versions of themes similar to those sung by neighboring populations that included only Wellfleet themes or only Chatham themes in their repertoires. Individuals which sang songs of both institutions sang fewer examples of Wellfleet themes ($n = 86$) than examples of Chatham themes ($n = 447$).

Since some Eastham populations sang only Wellfleet themes while others sang only Chatham themes, I considered the songs in this region to represent both the Wellfleet and Chatham song institutions. The reticulate pattern of song distribution in this town suggested cultural traditions were in flux at the time of my data collection. It appeared that populations of both the Wellfleet (from the north) and Chatham (from the south) song institutions had only recently expanded into north Eastham allowing the two traditions to come in contact.

Truro dialect

The introduction sung in the Truro version of theme W1 was a pronunciation variant of the most commonly sung introduction for theme W1 in the Wellfleet population's repertoire. This was followed by a core composed of syllable 501 plus two examples of syllable 530 (unique to this population, see Figure 24). This population varied the ending of theme W1 rather than the introduction (which was varied in the repertoires of birds singing the Wellfleet dialect). The ending of theme W1, as sung in the Truro dialect, was (most often) composed of two syllables (buzzy variants of syllables 504 and 505, sung in one hundred twenty four of two hundred thirty two songs), or three syllables (syllables

504, 505, and 821, sung in thirty seven songs), or the eight syllables seen in sonogram A, Figure 24 (syllables 504, 505, 821, 822, 502, 503, 822, and 906, sung in seventy one songs). The core syllables 504 and 505 of the Wellfleet dialect were sung as a buzzy ending routine in Truro. In addition, the core syllables 502 and 503 of the Wellfleet dialect were sung in the ending of the Truro version of this theme (Figure 24).

The Truro dialect's version of theme W2 included a complex introduction. This may have been improvised from the second most commonly sung introduction of the Wellfleet dialect's theme W1 (see sonograms C and D, Figure 24). The core of theme W2 was composed of only syllable 516 (trilled as it was in Wellfleet). The ending of this theme, as described above, was improvised from core syllables 502, 503, and 822 of Wellfleet's version of theme W1 plus a variant of syllable 906 (sonogram D, Figure 24).

Approximately one percent of the songs sung in south Truro (4 of 320 songs) were examples of theme F1A as sung by the Truro population of the Falmouth institution (see the Falmouth institution below). These songs were sung by only two birds which together sang 113 songs). This suggests either (1) cultural diffusion between neighboring Truro local populations, or (2) selective attrition of the Falmouth cultural tradition was occurring in these bilingual individuals (Baptista 1973, Nelson 1992).

Summary

The Wellfleet institution was composed of two dialects which differed to a great extent in lexicon as well as phonology. To the north, the Truro dialect of the Wellfleet institution shared a song tradition (theme F1A) sung elsewhere in Truro by members of a different institution. To the south, in Eastham, some individuals singing the Wellfleet dialect shared other traditions sung in the Chatham institution. This cross-institution sharing at each end of the Wellfleet institution suggested the Wellfleet institution had recently come in contact with the Truro and Chatham traditions.

The Barnstable Institution

This institution was characterized by themes B1 and two versions of theme B2: B2A and B2B. These themes were sung in several regions with some lexical variation (Table 4). Distributions of pronunciation variants in other portions of the Barnstable institution involved the lexicons of entire themes. Populations singing one variant were abruptly separated from populations singing other variants. Isogloss analysis of the Barnstable institution indicated nine dialects: seven dialects in which minor or local themes were sung in place of one or more of the Barnstable themes (lexical dialects), and two dialects based primarily on pronunciation differences (Figure 27). The Hyannis dialect (1) was the largest dialect and was located in the western portion of the institution. It may, therefore, contain the site of the original colonization of this institution. The repertoire of the Hyannis dialect included themes B1A, B1B, and B2 (Figure A.2). Four of the

lexical dialects included pronunciation variants of syllables sung in the largest dialect of the Barnstable institution.

Well defined, lexical dialects

There were three lexical dialects which differed from the Hyannis dialect by the substitution of one or two themes. (1) A small population in Osterville (dialect 2, Figure 27) replaced theme B1 with a variant of theme SP1 which included a routine derived from Yellowthroat song (Appendix C, Figure C.2). (2) A population at Doane Road (dialect 9, Figure 27) in Harwich replaced theme B1 with theme DR1 (sonogram B, Figure A.17) that ended with a derivation of a Flicker's "wicka wicka" call (Figure C.6). (3) The Long Pond dialect (7, Figure 27) retained syllables of theme B1, but substituted theme LP1 (sonogram A, Figure A.17) and C2 (sonogram B, Figure A.3) for sub-themes B2A and B2B.

Well defined, pronunciation dialects

The Hyannis dialect included the most commonly sung syllable pronunciations in the Barnstable institution. The Hyannis dialect (1, Figure 27), then, was the standard against which pronunciation variants were measured. The Dennis dialect (5, Figure 27) included the Hyannis variant of theme B2 plus pronunciation variants of themes B1A and B1B (Table 4).

Lexical and pronunciation dialects

There were four dialects that differed from the Hyannis dialect both lexically and in pronunciation. (1) The Harwich dialect (8, Figure 27) substituted theme H1, a derivative of Yellowthroat song (Figure C.1), for theme B1B, and sang a

pronunciation variant of theme B2. Dialect 8a included a different variant of theme B2 with theme H1. (2) The Herring Brook dialect (6, Figure 27) substituted a theme derived from Goldfinch song (Figure C.4) for theme B1A and sang a pronunciation variant of theme B1B. (3) The Yarmouth dialect (4, Figure 27) substituted many syllables that appeared to be derived from a Downy Woodpecker call into theme B1A (Figure C.5), changing theme B1A into theme YM1 (sonogram B, Figure A.15), and sang pronunciation variants of themes B2 and B1B. (4) The Phyllis Lane dialect (3, Figure 27) substituted theme PL1 (sonogram A, Figure A.15) for theme B1A and sang pronunciation variants of themes B2 and B1B.

Populations sharing songs with other song institutions

Two populations in the western portion of this region (shaded areas A and B, Figure 27) were more culturally related to the Mashpee institution. These populations sang only one Barnstable theme and two (population B) or three (population A) Mashpee themes. Several populations in the eastern portion of this region (shaded areas C, D, and E, Figure 27) were part of the Chatham song institution. Although they each sang portions of one Barnstable theme, the repertoires of these populations included two Chatham themes.

The Falmouth Institution: Poorly defined pronunciation dialects.

The Falmouth song institution was found at the base of the inner cape (Figure 28). Finches were not recorded in this area until four years after they were seen regularly in Chatham (Mundinger and Hope 1982, Chapter 1). Figure 2 (based on data in Mundinger and Hope 1982) shows the progressive expansion of the winter range of House Finches along coastal New England in the late 1960s. Because of this pattern of expansion, the songs of the Falmouth institution may have been culturally derived from songs along coastal New England.

Isogloss analysis of the Falmouth institution (Figures 28 and 29) indicate that most populations singing the Falmouth song institution were located at the periphery of the institution. No populations were recorded in the center of this institution's range. There were two reasons for this unusual geographical distribution of populations: (1) vegetation in the central portion of this region was composed of dense pine/oak forest which was shown by Mundinger and Hope (1982, Figure 5) to delay House Finch colonization. (2) I was not allowed access to the military installations (Otis Air Force base and the Camp Edwards Coast Guard reservation) located in the northern portion of this region. As there probably were established House Finch populations on these installations, lack of access to them may have resulted in errors in plotting routine distributions for this song institution. Since I did not know the distribution of alleles in the military installations, isogloss lines that crossed these installations appear as dashed lines in Figure 28.

Themes of the Falmouth institution were easily recognizable. The songs of local populations differed primarily in syllable pronunciation. House Finches within this song institution sang up to three sub-themes: F1A, F1B (Figure 18), and F2 (Figure A.1). Themes F1A and F1B shared several homologous syllables, but theme F1B included several syllables in addition to those shared with theme F1A (Figure 18). Populations in Wareham (north western region of the institution) and Truro (satellite) sang variants of themes F1A and F1B (Figure 19), and omitted theme F2.

In the Falmouth institution, microgeographic variation in song routines was less well defined than in the Wellfleet and Barnstable institutions. Relationships between populations were often indistinct when syllable distributions were mapped. When distributions of song routines were examined, however, cultural relationships within the Falmouth institution surfaced. In the Barnstable song institution (where dialects were based on the distribution of syllables), most syllables were widely distributed (Figure 27). In contrast, less than one half the song routines ($n = 25$ of 54 routines) sung in the Falmouth institution were recorded from more than ten of the fifty six populations (Figure 18). The remaining routines of the Falmouth institution ($n = 29$) were sung by one to ten populations (Figure 29). I analyzed routine distribution at two levels for this institution: (1) common routines, sung by more than ten populations (Figure 28) and (2) uncommon routines, sung by ten or fewer populations (Figure 29).

Separation of analysis in this manner clarified dialect relationships that were obscured when all routines were examined.

Common routines in the Falmouth song Institution

Two populations that shared the largest number of the common routines ($n = 19$ routines) were located in the town of Popponesset at the south eastern corner of the institution, nearest the Barnstable song institution (Figure 28). Many Popponesset syllable alleles sung in their routines were also shared with theme B1A of the Barnstable institution. These alleles were intermediate in pronunciation between alleles sung in theme B1A and by other populations of the Falmouth institution (Figure 28). Unlike most Falmouth populations, which included trills in theme F1A and F1B, the Popponesset populations only included a subterminal trill in theme F1B.

Moving westward and northward from Popponesset, populations sang only a subset of the common routines sung in Popponesset. Popponesset populations shared greater than one half their common routines with populations located in the southern and north-eastern areas of this institution (in the towns of Falmouth, Woods Hole, southern Bourne, and Sandwich). Popponesset populations shared less than one half their common routines with populations located along the western edge of this institution (in the towns of North Falmouth, Buzzards Bay, and Wareham, Figure 28).

The repertoires of the populations in the town of North Falmouth, Truro, and Buttermilk Bay in Wareham included small numbers of common Falmouth

institution routines (Figure 28). Most of these populations sang variants of theme F1 exclusively (F1A and F1B with and without the subterminal trill). The populations in North Falmouth comprised one dialect of the Falmouth institution, the Truro population, a second.

Uncommon routines in the Falmouth song institution

Uncommon routines had three distribution patterns in the Falmouth institution: unique, aggregated, and elongated (Figure 29). Unique routines were sung by only one population each. Routines with aggregated distributions were sung by clustered groups of populations in eastern Wareham (around Buttermilk Bay), southern Wareham (in the Wareham institution), and Sandwich. Routines with elongate distributions connected some populations in the northern portion of the institution with populations in the southern portion of the institution and other populations in the west with populations in the east.

Routines with local (aggregated and unique) distributions distinguished three additional, small dialects of the Falmouth institution: the Sandy Pond (unique), Buttermilk Bay (aggregated), and Sandwich (aggregated) dialects. Routines with elongate distributions suggested possible migration routes between the large, southern Falmouth dialect and northern populations (see Chapter eight).

Song traditions shared with other institutions

Some northern and eastern populations sang themes of the Wareham, Mashpee and Salt Marsh institutions in addition to Falmouth themes (Figure 28). In Wareham and Mashpee, Falmouth themes accounted for less than thirty

percent of the songs sung and the primary cultural relationships were with the named institution bordering the Falmouth institution. In Figure 28, populations 1 to 4 (to the west of the heavy line in Wareham, the boundary of the Wareham song institution) included about fifteen percent Falmouth song routines in their repertoires. Populations 5 to 8 (to the east of the heavy line curving northward to Sandwich from Popponesset, the boundary of the Mashpee song institution) included twenty to twenty eight percent Falmouth song routines in their repertoires. Although sixty eight percent of the repertoire of population 9 was of the Falmouth institution, population 10 sang only Salt Marsh themes.

When song similarities were looked for in coastal towns to the west of Cape Cod, an institution in Mattapoiset MA (about 15 km west of Buzzards Bay) included a possible variant of theme F1B (but no other Cape Cod themes) in its repertoire (Appendix B, sonogram B, Figure B.1), while an institution in Marion (about 8 km west of Buzzards Bay) sang a different possible variant (sonogram C, Figure B.1). In Portsmouth, RI, a theme related to theme F1A was also found (sonogram C, Figure B.3).

Summary

The Falmouth institution included six poorly defined dialects: lower Falmouth (which included Woods Hole and Popponesset), North Falmouth, Truro, Buttermilk Bay, Sandwich, and Sandy Pond in Plymouth. Populations in peripheral areas shared Falmouth themes with these dialects, but also themes

with the Wareham, Mashpee, and Salt Marsh song institutions. There were some cultural relationships with song institutions west of Cape Cod.

The Chatham Institution: non-dialects with pronunciation variants

The town of Chatham was the first Cape Cod location at which House Finches were recorded (Hill 1965, Mundinger and Hope 1982). The songs sung in Chatham are of interest because this may have been the site of the first House Finch colony on Cape Cod. The founders of this colony may have brought with them the cultural traditions that evolved into this institution (see ancestral traditions, Chapter 6). Since the arrival of House Finches on Cape Cod was almost certainly a result of jump dispersal (Mundinger and Hope 1982), the songs of the Chatham institution could have a cultural heritage with many possible institutions to the south west.

The Chatham song institution is characterized by two regional themes: C1 and C2 (Figure A.3). Isogloss analysis of the Chatham song institution indicated broad distributions for most syllables (Figure 30). Thirty seven of the fifty four syllables examined were sung by more than thirty populations. The other seventeen syllables were sung by fewer than twenty populations (twelve were sung by only one population each).

Of sixty two populations in this institution, fifty sang one or two pronunciation variants of theme C1. The twelve populations that did not sing theme C1 were located in Brewster (Figure 30). These populations included Barnstable theme B1 and/or theme B2 in their repertoires instead. The Brewster

populations thus formed a cultural intermediate between the Chatham and Barnstable song institutions. The eastern populations in Chatham, Orleans, and Eastham included both themes C1 and C2 in the repertoires of most populations.

Thirteen populations did not sing theme C2. Of these, eleven sang themes of either the Wellfleet ($n = 3$) or Barnstable ($n = 8$) song institutions with theme C1. These populations were neither geographically near each other, nor did their songs include a uniform lexicon of theme C1 syllables.

There were differences in pronunciation of some syllables across the institution. Syllables 309, 313, 315 (Figure 31), 356, 358, 363, 364 (Figure 32) exhibited distinct variation. This variation was distributed heterogeneously in a generally south to north direction across this song institution (Figures 33 and 34).

Alleles of syllables in both theme C1 and theme C2 had overlapping, non-random geographic distributions, but were sometimes randomly sung within an individual's repertoire. For example, one individual in Eastham sang songs with the following variants of syllables 309, 313, and 315.

309A 313A 315A (AAA), ACC, CBB, and CCB

A finch in Orleans sang songs with the following variants of the same syllables.

DCB, DAA, and CAA + 315B (sonogram E, Figure 31).

Thus the alternate alleles were neither separated geographically nor within an individual's repertoire.

Allelic forms of syllables in the same themes were rarely co-distributed (Figures 33 and 34). For example, syllable allele 309A had a much wider

distribution than did syllable alleles 313A and 315A. Syllable allele 309B had a much more restricted distribution than did syllable alleles 313B and 315B. Syllable alleles 309C, 313C, and 315C were distributed in about the same sized areas, but their geographic ranges differed (Figure 33). Similar differences in distribution and areas were seen for the alleles of syllables 356, 358, 363, and 364 (Figure 34). Thus the eastern portion of this institution was not divided into discrete phonological dialects.

Progressive changes in pronunciation of California House Finch songs along a transect were identified as "clinal changes" by Bitterbaum and Baptista (1979). I consider these sequences of alleles in the Chatham institution to also be clinal changes and that this institution does not have readily identifiable dialects. However, these clinal changes helped identify cultural relationships when I inferred migration routes (Chapter 7).

Cultural relationships with ancestral populations

Since Chatham was the first site on Cape Cod at which House Finches were observed (and nearby New England CBCs did not record this species until several years after they were recorded at Chatham, Munding and Hope 1982) I looked for similarities between songs of the Chatham institution and those of Long Island, and Westchester County, New York. I found suggestions of cultural relatedness in the songs sung in Chatham and Westchester County (see Appendix B and Figures B.4 through B.6).

The affinities between Chatham song themes and Westchester song themes are distant. There are similarities in a few syllables and in sequences of routines with these seemingly related syllables. The parallels between these distant populations are not as close as the similarities between the Falmouth song institution and the Mattapoiset song institution described above.

Summary

Two groups of populations singing the Chatham institution were distinguished by differences in distribution of themes C1 and C2. In Brewster (to the west), repertoires included theme C2 of the Chatham institution plus themes of the Barnstable institution. These western populations, therefore, had mixed cultural traditions. To the east, in the primary Chatham institution, repertoires included themes C1 and C2. To the north, in Eastham, populations singing the Chatham institution were interspersed with populations singing the Wellfleet institution (see the Wellfleet institution above), and some populations sang themes of both the Wellfleet and Chatham institutions. Like Brewster, these northern populations also had mixed cultural traditions. Syllable pronunciations in the core eastern portion of this institution tended to differ in a south-north direction in a clinal fashion.

There were suggestions of cultural relationships between the Chatham song institution and New York institutions. These relationships were not strong.

The Mashpee institution: non-dialects with lexical variants

In the inner and middle cape, isolated colonies of House Finches were often found encircling ponds surrounded by several square miles of unbroken woodland. Most colonies of the Mashpee song institution were isolated in this manner. Colonies were found in central Sandwich at Pimlico Pond and Spectacle Pond (PP and SP, respectively, in Figure 16). The repertoires of each of these colonies included distinctive local themes as well as themes of the Falmouth and Mashpee institutions.

Variation of Mashpee institution themes was unusually complex within local populations. Detailed analysis of microgeographic variation would be tedious for this institution, thus I describe variation within the songs of three individuals as an example of variation in the populations.

Twenty five finches were recorded at Pimlico Pond (Table 5). Six individuals sang a theme unique to this area (sonogram A, Figure A.13). The remaining nineteen birds' repertoires included material from two or three institutions: Falmouth, Mashpee, and Pimlico Pond. Although some individuals' songs were derived from themes of two song institutions (Table 6), the sequencing of routines in other birds' songs deviated from the usual sequences sung in the respective institutions (Table 7).

Two Pimlico Pond Individuals

The songs sung by bird 1 (Table 6) were derived from the Mashpee institution. The sequencing of routines in these songs, however, was altered and

the songs sounded quite different from standard Mashpee themes. Two of the songs selected (songs #4 and #7) were derived from a single, different Mashpee theme; two other songs (#14 and #15) were derived from two themes, while the remaining six songs were derived from three themes. The arrangement of song routines in the songs sung by this bird demonstrate the pattern called "combinatorial improvisation" by Marler and Peters (1982). This bird used learned routines in its songs, but arranged them in different sequences.

All songs sung by bird 2 (Table 7) were either the Pimlico Pond theme (4 songs), derived from the Mashpee institution with a Pimlico routine at the end (4 songs), or derived from two Mashpee themes (song #21). With the exception of song introductions, the sequences of routines in both themes sung by this bird were constant. The repertoire of this bird appeared to have developed as a result of reticulate evolution (see Chapter 6, borders).

A Spectacle Pond Individual

Twenty three finches were recorded at Spectacle Pond (Table 5). Two birds sang Mashpee themes exclusively. One individual sang Spectacle Pond themes (sonograms B and C, Figure A.13) exclusively. One individual sang Barnstable themes exclusively. Each of the remaining nineteen finches sang songs containing material derived from two of three song traditions: Falmouth, Mashpee, and Spectacle Pond.

Table 8 lists some examples of the sequence of routines in songs sung by one bird at Spectacle Pond. These songs were rather constant in sequence, but

only nine were derived from one institution. Six of these were the Spectacle Pond theme SP2. Eleven songs were composed of routines from one institution followed by routines from a second institution (Table 8). Thus the pattern of theme organization seen in this bird is more complex than that of the birds at Pimlico Pond. This bird's repertoire also appears to have been derived by reticulate evolution.

Summary

The intricate combinations of themes and institutional traditions recorded from most populations of the Mashpee song institution prevented differentiation of the populations into distinct dialects. There were tendencies for one set of themes to comprise a high percentage of the repertoire sung at one site and be only occasionally sung at other sites. Distributions of song traditions, at any level of organization, did not convincingly indicate dialects, however.

CHAPTER 6

RELATIONSHIPS IN

CAPE COD HOUSE FINCH SONGS:

BOUNDARY EFFECTS,

THEME SHARING, AND

FOREIGN INFLUENCES

House Finches learn their songs from other birds (Mundinger 1975). In species that learn their songs, the model for the learned songs may be the male parent or a similar appearing individual (Mann et al. 1991), neighboring adult males of the same dialect (White-crowned Sparrow, Baptista and Morton 1988), resident males in the neighborhood in which the individual settles (Brown-headed Cowbird, Rothstein & Fleischer 1987a and b), or alien species (Baylis 1982). Song institutions are cultural traditions that become established in a region (Mundinger 1980), the songs of which most individuals in that region sing. Dialects are locally distinct variations of the song institution. Hybrid songs or repertoires are often sung by individuals at the boundaries of dialects (Mundinger 1975, Baptista 1975, Baker and Thompson 1985) and song institutions (Mundinger 1975).

The purpose of this chapter is to (1) describe House Finch song institution boundaries on Cape Cod, (2) demonstrate theme sharing between song

institutions, both (A) with other Cape Cod institutions and (B) with distant institutions, and (3) illustrate the effect of songs of other species on the songs of some House Finches.

A. CULTURAL RELATIONSHIPS AT SONG INSTITUTION BOUNDARIES

Several boundary patterns between institutions have been described in the literature: (1) sharply demarcated lines, (2) reticulate evolution, and (3) variously defined hybrid zones.

Demarcation

Mundinger (1975) found House Finch song institutions on Long Island and in Westchester Co., NY, typically have boundaries sharply demarcated with one vocabulary giving way to a new vocabulary, often over a narrow zone.

Reticulate evolution

Mundinger (1980) uses the term "reticulate evolution" to describe a process in which song traditions from two institutions are blended into a new culturally hybrid institution sung by an isolated population. These new traditions continue to evolve culturally and are analogous to Short's "hybrid swarm" (1969): "hybrid populations of small to large size that are nearly or actually . . . isolated from populations of the parental forms." Reticulate evolution thus results in the formation of new institutions by cultural evolution in isolated populations.

Hybrid zones

Three patterns of song sharing have been described as hybridization. I distinguish each pattern separately.

Zones of song intergradation

Mundinger (1975) reported zones where song institutions overlap such that individuals sang hybrid songs composed of syllables from themes of contiguous adjacent institutions. These hybrid songs differed between individuals. A given population's repertoire may include several song variants which contain syllables and routines from both institutions. There may be little correlation between the songs of neighboring birds other than their shared routines were derived from neighboring institutions. The organization of hybrid songs of this nature was not constant and uniform theme sequences were not apparent. Hybrid songs produced by intergradation differ from those resulting from reticulate evolution in that intergraded songs (a) show variation in syllable sequences along a transect, and (b) the syllables closely resemble those of the original themes. In themes produced by reticulate evolution, (a) syllable sequences are less variable along transects, and (b) the syllables are usually modified from their original pronunciations, suggesting a history of isolated evolution after the original blending of cultural traditions.

Intergradation is analogous to Short's "hybrid zone" (1969) in that (a) the songs are hybrid, (b) the zone connects two parental song traditions, (c) there is a more or less gradual change from one song tradition to another as you move

across the hybrid zone, and (d) each border of the hybrid zone with the parental tradition is marked by an increase in the parental phenotype of the immediately adjacent form. On Cape Cod, intergradation zones connected adjacent institutions. Improvisation leading to reticulate evolution should not have occurred in these regions because both song traditions remained available as models in intergradation zones.

Bilingualism

A small percentage (2 to 4%) of male White-crowned Sparrows near song boundaries sang entire song repertoires from the adjacent dialects (Baptista 1975, Baker and Thompson 1985). Baptista called this phenomenon "bilingualism". When the repertoires of marked males displaying this behavior were examined in subsequent years, they dropped one dialectical repertoire (usually the one sung in lowest frequency) and retained the other. Thus bilingual individuals seemed to be in the process of replacing their original song with a newly learned local song dialect, suggesting they had recently dispersed into the new dialect region (Baptista 1975). This term describes the situation where males sing much or all of the repertoires of two institutions. Implicit in this term is the idea that a bilingual individual may be in a state of cultural transition and may, as Baptista observed, be replacing themes of a previously learned tradition with themes of a newly learned one.

Stratification zones

In many areas on Cape Cod there were large areas in which entire populations paired themes of one institution with themes of an adjacent institution. There was no blending of themes of one institution into themes of the other (therefore this was neither reticulate evolution nor intergradation). Individuals that sang themes of the two traditions were neither found in low frequency, nor did they sing complete repertoires of either institution (therefore this was not bilingualism). Rather there was an abrupt, stepwise replacement of themes at discrete boundaries. Repertoires of birds located within these regions included either themes common to populations residing on either side of the region, or themes found only within the region plus themes found outside the boundary.

I name this pattern "stratification". The typical pattern of theme sharing in stratification was that population repertoires were composed of subsets of the repertoires of adjacent institutions. The themes were retained in toto, with no intergrades as if each song in the hybrid repertoire were selected from a song "menu" from each of the adjacent institutions. These finches did not sing hybrid themes composed of mixtures of syllables or routines from two institutions (as described for individuals singing the Mashpee institution, Chapter 5). Thus syllable repertoires (vocalizations), but not song themes, of individuals within a stratified region were hybridized. The finches appeared to have made up their vocabularies from the song themes they happened to have learned.

Baker and Thompson (1985) reported a situation in the Point Reyes National Seashore in which populations of White-crowned Sparrow at dialect borders sang songs that included the complex syllable of one dialect with the simple syllable of the second dialect. These syllables best represent the core routines of White-throated Sparrow songs. Thus these hybrid songs shared routines of two dialects: e.g. routines of one song tradition replaced some (but not all) routines of another. Baker and Thompson (1985) called these areas "zones of song intergradation". I would have defined these areas as stratification zones. House Finches sing more than one song theme in their repertoires while White-crowned Sparrows sing only one. Thus stratification in White-crowned Sparrow song is on a different level (the routine) than stratification in House Finch song (the theme).

Webster (1976) defined the term *intergradation* as "transition through a series of grades, forms, or kinds that vary only by consecutive and related differences". Rather than exhibiting a series of grades in song routines, Baker and Thompson's intergrades were repertoires in which (A) a routine of one dialect was replaced in a stepwise manner by the corresponding routine of another dialect (the complex syllable) at one line while (B) another routine (the simple syllable) was replaced at another line. In most cases syllable pronunciation was not intermediate between the dialects, but abruptly changed from one form to another in the songs of the transitional populations. There was only one intermediate stage, not a series.

Baker and Thompson's (1985) data are presented in Figure 35. Overlap between dialects is identified by cross hatching within dialect borders on the map, while overlap between different introductions and endings is identified by cross hatching to the right of the map. The crosshatched regions mark the ranges of the transition populations identified by Baker and Thompson.

Since each song (and each bird's repertoire) was composed of four routines (which can be ranked as tiers of the song or strata), Baker and Thompson's (1985) data could have been presented in another manner that also shows the sequential replacement of each of the song routines. Figure 36 shows the stratification analysis for the transect including the dialects in Baker and Thompson's analysis. The shaded areas in the second and third rows (complex and simple syllables) in Figure 36 correspond to the crosshatched areas on the map in Figure 35. The shaded areas in the first and fourth rows (introductions and endings) of Figure 36 correspond to the crosshatched areas beside the map in Figure 35. The transition populations occupy regions where one song tradition overlapped another and the routines of one dialect replaced those of the other at distinct demarcation boundaries. Because of separate demarcation (not intergradation) boundaries for the several routines of this species' repertoire, I considered this method of syllable replacement as stratification.

All of the above described boundary conditions were associated with each of the four regional institutions on Cape Cod: Falmouth, Mashpee, Barnstable,

and Chatham. Each of these institutions had sharply demarcated boundaries in some locations, intergradation zones at other locations, some bilingual individuals, stratification areas, and repertoires derived by reticulate evolution in still other portions of their boundaries.

Modes of Replacement of Barnstable Institution themes - Zones of complex stratification

Here I describe stratification of typical Barnstable themes in different populations singing the Barnstable institution. Since these populations also included local themes in their repertoires, this boundary region had a diverse cultural heritage.

Figure 37 indicates the theme replacements along a fifteen mile long by one mile wide transect running west to east through the middle cape. This transect began in the Barnstable institution, extended across a region of complex stratification, and ended in the Chatham institution. Nine themes were sung along this transect. Themes B1A, B1B, and B2 (west end of the transect) were of the Barnstable institution. Themes C1A, C1B, and C2 were of the Chatham institution. Themes D1, H1, and L1 were minor themes sung in areas surrounding this transect. The pattern of theme replacement along this transect was much more complex than the replacement of song segments in White-crowned Sparrow song (Figure 35). The distribution of all themes, except themes LP1 and C1A, were disjunct along the transect. The first and fifth populations sang Barnstable themes exclusively while the sixteenth population sang Chatham themes exclusively. The

intermediate populations sang themes of one or both of these two regional institutions plus most included one or more of the local themes.

Each of the nine themes sung in this region alternated with at least one other theme in population repertoires along this transect. Alternate groups of themes were: themes B1B and D1 (B1B/D1), themes B2 and C2 (B2/C2), themes B1A, H1, and C1B (B1A/H1/C1B), and themes C1A and LP1 (C1A/LP1).

Populations in the eastern and western portions of this transect sang strikingly different theme complexes. The double vertical line in Figure 37. marks a narrow boundary between populations 6 and 7 which separated populations which sang B1B/D1, B2, and B1A, from populations which sang B1B, B2/C2, H1/C1B, and LP1/C1A/ Themes D1 and B1A were not sung east of this location. Themes H1, LP1, C1A, and C2 were not sung west of this position. Although themes B1B and B2 were sung on both sides of this boundary, only 25% of the populations that sang B1B were west of the point and only 33% of the populations that sang B2 were east of the point. This distribution of song themes seemed to be a result of historical migratory events and is further treated in Chapter seven.

Theme D1 of populations 3, 4 and 6 was a pronunciation variant of theme B1B of the Barnstable institution. Several syllables in theme H1 seemed to be derived from the song of a Yellowthroat. Theme LP1 appeared to be unrelated to other Cape Cod themes. The repertoires of populations 8, 10, and 12 through 15 included themes of both the Barnstable and Chatham institutions, and thus these populations were culturally transitional between these two song institutions.

The distance separating some differing theme complexes in Figure 37. were small. Populations 2 and 3 were found on adjacent parallel streets, separated by about 200 feet of wooded suburban yard. Populations 6 and 7, separated by a major boundary, were found on the south and north sides of a tidal creek and were separated by about 150 feet of salt marsh. Populations 10 and 11 were found in adjacent suburban yards. Several times singing individuals of one of these populations would leave a perch to be replaced by singing individuals of the other population. At other times members of one population would be singing on a perch while members of the other population were singing less than thirty meters away. Thus the effective ranges of several populations overlapped at the sites I recorded their repertoires.

The distribution of song themes in the eastern portion of the Barnstable song institution was extremely complex and suggested a historical pattern of multiple jump dispersals, either from a neighboring (Mashpee, Barnstable, or Chatham) institution or from an unknown source (the Yarmouth dialect). The complexity of this region's song pattern distributions resembled that of the "fragmentation zone" of central Africa in which hundreds of languages are sung in a small geographic area (Greenberg 1966, Gregersen 1977). Greenberg (1966) also interpreted the language distributions in Africa as originating from multiple colonizations (jump dispersals) followed later by diffusive dispersal.

Modes of Replacement of Falmouth Institution Themes by Songs of Other Institutions - A case study

In the preceding section, I demonstrated (1) that themes of the Barnstable and the Chatham song institutions are separated by zones of stratification. Here I present a detailed account of the distribution of another song institution, Falmouth, and describe the patterns of theme replacement at the edges of its range. I selected the Falmouth institution because most of its boundary patterns were distinct and small. For the other institutions, most boundary regions included more than one pattern of theme replacement.

The Falmouth institution was bounded by the Wareham institution in the north-west portion of its range, the Sandwich institution in the north portion of its range, the Mashpee institution in the eastern portion of its range, and the sea in the southern and western portions of the range (Figure 4). Variants of theme F1A were sung in the Barnstable institution as sub-themes B1A and B1B (see below, Sharing themes). Since sub-theme B1A as sung in the western portion of the Barnstable institution was nearly indistinguishable from theme F1A as sung in the eastern portion of the Falmouth institution, I treat it here as a variant of theme F1A. Songs in all areas of the Falmouth institution were recorded in both 1985 and 1986. Themes remained constant within this song tradition over the two years.

Here I describe three modes of theme replacement along transects located at different boundaries (Figure 38). The selections were made because they exhibit variation in theme replacement at this institution's boundaries.

Falmouth/Mashpee boundary - sharp demarcation

This crescent shaped transect extends from sectors 2605 and 2813 in Falmouth to sectors 4722 and 4719 in Barnstable (FM in Figure 38). Fifty two House Finches were recorded in seventeen sectors in this transect. Table 9 indicates the cultural relationships of the themes sung in each of the 17 map sectors making up this transect. Twenty four individuals sang Falmouth themes exclusively. Eighteen birds sang Mashpee themes exclusively. Three individuals sang only local themes. One bird sang one Mashpee theme and one local theme. No finches sang both Falmouth and Mashpee themes. Of the twenty two birds recorded directly on the border between these institutions (sectors 3608 - 3912), no finches sang themes of two institutions. The two song traditions are sharply demarcated at this boundary.

Falmouth/Sandwich boundary - a zone of intergradation

This transect extends from sectors 3231 and 2936 in Bourne to sector 3731 in Sandwich (FS in Figure 38). Along this transect the Falmouth institution borders the minor, Sandwich, institution and the local, Salt Marsh, institution. Forty finches were recorded in nine sectors (Table 10).

Eleven finches sang Falmouth themes exclusively. Two individuals sang Sandwich themes exclusively. Seven individuals sang Salt Marsh themes exclusively. Eighteen birds sang themes of both the Falmouth and Sandwich institutions. Two birds sang both Falmouth and Salt Marsh themes. Many of the songs sung by the birds that sang two institutions were hybrid songs including

syllables and routines of both institutions. There was little consistency of syllable sequencing in these hybrid songs. The song patterns are typical of those found in an intergraded hybrid zone.

Falmouth/Barnstable boundary - song stratification

This transect extends from sectors 4230 and 4429 in Barnstable to sectors 4719 and 4722 in Barnstable (FB in Figure 38). Thirty two birds were recorded in twelve sectors (Table 11).

Fourteen of the finches sang Barnstable themes exclusively, thirteen of these were located in the north-western portion of the transect. This area is nearest the boundary of the Falmouth institution. One bird sang two Mashpee themes M5 and M1 exclusively.

Fifteen finches sang a variant of theme B1A (here identified as F1) that was derived from the Falmouth theme F1 with the other Barnstable themes. Twelve of these were located in the south eastern portion of the transect, at least five miles from the nearest populations singing the Falmouth song institution. Two individuals sang Mashpee themes with the Falmouth variant of theme F1. Figure 14 shows that the Barnstable derivative of theme F1 (B1A) is sung throughout the (primarily) southern portions of Barnstable, Yarmouth, Dennis, and Harwich. This theme's routines were characteristic throughout this entire region. The transect presents an example of song stratification where Falmouth theme F1 was incorporated into the repertoire of the (incipient) Barnstable song institution.

Summary

Vocal interaction patterns between birds were not the same at all boundaries. Different populations of birds responded to birds singing other song traditions in different fashions. The modes of replacement of song institution themes at institution boundaries included each of the five described patterns: demarcation (sharp boundaries), intergradation zones (routine substitution with little cultural evolution), bilingualism (mixed routine and theme substitution), stratification (theme substitution), and reticulate evolution (routine substitution with cultural evolution).

Isolated colonies, such as Pimlico Pond and Spectacle Pond, demonstrated reticulate evolution and bilingualism more than other boundary regions. Other boundary regions developed intergradation zones, became sharply demarcated, or exhibited stratification with other institutions.

B. THEME SHARING

Each of the regional song institutions included distinctive themes in their repertoires. Notwithstanding, portions of several song themes were shared between song institutions .

Influence of Other Cape Cod populations

Mundinger (1975) found instances of at least partial sharing of themes across song institutions. For different populations, he attributed this sharing to reticulate evolution, improvisation after jump dispersal, and intergradation. On

Cape Cod, I found sharing of themes at institutional borders to be the norm (see "borders" above), and a given theme of one song institution was often culturally related to a theme of an adjacent institution.

Both themes of the Barnstable song institution (B1 and B2) were related to adjacent institutions. Theme B1 was culturally related to theme F1 of the Falmouth institution, while theme B2 was culturally related to both theme C2 of the Chatham institution and theme W1 of the Wellfleet institution. Figure B.7 (Appendix B) portrays similarities between theme B1 and theme F1 and theme PS1, sung in Portsmouth, RI. A technical analysis of culturally related themes from different institutions follows.

Themes F1, B1, and PS1: case study #1

Since these themes were similar, yet sung in different song institutions, the first identifying digit of the syllables identified the institution (e.g. 1xx = Falmouth, 2xx = Barnstable, 3xx = Chatham, 5xx = Wellfleet), while the second two digits identified the syllable type (e.g., x06 represents one syllable in a series, x07 a second, and x08 a third). Since Portsmouth was not in the study area, its syllables are identified with a S in the first digit's position. Syllables x06, x07, and x09 were sung in all of the themes and their sub-themes (F1A, F1B, B1A, B1B, and PS1). Syllable x08 was sung in sub-themes F1B, F1A, and B1B. In theme F1A, syllable x16 was inserted after syllable x06. Syllable x16 was also sung after

syllable x06 in sub themes B1A and B1B, and in theme PS1¹. Barnstable sub-theme B1B often included a more complex introduction (sonogram C, Figure 20). Pronunciation differences and the presence of syllable 208, however, were sufficient to distinguish between theme B1A and B1B.

Themes C2, B2, and W1: case study #2

Figure 39 shows the similarities between theme B2 and themes C2 and W1. The routine x34 x35 x36 was sung in each of the themes. The Wellfleet theme inserted syllable 540. Syllable x37 was probably modified to syllable 501 in Wellfleet. In the Barnstable theme, syllables 238 and 251 were inserted after 237. These syllables distinguished Barnstable theme B2 from Chatham theme C2. Syllable 238 was probably modified to syllable 502 in the Wellfleet theme. Syllable 251 was modified to syllable 503. Syllables x58 and x63 were not sung in Wellfleet. Syllable x59 and x64 may have been modified to form syllables 504 and 505. Syllable 821.6 was modified as syllables 821.3 and 821(506) in Barnstable and Wellfleet, respectively. The three forms of syllable 822 were more conservative modifications. Syllables 931, 932, and 933 were included in the songs of both Chatham and Barnstable, but were absent from Wellfleet. Individuals singing the Barnstable theme often replaced syllables 932 and 933 with the sequence 981 and 982, then sang another song theme (usually theme B1A).

¹Although the trill composed of syllables 110 and 111 was found only in Falmouth songs, a trill of two to five repetitions of syllable 931 (having different derivation from syllable 110) was sung in Barnstable theme B2(see routine bEM, Figure 21, and Figure 39).

Themes C1 and W2: case study #3

Figure 40 compares theme C1 of the Chatham institution with theme W2 of the Wellfleet institution. There were three homologous syllables shared between these themes: x20, x16, and 906. Theme W2 shared syllables 534 to 540 and 505.1 to 822 with theme B2 and W1 (discussed above).

In sum, Each group of related themes (F1-B1-PS1 and C1-B2-W1) contained common syllables sung with pronunciation variations. Theme B2 included several syllables in addition to those it shared with theme C2. Themes F1 and B1B included several syllables in addition to those they shared with theme B1A. Thus the themes of the Barnstable institution were related to two of the three neighboring institutions and a distant institution.

The introductory and core syllables of theme W1 were more similar to those of Barnstable theme B2 than to Chatham theme C1. Theme W2 of the Wellfleet song institution shared a trill and ending syllables with theme C2 of the Chatham institution.

The Truro population shared most of its syllables with themes F1A and F1B as sung in southern Falmouth. The themes sung in Truro were so similar to those sung in Falmouth that the repertoire of the disjunct Truro population was classified as a dialect of the Falmouth institution (Chapter 4).

Song themes of the Provincetown population included a few syllables and routines from each of the Falmouth, Chatham, Wellfleet, and Barnstable institutions. The songs of this population appeared to have been derived by

reticulate evolution, combining syllables from themes from each of these institutions. Some Provincetown themes were also intergraded with the themes sung in the Truro dialect along their common border.

Ancestral influences of off-cape populations

"I will sing of the mercies of the Lord forever.

With my mouth will I make known thy faithfulness to all generations. . . ." (Psalm 89)

The populations that founded Cape Cod colonies were probably derived from populations that arose in New York or locations along the New England coast. For this reason, I examined the songs of coastal New England towns and New York song institutions for similarities in syllables and routines. There were several populations that sang one or more songs similar to those found on Cape Cod.

Similarities with off-Cape populations: Ancestral Patterns

House Finch populations disperse by both diffusion and jump dispersal (Mundinger and Hope 1982). I expected colonies originating from an established song institution to sing songs similar to those of the source population. Thus I sampled the songs of several coastal New England House Finch populations in an attempt to locate populations singing songs similar to those sung by Cape Cod populations. Although most of the themes I recorded differed from Cape Cod themes, a few populations sang recognizable variants of themes also sung on Cape Cod. The closest population was located in Marian, about 5 km from

Bourne, the base of Cape Cod. Two other off-cape populations were located in Plymouth and Mattapoiset, within 35 km of Bourne. More distant populations were located in Portsmouth and Newport, RI, about 75 km from Bourne. Still further off, others were located in East Lyme, New London county, CT (about 200 km), and Farmingdale, NY (about 350 km). Technical comparisons of sonograms of these themes with those of Cape Cod songs are found in Appendix B: Marian (Figure B.1), Plymouth (Figure B.4), Mattapoiset (Figure B.1), Portsmouth, RI (Figure B.2), Newport, RI (Figure B.3), East Lyme, CT (Figure B.3), Farmingdale, NY (Figure B.3).

I also compared Cape Cod song themes with themes published by Mundinger (1982): Peningo (Figure B.5), Harrison (Figure B.6), and Larchmont (Figure B.7). Song patterns of Chatham finches were distantly related to these metropolitan New York patterns. The resemblances between New York patterns and eastern Cape Cod (Chatham) patterns were on a much lower level than relationships between western Cape Cod (Wareham, Falmouth, and Barnstable) patterns and other populations above. Technical comparisons of similarities between Cape Cod song patterns and those of distant populations are found in Appendix B.

Each of the off cape populations sang only one theme in common with its paired Cape Cod population. The repertoires of each member of a population pair contained themes unrelated to themes sung by the other member of the pair. These song distribution patterns suggested that some colonizers

either learned only a portion of their source population's repertoires or substituted new material for part of their learned repertoires after dispersal.

Themes of the Chatham institution included phrasing and syllable pronunciations that appeared to be related to Long Island songs - notably themes recorded by Mundinger (1975) in Peningo (or Mamaroneck), Harrison, and Larchmont, N.Y. (Appendix B, Figures B.4 to B.7). Sequences of possibly homologous syllables sung in Chatham were similar to syllable sequences in metropolitan NY songs, although there were deletions, insertions, and substitutions.

Summary

Taken individually, the similarities seen between any of the Cape Cod themes and off-Cape themes could be explained as convergence. As a group, however, they suggested a cultural connection between House Finch songs sung on Cape Cod and those sung in several localities scattered in south-eastern New England.

Foreign influences

"O sing unto the Lord a new song; sing unto the Lord all the earth. . . ." (Psalm 96)

Payne, et al. (1988) noted that a population of House Finches in Illinois included some trills and routines of Canary song in its repertoire. Mundinger (personal communication) found a population of House Finches in Cairo, New York, for which individual repertoires were seemingly based on Cardinal song and included trills in their themes. I found trills to be common in Cape Cod House

Finch song (Chapter 4), often resembling Cardinal, Goldfinch, Song Sparrow, or Yellow Warbler songs in tempo, pronunciation, or frequencies. Many authors have shown that individuals of normally non-mimetic bird species may adopt the songs of other species (Buffon 1791, Rennie 1833, Witchell 1896, Hartshorne 1973, Baylis 1982, McNair and Forster 1983, McNair 1985, Payne et al. 1988). I found numerous examples of House Finches on Cape Code mimicking syllables or routines of other species as part of their songs, but, like Payne et al. (1988), found no examples where the finches mimicked entire songs of other species. A detailed comparison of the songs of Cape Cod House Finch songs with the songs of their possible models is found in Appendix C. Several Cape Cod populations sang songs that appeared to be influenced by the vocalizations of other species.

The list of probable model species from which the finches copied is extensive: Yellowthroat, Geothlypis trichas (Figures C.1 and C.2); Ovenbird, Seiurus aurocapillus, (Figure C.3); Purple Finch, Carpodacus purpurea (Figure C.3); Goldfinch, Spinus tristis (Figure C.4); Downy Woodpecker, Picoides pubescens (Figure C.5); Common Flicker, Colaptes auratus (Figures C.5 and C.6); Indigo Bunting, Passerina cyanea (Figure C.7); Song Sparrow (Figure C.8); Cardinal, Cardinalis cardinalis (Figure C.9); and possibly Yellow Warbler (Figure C.10). Most routines that were borrowed from other species were derived from the song of the model species, but with the Flicker and Downy Woodpecker, call notes were copied. In almost every alien-derived House Finch song, the

mimicked pattern was trilled, as it was in the alien model. See Appendix C for technical comparisons of House Finch songs with songs of these other species.

House Finch renditions of alien patterns were neither note-to-note matches (pronounced the same) nor sung at the same frequencies as the models. Witchell (1896), Baylis (1982), and Payne et al. (1988) described similar improvisations on model song by mimics. Often the unusual patterns, inter-note timings, and overall sounds of the finch songs were only suggestive of those of the alien models.

Witchell (1896) and Baylis (1982) noted that included alien materials were usually found at the end of songs. I found that the mimicked portions of House Finch themes were usually followed by syllables and/or buzzy ending routines typical of finch songs. The only apparently mimicked elements of House Finch song that were found at or near the end of House Finch songs were trills. These trills were sometimes close copies of Cardinal trills, and, although they sometimes ended the song, they still were usually followed by typical House Finch ending routines. Still other alien-derived routines were found in the introductions. Alien-derived material was rarely in the core of House Finch songs.

Except for themes including trills similar to those of Cardinal routines, themes containing mimicked material were usually confined to smaller geographical regions than more typical House Finch themes. Included alien routines were usually degraded by replacement syllables of regional routines at the boundaries of the unusual dialects. In each case the mimicked alien routines

were included as fragments rather than being the entire theme of the song. This was noted also by Witchell (1896), Hartshorne (1973), and Payne et al. (1988).

The incidence of mimicry by House Finches was greater on Cape Cod than reported in other House Finch studies (Bitterbaum and Baptista 1979, Mundinger 1975, Payne et al. 1988). Mundinger focused on new House Finch institutions being derived from previous song traditions or by improvisation and essentially dismissed the plausibility of influence by foreign song (personal communication). Bitterbaum and Baptista (1979) did not suggest foreign influences in the songs of California House Finches. Payne et al. (1988) described the inclusion of Canary routines in a few wild House Finch songs. As in this study, Payne's group found that the Canary influence was modified and Canary elements rapidly blended into the local House Finch song traditions. The appearance of alien species' song patterns in House Finch songs may be a result of colonizers being isolated from finches singing the ancestral song patterns and so adopting local songs of other species instead (Baylis 1982).

Songs learned from non-House Finch species tended to be modified to resemble the songs of neighboring finch populations. Initially the mimicked songs do not sound like finch songs and individuals singing these song patterns are subject to social pressure from conspecifics (Baptista 1975, Nelson 1992). Since most species tend to sing species specific songs, song routines mimicked by

House Finches would be subject to improvisations² which would alter frequency, timing, and pronunciation to more closely approximate finch song (Baylis 1982).

Payne et al. (1988) described the process of modification of mimicked song by a local population of House Finches in Illinois that incorporated a song sequence from a Canary into the wild birds' repertoire. The songs of the Illinois population exhibited rapid mutation of Canary song patterns followed by their replacement with regional House Finch patterns normally sung in the area. I found the same mutation and replacement of alien-derived patterns at dialect borders of these themes.

The relatively common incidence of several different dialects that included non-House Finch songs suggests that dispersing House Finches appear to learn at least part of their song repertoires from non natal songs, perhaps from the resident population. In the case that non-House Finch songs were copied, I presume that colonizing House Finch accepted the songs of these alien species because there were no resident House Finches to learn from. Baylis (1982) called this primary mimicry. As subsequent generations of finches learned their songs from residents singing alien routines, copy errors would account for much of the dissimilarities between the mimicked songs and their original alien models.

²Baylis (1982) called the process of adoption of alien songs "primary mimicry," and the process of learning alien-derived patterns by juvenile finches from finch tutors "secondary mimicry." He noted that improvisation could occur during both primary and secondary mimicry.

Range expansion data show the House Finch is a rapidly dispersing species (Mundinger and Hope 1982, Taylor 1992). Under conditions that prevail in most parts of the US today, dispersing House Finches would now probably settle in regions that already have established populations. Immigrating finches would be under pressure to learn the local dialect or be forced out of the area. Other studies on song learning show that dispersing individuals often learned the songs of the adopted population (Baptista 1973; Baker and Jenkins 1987; Rothstein and Fleischer 1987a, 1987b; Baptista and Morton 1988).

I suggest the uncommonly high frequencies of mimicry of alien species songs may be a result of a proclivity of dispersing individuals to learn the dialect of their adopted territory. This would allow immigrants to more easily fit into the social hierarchy of their newly adopted neighbors (Rothstein and Fleischer 1987 a, b). Because of this proclivity, selective attrition of previously learned cultural traditions (Nelson 1992) and learning of local song traditions (Baptista 1973) - even though they were alien - would result in interspecific song sharing on the part of colonizing House Finches.

Adoption of alien song

Although many alien-derived patterns were modified into more House Finch-like patterns, some colonizing House Finches often seemed to retain the alien patterns, adopting the songs of other species as though they were songs of their own species. Baylis (1982) noted four hypotheses which could account for this. (1) The resemblance is due to chance. In species with large repertoires

chance alone should account for song similarities between species. (2) There are shared environmental factors which affect the songs of the two species in common. Adaptation of song to these factors may result in independently derived song similarities. (3) House Finches may adopt the songs of alien species when they imprint on the alien species' song after dispersal to a location where there is no conspecific song. (4) Juveniles raised by alien species may learn the songs of the foster species.

The number of instances of alien mimicry in House Finch song on Cape Cod, while not recognized in New York (Mundinger 1975) or California patterns (Bitterbaum and Baptista 1979), does not support the hypothesis that the resemblance of songs is a chance event. Some of the mimicked songs are sung in a wide variety of habitats from the ocean's side through suburban neighborhoods and into woodlands. The varied types of habitats occupied by finches singing an alien-derived pattern, thus, does not support the hypothesis the songs are influenced by common environmental factors. Since House Finches are not social parasites, whose offspring would be raised by other species (Bent 1968), they would not learn the song traditions of foster parents. This leaves hypothesis (3), that House Finches adopted the alien patterns after dispersal to locations void of conspecific song.

When House Finches founded colonies the founders were deprived of conspecific song because conspecifics had not yet taken up residence in the adopted locations. If founding finches were to adopt the songs of local residents,

they had nothing other than alien song to learn. Thus the deprivation hypothesis seems the most likely hypothesis to have effected the song mimicry observed in these populations.

Founding colonizers appeared to have used one or more of the following criteria when adopting non-specific vocalizations: (1) Songs sung by similar appearing birds, such as Cardinals, or Purple Finches; (2) Songs which were common in the acoustical environment, eg. those of Cardinals, Yellowthroats, Goldfinches, woodpeckers, Song Sparrows; or (3) songs which were similar to previously learned or genetically programmed patterns. At least the first two processes appear to have been used by different populations of House Finches on Cape Cod. Once adopted, a foreign species song would be modified to conform to patterns that House Finches are culturally or genetically programmed to sing (Hartshorne 1973, Baylis 1982).

Discussion

Reduction in both genetic and cultural diversity on islands occurs when the founding group leaves the source population. Secondary reduction of cultural diversity in colonizers may occur after the colonies become established. Swamp Sparrows selectively learn conspecific song when provided a choice between conspecific and alien song. This species incorporates alien song elements when not provided a choice, but only if the alien elements satisfy apparently inborn criteria (Marler and Tamura 1964). In the absence of acceptable tutoring models,

sparrows tutored with alien songs produced shorter songs than characteristic for the species. These songs were usually composed of improvised syllables.

Founding groups (A) composed of cohorts of juveniles that either (1) did not learn the songs of their natal population or (2) normally learn song after dispersal, or (B) whose repertoires became reduced by attrition and lack of transmission, would not be tutored by conspecifics other than themselves. If individuals of these groups adhere to constraints in accepting song models when learning songs (as Swamp Sparrows seem to do), they might extract from alien songs elements that meet their criteria and improvise other elements. This could result in the production of songs that are partially alien, partially improvised, and have fewer syllables when compared with songs of the source population.

Once a population incorporates routines from alien song into their repertoires, they may encounter other populations which sing more species-typical patterns. The unusual songs may be (a) retained intact, (b) incorporated into the species-typical songs (by reticulate evolution, Mundinger 1982), (c) modified to sound more like species-typical songs (Baylis 1982), or (d) be discarded. I found examples of the first three of these processes on Cape Cod, and assume the fourth process also occurred.

Song routines that were easily matched with alien songs were found in the Woods Hole (Song Sparrow) institution, and in the Harwich (Yellowthroat) and Doane Road (Yellow-shafted Flicker) dialects of the Barnstable institution. Song routines that were recognizable as being based on alien songs, yet were part of

more typical House Finch songs were found in the Plymouth Rock institution (Indigo Bunting), in the Sandwich dialect of the Falmouth institution (Yellow Warbler), and in the Osterville (Yellowthroat) and Herring Brook (Goldfinch) dialects of the Barnstable institution. Song routines that were somewhat modified from their original traditions were found in the Crosby Landing (Ovenbird and Purple Finch) institution, throughout the Yarmouth (Downy Woodpecker) dialect of the Barnstable institution, and at the peripheries of the Harwich (Yellowthroat) and Doane Road (Yellow-shafted Flicker) dialects of the Barnstable institution.

Summary

Several House Finch song themes included routines that seemed to have been modelled after the songs of alien species. Sometimes these routines closely resembled alien patterns, at other times the resemblance was less conspicuous. A possible reason why alien songs were mimicked is that some colonizing units did not bring with them previously learned or had only partially learned traditions and, when they entered song environments that were void of conspecific song, patterned their songs after those sung locally by other species.

CHAPTER 7

HISTORICAL PROCESS

AND DISPERSAL ROUTES

ON CAPE COD

Baker and Thompson (1985) used the distribution of song in bird populations to suggest historical relationships between song populations. Their interpretations of cultural relationships and colonization events were based on song distribution. These researchers used zones of intergradation and hybridization, geographic variation, and clines to make their deductions. Similar patterns of genetic distribution provided data for interpreting the process of organic evolution (Mayr 1963).

I developed a model of dispersal on Cape Cod because interpretation of historical changes in song populations of a known age may enhance our understanding of the process of cultural evolution of avian communication signals. My model is based on song variation within and among the populations of House Finches residing both on Cape Cod and along coastal New England and New York. I inferred House Finch dispersal routes from geographic patterns. Besides using criteria similar to those Baker and Thompson (1985) used for the White-crowned Sparrow in the Point Reyes National Seashore, I also compared the sizes of repertoires of related populations to determine cultural relationships. After

dispersal, populations appeared to initially reduce then secondarily increase repertoire size. Thus, there seemed to be a correlation between dispersal and repertoire size.

This chapter has two main objectives: (1) describe initial and secondary changes in repertoire size after dispersal, and (2) present the model of colonization of Cape Cod by the House Finch.

A. HISTORICAL PROCESSES:

CHANGES IN REPERTOIRE SIZE AFTER DISPERSAL

Island populations of birds have both lower genetic diversities (Barton and Charlesworth 1984) and sing reduced repertoires (Nottebohm 1969, Thielke 1973, Baptista and Johnson 1982, see review in Miller 1982, Baker and Jenkins 1987, Morton 1987, Naugler and Smith 1991) when compared with mainland populations. Reduced genetic diversity and repertoire size are often correlated with size of the island (affecting population size) and increased distance from the source population (affecting the number of dispersal events). Reduction in repertoire size of island populations, then, culturally parallels MacArthur and Wilson's distance - area thesis for colonization (1967).

Evolutionists and behaviorists have found that small founding groups bring with them only a subset of the parental population's genetic and cultural traditions. This reduces variation in both genetic and cultural traditions of colonies below those of the source populations. Besides reduced diversity, insular populations often have unique genetic and cultural traditions.

Changes in genetic diversity

The reduction of genetic diversity of founder populations (called the founder effect, Mayr 1966), is responsible for primary reduction in genetic diversity. These founder populations have higher than average frequencies of some gene alleles and lower than average frequencies of their alternate alleles. After establishment of a colony, genetic drift often causes secondary loss of other gene alleles.

In the event new alleles are formed by mutation, small population size may allow these alleles to become homozygous, and these new alleles become established more frequently in small populations than in large ones. Thus, colonies often become homozygous for some gene alleles without regard to their phenotypic fitness. This loss of heterozygosity sometimes reduces the ability of a founding colony to survive (Mayr 1966).

Changes in cultural diversity

Similar processes occur on the cultural level. If the members of founder populations are culturally related, they would bring with them relatively homogeneous cultural traditions. This reduction of the original population's traditions to a subset effects a primary reduction in cultural diversity (Nottebohm 1969). Once a colony is established, there could be a secondary reduction in cultural diversity resulting from (1) lack of use of some traditions by individuals that had learned them earlier (attrition) and (2) inability to transfer a tradition to others (Thielke 1973, Baker and Jenkins 1987). Thus for cultural traditions (as for

genetic traditions), the founder effect may be only partially responsible for reduction in diversity.

Other changes in cultural traditions would take the form of (1) miscopying (Baylis 1982, Miller 1982); (2) replacing learned traditions with improvisations (Mundinger 1980); and (3) replacing learned traditions with local, alien-derived traditions (this thesis). Small population size would allow receptive individuals to learn these altered songs and incorporate them in their repertoires. Thus old cultural traditions may rapidly become lost in new colonies even as new unique traditions become established (also without regard to their evolutionary fitness).

Although genetic and cultural diversities are similarly reduced in isolated populations, their modes of transmission differ. Individuals receive full $2N$ (diploid) complements of genetic material at conception. The size of a species' genome (genetic complement) is constant and essentially does not vary from individual to individual. On the other hand, the size of a vocabulary is not predetermined and often varies dramatically. In this study, the number of themes and sub-themes sung by individuals varied threefold from two to six, the length of themes varied fourfold from eight syllables to over forty, and the number of syllables in an individual's lexicon varied fivefold from fourteen to over seventy.

Some gene alleles are transmitted covertly without expression as hidden recessive alleles. These recessive alleles can express themselves in succeeding generations if they subsequently become homozygous. The transfer of cultural traditions, however, is overt: a tradition cannot be copied if it is not first expressed

by a model, and when a cultural tradition is no longer expressed, that tradition is dropped from the population's repertoire (Thielke 1973).

A constant feature of cultural traditions (e.g., bird song) is change (Mundinger 1980). Once a population's song repertoire has been established, it will begin to undergo change, and this change will continue throughout the span of the population's existence. Individuals miscopy learned traditions (cultural mutation), fail to learn traditions (causing attrition), copy from more than one model (producing hybrid songs or repertoires), or substitute learned or improvised (mutated) traditions for other traditions. In this study these changes resulted in both relatively stable and reduced repertoire sizes. Stable repertoires were found in some stratification zones and zones of intergradation where themes or portions of themes of similar length were substituted for each other. Reduced repertoires were typically found in satellite and dialect populations in which one or more themes of the primary institution were lost.

Some forms of change would result in additions to repertoire sizes. In this study, additions took the forms of newly improvised or copied themes (stratification) where the new theme was either added to the repertoire or replaced a shorter theme, insertion or duplication of syllables in established themes, or improvisation of new syllables from the notes of complex syllables. Sometimes these additions resulted in the evolution of one theme into a series of sub-themes (Chapter 5), in other instances the addition of themes resulted in the formation of complex population repertoires. These historical processes were sometimes

traceable when their intermediate stages were preserved in the repertoires of related populations (see Chapter 5).

Reduction of previously learned repertoire size

The shared repertoires of Cape Cod satellite and dialect populations of most song institutions exhibited reductions in numbers of themes (Table 4), numbers of syllables (Tables 12 and 13), and/or numbers of alleles per syllable when compared with their probable source populations. There were on average 27 percent reductions of primary repertoires (as measured by syllables held in common) when populations separated by less than seventy kilometers were compared (28% between satellite populations and their source institutions, Table 12; 27% between dialect populations and the primary dialect of the institution, Table 13; and 27% between local song institutions, Table 14); and a 37 percent reduction between disjunct song institutions separated by more than seventy kilometers (Table 14).

For satellite populations whose source population was identifiable, each adopted theme commonly included a subset of the original theme's lexicon. Thus when two institutions shared a theme, the institution with the smaller of the two versions of the theme was typically considered the secondary institution (but theme B2 of Barnstable had more syllables than theme C1 of Chatham - other factors indicated theme B2 was derived from Chatham, see below).

Secondary expansion of repertoire complexity

Three large, primary Cape Cod institutions (Falmouth, Barnstable, and Chatham) included themes that had evolved into sub-themes (Chapter 4). For each theme that was sung in two forms, one of the sub-themes was shared between two institutions (e.g., sub-theme F1A of Falmouth was shared as sub-theme B1A of Barnstable, and sub-theme C1A of Chatham was shared as sub-theme B2 of Barnstable). The other sub-themes were not shared between the two institutions, differed in pronunciation and lexicon from the shared sub-themes, and had on average 26 percent more syllables than the shared sub-themes (Table 15). The shared sub-themes were more conservative within an institution than the unshared sub-themes. Shared sub-themes had on average 5.2 percent more syllables than the shared core of syllables, while the unshared sub-themes were on average 33.3 percent larger than the shared core (Table 15)

Sub-themes F1A and B1A: a case study

Sub-themes of themes F1 (Falmouth) and B1 (Barnstable) were good examples of differences between institutions. Theme F1 was sung as two sub-themes (F1A and F1B), while theme B1 also had two variants (B1A and B1B). Sub-theme F1A was similar to sub-theme B1A (Figure B.1), but sub-themes F1B and B1B were not shared by the two institutions (compare sub-themes F1B, Figures 18 and 19, with sub-theme B1B, Figure 20). Sub-theme F1A shared a subterminal trill with sub-theme F1B, but this trill was not found in either sub-theme B1A or sub-theme B1B.

The dissimilar (unshared) sub-themes (F1B and B1B) differed in both pronunciation and lexicon from the shared sub-themes and each other. Sub-theme F1B included a trilled routine composed of core syllable 115 (routine FC, sonograms C, E, and G, Figure 18) that was not shared with sub-theme F1A. Additionally, the syllables shared between sub-themes F1A and F1B were sung with different pronunciations. In sub-theme B1B, syllable 208¹ was found in routine BB (sonograms B and C, Figure 20). Sub-theme B1B added introductory routine b1B and altered the pronunciation of the core syllables shared with sub-theme B1A. The pronunciation of all syllables shared by sub-themes F1A, F1B, B1A, and B1B differed. Changes in pronunciation added to repertoire complexities as the new syllable pronunciations generated new routine variants (which appeared to be the way new routines evolved in Falmouth [see syllable 106, Figure 18] and Provincetown).

The similar (shared) sub-themes (F1A and B1A) were composed of seven syllables each (Table 14) and shared no trills. Dissimilar sub-themes were composed of nine (F1B) and twelve (B1B) syllables each. These sub-themes shared three syllables, but the pronunciations of these syllables differed.

Similar differences in pronunciation, lexicon, and increase in syllable numbers were found when sub-theme C1A of the Chatham institution is compared with theme B2 of the Barnstable institution, and also when sub-theme B2 of the

¹Syllable 208 was derived from syllable 108 that was found in both the presumed primary form of theme F1 and sub-theme F1B.

Barnstable institution is compared with theme W1 of the Wellfleet institution. Thus, evidence of secondary increase in the complexity of cultural traditions is seen in the development of sub-themes in the several song institutions.²

B. DISPERSAL ROUTES

Assumptions

For this analysis I made several assumptions which are substantiated either in the literature or by findings reported in this thesis.

1. Populations with similar vocal patterns are culturally more closely related than populations with different vocal patterns (Mundinger 1980, Baker and Thompson 1985).
2. Older populations will be found over greater areas and serve as sources for colonies produced as a result of jump dispersal more frequently than populations established later. As examples of this, the southern population of the Falmouth institution and the Hyannis dialect of the Barnstable institution sing the most widely spread variants of their respective institutions.

²The population in Truro that sang theme F1 of the Falmouth institution did not follow this convention. Both sub-themes of this population were sung with similar pronunciation and fewer syllables than the same sub-themes that were sung in the source population (in North Falmouth). Since the Truro population's patterns were simpler than, and pronunciations were similar to those of the North Falmouth population's, the Truro population was considered a dialect of the Falmouth institution culturally derived from the Falmouth institution, not a separate institution.

This assumption must be used cautiously, however, as inhospitable terrain slows the ability of House Finches to disperse (Mundinger and Hope 1982). Finches were absent from unbroken forested areas (Chapters 1 and 5), and residential neighborhoods in the eastern scrub and dune areas on the Atlantic coast of the outer cape (see Chapter 1, Figure 3). Since wooded regions and areas of scrubby vegetation inhibit the spread of finches, colonies founded in open residential areas would be expected to expand more rapidly than colonies founded in dense woods or scrub.

3. New variants of routines will tend not to revert to an earlier form of that routine.

Sub-themes with pronunciation variants were found in the three primary song institutions: Falmouth, Barnstable, and Chatham. In some populations the pronunciations of the shared syllables of sub-themes were similar. In other populations these syllables were pronounced differently in sub-themes, and the alternate pronunciation forms diverged in a clinal fashion (Chapter 6).

There were several variants of one or more Barnstable themes found in the Harwich, Yarmouth, Phyllis Lane, Dennis, and Herring Brook dialects (Table 4). These variants often retained their identities at sharply demarcated boundaries - even where the Hyannis dialect or a dialect closely resembling the Hyannis dialect was also sung at the boundary.

4. A group of culturally related populations radially arranged around one population would probably have arisen by dispersal from the hub

population. The distributions of satellite (Figure 17) and dialect populations (Figure 27) of institutions were sometimes radially arranged. Typically, the songs of disjunct satellite populations were similar to those of the source populations, while songs of nearby dialect populations characteristically were dissimilar from the source population and from related dialects.

5. The repertoires of colonies established as a result of jump dispersal included fewer syllables and syllable alleles than repertoires of populations that expanded their range by diffusion. This phenomenon has repeatedly been observed in island populations of birds (Thielke 1973, Baptista and Johnson 1982, Baker and Jenkins 1987, Morton 1987, this thesis).

Macrogeographic view of dispersal routes

Colonization of each of the major (and two minor) song institutions can be traced through song pattern sharing with other institutions. The initial colonization events are presented in this section.

Chatham

The boundaries of the Chatham institution enclosed the location where House Finches were first recorded on Cape Cod in 1964 (Hill 1965, Mundinger and Hope 1982). Finches were not seen at other areas of Cape Cod until four years after they had been recorded at Chatham. Consequently, I assumed the Chatham song institution was derived from song traditions of the first colony to become established on the cape. At the time of first sighting, the nearest

Christmas Bird Censuses (CBCs) to Chatham that recorded House Finches were located at Newport, RI (about 175 km away), New London, CT. (about 300 km away), and Montauk, NY (about 350 km away).

I compared Cape Cod song patterns with songs I recorded in and near Newport, RI., and New London, Ct., and with published songs from New York and western Connecticut institutions (Mundinger 1980). Several syllables and routines of Chatham songs more closely resembled patterns characterizing institutions found in metropolitan New York and western Connecticut (Figures B.5 to B.7). Chatham patterns did not resemble patterns sung near Newport, RI., or New London, CT. This suggested that, although the patterns of Chatham songs were not identical to New York patterns, the founders of this institution were culturally related to a New York song institution.

Colonizing individuals may or may not have learned their repertoires in a metropolitan New York song institution, in which there were similar song patterns. Mundinger (1975) found some syllables of the Mamaroneck song institution were also sung by (his) institution number 16, at the tip of Long Island (see Figure 1). This indicated to him that the founders of this Long Island institution were culturally related to the Mamaroneck institution. Whether the founders of the Chatham institution dispersed from an established metropolitan New York institution like Mamaroneck or a satellite population like that on the tip of Long Island, ultimately the Chatham institution was culturally related to the established metropolitan New York tradition. This relationship is indicated in Figure 41.

Falmouth

Winter CBC records first identified House Finches in Bourne (part of the area in which the Falmouth song institution was sung) four years after they arrived in Chatham (Mundinger and Hope 1982). At the theme level, the Falmouth theme F1 was related both to the Mattapoiset theme MP1 (to the west, Figure B.1) and the Barnstable theme B1 (to the east, Figure B.2). At the syllable level, pronunciations of syllables of Falmouth theme F1B were almost identical to Mattapoiset theme MP1, while syllable patterns of Falmouth theme F1A were more closely related to those of Barnstable theme B1A than to theme MP1 of the Mattapoiset population. These similarities suggested a west-east linear relationship among the three institutions: dispersal from Mattapoiset to the Falmouth founding site; dispersal to Barnstable either from Falmouth or a second founding from Mattapoiset.

Further support of the concept of west-to-east migration comes from the eastward pattern of winter dispersal along coastal New England. Christmas Bird Census data for the colonization period showed a gradual eastward expansion of the House Finch along coastal New England (Mundinger and Hope 1982, Figure 2). This expansion suggested the Falmouth institution may have been founded

by dispersers from the west (Mattapoiset) rather than from the east (Barnstable or Chatham)³.

The combination of song patterns (Figures B.1 and B.2) and historical dispersal patterns (Figure 2) of this species supported the possibility that the Falmouth institution was derived by an eastward diffusion of finches into Falmouth. I suggest, therefore, the Falmouth institution was originally a satellite or extension of the Mattapoiset institution (Figure 41). This would make the Falmouth institution the second Cape Cod institution to become established. If so, then the Falmouth theme F1 would be a primary modification of the Mattapoiset theme, and the Barnstable theme B1 would be secondarily modified from the Falmouth theme (or a second primary modification of Mattapoiset if Barnstable was settled by a second jump dispersal from there).

Barnstable

Cultural affinities to both Chatham and Falmouth themes indicate that the Barnstable institution may have been founded when dispersers from both the east (Chatham) and west (Falmouth) settled near the town of Hyannis near the same time (Figure 42). This caused a cultural blending of these song institutions of diverse cultural histories.

³Still other suggestion of a west-to-east relationship was found in similarities between theme A1 (Wareham), metropolitan New York (Farmingdale, Long Island), and coastal New England (East Lyme, New London County, CT, and Newport, RI) themes (Figure B.3). See Appendix B for a technical analysis of these songs.

The cultural similarities linking Chatham theme C2 with Barnstable theme B2 and linking Falmouth theme F1A with Barnstable theme B1A (described in Chapter 6) are very close (Figure 39). The Barnstable institution's repertoire is, therefore, a hybrid repertoire that included a Chatham theme and a Falmouth theme. This hybridization is interpreted as an incident of stratification between the two institutions (as theme B1 was derived from theme F1 of the Falmouth institution and theme B2 was derived from theme C2 of the Chatham institution). After the early Barnstable population became established, the two Barnstable themes (B1 and B2) each evolved a sub-theme different from the original forms (Figures 20 and 21). Implications of this evolution are discussed below (microgeographic view).

Mashpee

Mashpee institution song traditions were very complex. The institution was characterized by only one theme. Although two or three themes were sung by all populations, theme M1 was the only one common to the repertoires of all populations singing this institution. Some populations included theme M4, while others sang themes M2 and M3 with theme M1. Still others sang local theme(s) with theme M1 (and sometimes themes of a neighboring institutions). The small John's Pond and Salt Marsh institutions bordered the Mashpee institution.

Most of the township of Mashpee and parts of southern Sandwich were forested with several isolated residential neighborhoods at Spectacle Pond, Pimlico Pond, John's Pond, and near the Mashpee town hall in central Mashpee

(Figure 43). Each of these neighborhoods contained populations of House Finches that sang one or more unique themes in addition to the shared M1 theme. The population in central Mashpee, near the town hall, inhabited a moderately large residential area. Presumably, this optimal habitat type allowed the central Mashpee population to expand rapidly after its initial founding. The other Mashpee populations were found in geographically small residential areas enclosed by woodland.

Finch populations in coastal areas of Mashpee generally sang the Falmouth institution, but finches on the northern end of the Popponesset peninsula (Figure 43) sang Mashpee themes M1, M2, and M3. That boundary between the Falmouth and Mashpee institutions was sharply demarcated (Table 9)

The high levels of endemism in song themes in this institution suggested that each of the residential areas was colonized by a cohort of finches that established distinct, highly localized institutions. Presumably, dispersing groups from the central Mashpee population secondarily settled in areas that had previously been colonized at John's, Spectacle, and Pimlico Ponds (arrows from MC leading to JP, SP, and PP, Figure 43). Populations at John's Pond, Spectacle Pond, and Pimlico Pond, therefore, sang traditions from both the Mashpee institution and the respective local institution.

Two of these secondary colonizations (Spectacle and Pimlico Ponds) partially replaced the previously established local traditions. The song repertoires of individuals recorded at these sites were sometimes based solely on the local

institution. In other instances, the repertoire was a blend of stratified and intergraded songs including portions of both the local and Mashpee patterns (Table 7). Sometimes a repertoire was derived solely from the Mashpee institution, although there were alterations in routine sequencing (Table 6).

At the other two sites (John's Pond and Popponesset peninsula) the Mashpee institution spread and met other populations singing other traditions along sharply demarcated boundaries. At these sites, then, hybridization of traditions had not occurred.

Wellfleet

The Wellfleet institution was culturally intermediate between the Barnstable and Chatham institutions. Versions of themes B2 and C2 were included in the repertoire. Theme W1 of the Wellfleet institution seemed more culturally related to the Barnstable institution than to the Chatham institution (Figure 39). Theme W2 contained two syllables (520 and 516) that were part of the Chatham repertoire (320 and 316), but were not sung in the Barnstable institution (Figure 40).

The Wellfleet repertoire did not include theme B1, but two individuals in the northern dialect of the Wellfleet institution sang theme F1. Pronunciation and lexicon of theme F1 sung by these Wellfleet birds were identical to the theme as sung by the Truro dialect of the Falmouth institution. Theme F1 of the Truro dialect did not resemble theme B1 as sung in Barnstable (which was also derived from theme F1). I surmised, therefore, that the inclusion of theme F1 in the

Wellfleet repertoire was a result of secondary contact with the Truro dialect of the Falmouth institution, and that this theme had not been part of the repertoire of the original founders.

Three alternative scenarios could account for the inclusion of themes of both the Barnstable and Chatham institutions in the Wellfleet repertoire: (1) individuals from both the Barnstable and Chatham institutions colonized Wellfleet, (2) the founders of the Wellfleet institution were derived from the population (or a similar one) that founded the Barnstable institution - possibly at or near the time the Barnstable institution was founded, either before (more likely) or after theme B1 was added to the Barnstable repertoire (recall that Wellfleet birds do not sing theme B1); or (3) Barnstable/Chatham hybrids founded the Wellfleet institution.

Pronunciation and lexical relationships of the Wellfleet themes were closer to Barnstable traditions than to Chatham traditions. Although the first scenario cannot be ruled out, syllable relationships pointed to the second scenario. The third scenario probably did not result in formation of the Wellfleet institution for reasons that follow. Consequently, I suggest the Wellfleet institution was founded by a cohort from the newly formed Barnstable institution (Figure 43).

Although the few individuals singing this institution were not geographically wide spread, which might suggest a relatively recent colonization, the time of colonization of the Wellfleet institution was difficult to determine for several reasons. First, the town of Wellfleet was surrounded by inhospitable terrain which may limit subsequent spread (Mundinger and Hope 1982, Chapter 5 this thesis).

Second, at the time of my data collection, the Wellfleet institution had differentiated into two distinct dialects: a relatively large one in Wellfleet and a smaller one in Truro, and a less distinct sub-dialect in Eastham. In addition, Wellfleet themes had evolved into distinct forms (Figures 24 and 25). Also, the Chatham institution and the Wellfleet institution were both sung in a reticulate hybrid zone in northern Eastham (Figure 23) with both traditions retaining their identities. All of these processes require some time to evolve. Thus, this institution was probably founded early in the history of the House Finch on Cape Cod.

Truro

The Truro population was considered a dialect of the Falmouth institution (Figure 44). The songs sung there at the time of my data collection were good representatives of sub-themes F1A and F1B. Since (A) the population size was small (I found less than 50 singing individuals) and (B) the songs had not diverged to any extent from their parental forms in Falmouth, I concluded this population had only recently dispersed from the parental population.

Provincetown

Cultural relationships of the population located in Provincetown were very complex. Individuals were found there that sang examples of all the regional institutions except Mashpee, plus the Wellfleet institution and two themes I did not find models for. Thematic relationships of this population were such that some individuals sang primarily a stratified repertoire while others sang reticulate

(hybrid) themes incorporating routines from more than one institution (theme P1, sonogram C, Figure A.9).

Individuals of diverse cultural heritages may have settled in Provincetown several times (Figure 44), and will probably continue to do so for some time. Since Provincetown is at the very end of Cape Cod, fall and winter dispersers from the south and western parts of the cape would have to settle there or retrace their outward route back to the south the following spring. If the birds have spent some time looking for a place to settle, and were still in Provincetown as the breeding season commenced, it would make sense for them to stop there.

Summary

There were two types of cultural complexes on Cape Cod: those derived from (nearly) homogenous cultural backgrounds with one (or at most two) cultural tradition(s), and those derived from a heterogenous cultural background (multiple source traditions). The first colonization events were of the homogeneous type. Later colonizations were often heterogenous.

Finches with cultural affinities to New York probably jump dispersed to Chatham, Cape Cod about 1965. This was followed less than five years later by dispersal of finches from Mattapoiset to Falmouth. Cultural traditions of these early colonies differed and each derived a unique song institution. Soon after these populations became established, emigrants from both institutions met in central Barnstable (near the town of Hyannis). The resulting hybrid cultural tradition evolved into the Barnstable institution which retained affinities to both

parental song institutions (theme B2 resembled theme C1 from Chatham, and theme B1 resembled theme F1 from Falmouth). Some finches dispersed from Barnstable to Wellfleet after the Barnstable theme B1 evolved from theme C1, but before theme C2 was completely dropped from the Barnstable population's repertoire.

Multiple colonizations in Dennis, Brewster, Harwich, and Mashpee generated many unique local institutions. The Hyannis dialect of the Barnstable institution hybridized with several of these, producing the zones of complex stratification seen in the eastern part of that institution. An institution in central Mashpee hybridized with two isolated institutions (at Spectacle Pond and Pimlico Pond), forming a second complex cultural system. Multiple immigration events in Provincetown with successive waves of reticulate evolution resulted in yet another complex system of hybridization at the tip of Cape Cod.

Microgeographic view of dispersal routes

Within song institutions there was variation in the patterns of dispersal. Here I discuss dispersal within the three early, large song institutions: Chatham, Falmouth, and Barnstable. These institutions are described in the sequence suggested by the chronology of the macrogeographic model.

Chatham institution

The most probable scenario for the colonization of the Chatham institution is that this song tradition became established in the town of Chatham and rapidly diffused outward in all directions wherever there was suitable terrain. At the time

of colonization, densely forested regions in Brewster and Harwich and scrub dune vegetation in northern Orleans and Eastham would have restricted diffusion (as these regions continued to do in central portions of the inner and middle cape, and the outer cape in the 1980s). It was not until the late 1970s that a surge of new construction began on Cape Cod⁴ and made available for colonization tracts that were previously inhospitable.

Distributions of syllable alleles of Chatham themes (Figures 33 and 34) suggested the original colony may have rapidly established two sub-populations (Figure 45A), each of which developed its own sub-dialect founded on pronunciation variants of theme C1 (which in this thesis are called sub-themes C1A and C1B). Subsequently these sub-populations seemed to meet with one apparently divided by the second. Presumably, the "divided" population was pushed to the north into Eastham and to the south into Harwich (Figure 45B) as the other population spread west.

A successful satellite population also seemed to migrate by jump dispersal into or near the town of Hyannis in Barnstable (Figure 42). This satellite population, then, became established in the largely residential southern portion of Cape Cod and, together with birds from Falmouth, formed the nucleus of the new Barnstable institution.

⁴Many neighborhoods in Brewster and Harwich were under construction in 1985 and 1986.

I frequently recorded birds with the sounds of hammers and staple guns in the background.

Secondary spread of the Chatham institution probably occurred at a later time. Populations singing Chatham traditions diffused into eastern Harwich and Brewster meeting with others singing Barnstable traditions even as these wooded regions were being converted into newly established residential neighborhoods. Other populations moved northward through Orleans and Eastham where they met members of the Wellfleet institution (Figures 23 and 30). In each of the mixed colonies, the population repertoires were stratified (e.g. they contained song themes of both the Chatham and Barnstable institutions in the townships of Brewster and Harwich, and the Chatham and Wellfleet institutions in the township of Eastham).

Satellite populations of the Chatham institution were also recorded at the western boundary of the Barnstable institution and in Dennis (Figure 17). In both of these locations individuals singing the Chatham institution were heard countersinging with individuals singing the Barnstable institution.

There was a distinct Chatham influence in Provincetown. A few individuals in Provincetown sang modified Chatham themes. In some neighborhoods, these themes had undergone reticulate evolution with other traditions, while in other neighborhoods one or more themes were based entirely on Chatham traditions. Since there was more than one pattern of theme organization, Provincetown seemed to have received more than one dispersing group from Chatham.

In summary, the Chatham institution increased during an early period of diffusive spread into available habitat. Some finches travelled more than forty

kilometers and established new colonies in Barnstable, Sandwich, and Dennis. Others dispersed to Provincetown where they settled alongside dispersers from other institutions. No other populations singing modified Chatham themes were found. As new construction resumed in the 1970s dispersers from this institution were again able to find suitable terrain. The cultural traditions of many of these new colonies were mixed. It is possible they were founded almost simultaneously by individuals singing other traditions (the Barnstable institution, in the middle cape, the Wellfleet institution, in the outer cape).

Falmouth institution

The founders of the Falmouth institution probably dispersed from coastal Massachusetts between 1968 and 1970 (Mundinger and Hope 1982). Analysis of the songs of the Falmouth institution suggest the original colony may have been centered in the town of North Falmouth (Figure 41). There are several reasons for this deduction.

- (1) The lexicon and pronunciation of the Falmouth sub-themes of theme F1, as sung in North Falmouth, were similar to those of the Mattapoiset theme MP1. The songs of North Falmouth contained only a few routine variants. This is somewhat misleading because it could be interpreted that the populations making up this dialect did not have a full repertoire of themes. The North Falmouth populations sang both themes F1A and F1B, but with little variation in pronunciation.

- (2) The version of theme F2 sung in North Falmouth was uniformly sung with a subterminal routine borrowed from theme F1. Thus, although the North Falmouth populations sang fewer routine variants, their repertoires included the full complement of Falmouth themes.
- (3) Repertoires were enriched and variable (with individuals singing more than one set of routines for the same sub-theme) in all other areas of the Falmouth institution (Figures 28 and 29). Most populations sang separate routine variants for sub-themes F1A and F1B. Since the routine variants of all themes sung by other populations usually differed from those in North Falmouth, there were few shared isoglosses between these populations and North Falmouth.
- (4) Finally, only one of twenty nine rare routine variants was sung by one of the North Falmouth populations. This suggests themes sung in areas other than North Falmouth had undergone secondary enrichment through song drift, improvisation, and incorporating the traditions of other populations.

The picture in North Falmouth was that the colony founded in this region diffused along the coast, establishing several sub-populations (Figure 42). Syllable pronunciations of each sub-population varied slightly from pronunciations of other groups. Within the repertoires of a sub-population, however, the sub-themes were generally similar (each local population sang the shared syllables with similar pronunciations).

As the North Falmouth tradition diffused southward, birds settled in Woods Hole and then moved eastward along the southern shore to the town of Falmouth. This coastal expansion continued eastward until the entire town of Falmouth and coastal areas of the Mashpee township were populated. The eastward diffusion of finches singing Falmouth traditions stopped at the Popponesset peninsula (PP1 and PP2, Figure 28; Figure 42 [macrogeographically]; and Figure 46 [microgeographically]), where they met others singing Mashpee traditions.

It appeared that a cohort from the town of Falmouth or Popponesset area migrated by jump dispersal to Hyannis almost simultaneously with a group from the Chatham institution (Figure 42). Finally some diffusion occurred northward from North Falmouth into the southern coastal portion of the Bourne township (Figure 46). Song patterns of North Falmouth and southern portions of Bourne are related through several rare variants of syllables (but not routines).

A small colony was established at Buttermilk Bay in northern Wareham (Figure 46). Since there were few pronunciation similarities between the themes sung at Buttermilk Bay and those sung elsewhere in the Falmouth institution (sonograms C and D, Figure 19), it seemed this colony had been isolated for some time before secondary contact with other members of the Falmouth institution. There was no way to tell if the Buttermilk Bay colony had originally been derived from the Falmouth or Mattapoiset institutions.

Other instances of jump dispersal occurred somewhat later. Separate colonies were settled in Bourne and Sandwich from southern Falmouth

populations (Figure 46). Several rare routine variants tie Bourne and Sandwich to southern Falmouth populations. The two northern colonies' pronunciations and lexicons of theme F2 differ such that the Sandwich population seemed more closely related to populations on the south shore (peninsular region of Falmouth or Popponesset), while the Bourne population's relationships were closer to the area just north of Woods Hole. Sandwich song patterns hybridized with patterns of a population singing another institution to the north (the Sandwich institution, SG, Figure 46), forming an integrated zone. The Bourne colony hybridized with a population singing the Wareham institution from the west (WH, Figure 46) and these traditions became stratified in the town of Wareham (populations 1 to 4, Figure 28).

A satellite dialect of the Falmouth institution was found in Truro (Chapter 4). Since pronunciation and lexicon of the songs in the Truro dialect were similar to those of the North Falmouth dialect, and syllable pronunciation of the syllables shared by sub-themes F1A and F1B were similar, I inferred the founding cohort for the Truro dialect dispersed from North Falmouth (Figure 44).

Barnstable institution

Sub-themes B1A, B1B, and theme B2 of the Barnstable institution were sung throughout the Hyannis dialect with little or no variation. Theme B2 was related to theme C2 of the Chatham institution. In comparison to other Barnstable dialects, the Hyannis dialect's variant of theme B2 was most similar to theme C2 (Figure 39). In contrast, sub-theme B1A was closely related to theme F1A of the

Falmouth institution. Again, it was the Hyannis dialect's variant of theme B1A that most resembled theme F1A (Figure B.2). These similarities suggested that the Barnstable institution was founded by dispersers from both the Chatham and Falmouth institutions settling in or near the town of Hyannis.

Although sub-themes B1A and B1B appeared to be derived from a theme sung in the south-eastern portion of the southern Falmouth institution (Figure B.2), these themes included shared syllables sung with different pronunciation variations. Relationships between sub-themes F1B and B1B are circuitous (the relationship being through sub-themes F1A and B1A). Theme B2 is not related to either variant of theme B1.

a. Song distribution patterns and relationships between song themes.

Table 4 summarizes dialect distribution in the Barnstable institution. Several local dialects were found (A through I) in which one or more of the regional themes or sub-themes (B2, B1A, or B1B) were either modified strongly or replaced by unrelated themes ("other", Table 4). Eight local themes (‡, Table 4) were closely related to the Hyannis dialect. Nine themes (*, Table 4) were also derived from the Hyannis homologue, but with strongly modified pronunciations of some syllables, and losses or substitutions. Five themes (‡, Table 4) were partially adopted from non-House Finch song (Appendix B) and additionally included either modified Barnstable syllables (themes Y1, in part, and HK1), syllables derived from other institutions (theme SP1, in part [Mashpee]), or improvised syllables

(themes Y1 and SP1, in part, and themes DR1 and H1). One theme (theme LP1) was derived from Chatham song patterns.

In five of the local dialects (C, E, F, G, and H), syllable pronunciations of the Barnstable themes were distinct from homologous ones sung in the Hyannis dialect. This suggested: (1) These four dialects were founded by dispersing Hyannis birds shortly after the Hyannis dialect was established, or (2) the birds markedly altered syllable pronunciations and added or subtracted other syllables. Note that in each of the four dialects, several syllables, and also some themes, were lost (Table 4).⁵

The syllables sung in the remaining local dialects were also similar to those sung in the Hyannis dialect, but were reduced in number. This suggested either:

1. These dialects were only recently founded by birds from the Hyannis dialect,
2. there was continued communication between the new and original dialect, or
3. these dialects were founded by finches that originally sang themes different from the Barnstable institution, and only secondarily incorporated Hyannis dialect traditions.

⁵Reduction in syllable repertoire size was also evident in the Truro population of the Falmouth institution. In that population, however, the repertoire was reduced without the addition of another theme. The repertoire reductions in Barnstable, as in Truro, included losses of number of syllables, syllable alleles, and themes.

When finches singing the Hyannis dialect encountered these local populations, some members of the local populations (e.g., Dennis) lost some local patterns and adopted Hyannis patterns. I am hypothesizing here that themes from the repertoires of the smaller (e.g., Dennis) populations were replaced with themes of the larger (e.g., Hyannis) population. These relationships suggest a temporal sequence of range expansion in this institution as outlined below.

Synthesis of migration routes in the Barnstable song institution

I interpreted the colonization of the Barnstable institution in the following manner.

1. A colony became established near Hyannis (Figure 42). Colonizers for this population may have had two sources: Chatham (providing theme B2) and Falmouth (providing theme B1).
2. As the Hyannis colony began to expand, other colonies became established in various locations. Populations D, HK, and W (Figure 43) were descendant from Barnstable, while LP probably dispersed from Chatham. The source for some colony YM was not obvious.
3. Continued expansion of the Hyannis and other dialects (YM, D, HK, and LP) resulted in increase of geographic size and further colonizations (Figure 47). Satellites of the Hyannis colony were established at Phyllis Lane (PL) and in Harwich (H). A satellite of the Spectacle Pond colony was founded in Osterville (O).

4. The Hyannis colony secondarily met several of these colonies, adopting portions of their repertoires. In the future this may occur as the Barnstable institution was just meeting a new colony (CL, Figure 48) established from other sources.
5. The less widespread song traditions (dialects 2 through 9, Figure 49) were partially adopted by dispersing birds from the Hyannis dialect. This usually resulted in stratification of Hyannis song themes (pure Barnstable) with the local repertoires.
6. A small cohort of individuals singing the Hyannis dialect dispersed WNW to Spectacle Pond. These birds were recorded countersinging with birds from the local Spectacle Pond tradition, which was a complex tradition unrelated to Barnstable (Hyannis) patterns.

Ultimately there were nine dialects in the Barnstable institution (Figure 49).

Summary

By examining similarities and differences in song themes, I derived hypothetical sequences of range expansion for the Chatham, Falmouth and Barnstable institutions on Cape Cod.

Based on both CBC records (Mundinger and Hope 1982) and song pattern similarities with metropolitan New York traditions, I have hypothesized the Chatham song institution was the first to be founded on Cape Cod after a jump

dispersal from a metropolitan New York institution (or an institution whose song traditions were derived from a metropolitan New York institution).

I have hypothesized the North Falmouth population reached Cape Cod after a jump dispersal from Mattapoiset. The North Falmouth population had the lowest number of routine variants of the populations in the Falmouth institution except for the Truro population. Reduction in the number of Falmouth institution syllables sung by the Truro population reflected typical reductions in repertoire sizes of other populations that dispersed and/or hybridized their repertoires with other dialects or institutions (see Chapter 6). Restriction of the Truro population's repertoire to a smaller number of syllables and alleles - even though it retained the two sub-theme variants of theme F1, indicated the repertoire of the North Falmouth population of the Falmouth institution was a subset of the repertoire sung by the original founders of the Falmouth institution.

I suggest a colony was founded in Hyannis after jump dispersal events from both the Chatham and Falmouth regions. The Hyannis dialect (1) has the largest range of all the dialects in the Barnstable institution, and (2) is one of only three Barnstable dialects in which the three regional themes (B1A, B1B, and B2) were sung in pure form.

The Hyannis dialect probably became the source of several satellite colonies which then learned new themes by improvisation or in some cases misimprinting from alien species, sometimes both. These satellite colonies did not expand as rapidly as the Hyannis dialect did as they were geographically localized

in 1986. As the Hyannis dialect spread, becoming regional, populations singing this dialect came in secondary contact with these smaller satellite colonies, producing local border populations with stratified repertoires as they assimilated themes of both traditions into their repertoires.

CHAPTER 8

SONG PATTERN DISTRIBUTIONS

AND DISPERSAL:

A REPRISAL

The model of dispersal and colonization routes for the House Finch was based on analysis of songs at the theme and institution level. I found these cultural traditions on Cape Cod distributed in much more complex patterns than they were on Long Island, New York (Mundinger 1975). Song patterns did not separate neatly into dialects and institutions in many areas. In the Chatham institution and parts of the Falmouth institution, syllables changed gradually in a clinal fashion, as reported for California finch traditions (Bitterbaum and Baptista 1979). In other areas, extensive hybridizations were manifest as zones of intergradation (Mundinger 1975), reticulate evolution (Mundinger 1980), and stratification (sensu Baker and Thompson's "intergradation," 1985; this thesis). In still other areas, boundaries were sharply demarcated as described for some New York populations (Mundinger 1975).

A. SONG PATTERNS

Songs were composed of three segments: an introduction, core, and ending. Each song segment was composed of one or more routines, which were, in turn, composed of syllables. Analysis of songs at the routine level made it easy to identify syllable substitutions, insertions, deletions, and mutations, as routines were more conservative than were individual syllables. In the Falmouth institution, where dialects were not well defined, dialect boundaries were determined by using pronunciation and

lexical variants of song routines. Mundinger (1975) interpreted dialect boundaries using pronunciation variants of syllables.

Nottebohm (1984) suggested that "the size of brain networks for song control may limit how much can be learned." Kroodsma and Verner (1978) found significant differences in repertoire size in Cistothorus wrens. A similar difference was found in the size of the brain nuclei controlling singing in these wren species (Canady et al. 1984, Kroodsma and Canady 1985), and others (reviewed in DeVoogd et al. 1993). Baptista (197) found individual bilingual White-crowned Sparrows stopped singing their previously learned tradition when they began singing adopted traditions after dispersal. He attributed this loss of song to a lack of use. Nelson (1992) found Field Sparrows show selective attrition of songs as they established their first territories (retaining songs similar to those of neighbors, while deleting dissimilar patterns). The Field Sparrows did not appear to learn new songs at this time, nor did individuals change to different songs once their repertoires were established. On the other hand, Indigo Buntings (Margoliash et al. 1991), and European Starlings (Eens et al. 1992) go through a period of singing plastic song each spring. After these periods of adult plastic song, individuals deleted some songs from the repertoires while they added new routines, or even themes.

Reduced repertoire size

In species that learn new repertoires after dispersal, the ability to reduce a previously learned song repertoire and learn new songs after dispersal would provide a social advantage. Whether a conscious or unconscious event, replacement of old song traditions would allow individuals to adopt the patterns of new neighbors and assume a position in the social hierarchy. The learned repertoires of insular populations (Baptista and Johnson 1982, Baker and Jenkins 1987, Morton 1987) and of both individual and

group isolates (Marler and Mundinger 1971) were often smaller than repertoires of mainland populations or of tutored individuals. On Cape Cod a similar reduction in House Finch repertoire size occurred in similar circumstances, but other processes occurred as well: (1) repertoire sizes of satellite and dialect populations were smaller than the repertoires of their source populations, (2) in some areas of overlap, themes were stratified with only a part of the total repertoire of one institution (the postulated ancestral institution) being sung with a part of the repertoire of another institution (presumably a type of substitution occurred), and (3) adoption of alien-derived patterns in their songs in populations that developed in previously uncolonized habitat.

Repertoire size of satellite and dialect populations

The Truro satellite population of the Falmouth institution included sub-themes F1A and F1B, but not theme F2, in its repertoire. When compared with Falmouth populations, this population sang both sub-themes of F1 in abbreviated forms. In addition syllables shared in the two sub-themes were sung with (nearly) identical pronunciation alleles. Although the probable source population in North Falmouth sang similar variants of shared syllables in their sub-themes, other populations in the institution sang different alleles in those two sub-themes.

When the themes of the Truro population were compared with those sung in the probable source institution, the song repertoire of the Truro population was only half the size of the source population's in total number of syllables (twenty-two syllables vs. forty-six), and number of alleles (twenty vs. forty). Similar reductions in the numbers of syllables and themes were found when other satellite (or dialect) populations were compared with their source populations.

Theme stratification

The occurrence of several song traditions on Cape Cod indicated that dispersing populations singing one song tradition (e.g., the large Hyannis dialect of the Barnstable institution) regularly encountered populations singing alternate traditions (e.g., small, local institutions found at Herring Brook, Yarmouth, Harwich, and Long Pond). Stratification of repertoires occurs when descendants of one tradition (e.g., Hyannis) meet finches singing an alternate tradition, and the descendants eliminate one or more themes of their ancestral repertoire, accepting one or more themes of the alternate traditions. Stratification appeared repeatedly in the eastern portion of the Barnstable institution, in the Mashpee institution, and in northern Eastham where the Chatham and Wellfleet institutions hybridized. Unless there were cultural or genetic guidelines, the selection of which themes would be lost from the newly combined repertoire would be randomly determined. My field data supported this proposition, since there was no regular pattern in regard to which Barnstable themes were substituted for in several different regions of complex stratification (Table 7.5). This lack of uniformity suggested that random eliminations and replacements of themes ensued when populations meet. Away from these contact zones, most members within a dialect conformed in their theme repertoires. This conforming suggests that social factors control an individual's selection process at the time of stratification of repertoires (when there were alternate themes available). Some juvenile birds may preferentially learn their songs from experienced birds (Williams et al. 1994). Others may learn from dominant individuals or groups (Krebs and Weary 1987).

Adoption of alien songs

When dispersing into territories where conspecifics reside, reduction of repertoires upon dispersal (followed by learning new patterns sung by residents) would provide a social advantage to dispersing birds. Colonizing groups, however, found no conspecifics singing songs that they could add to or substitute for portions of their repertoires. If a post-dispersal learning species also spontaneously and irreversibly eliminates part of the repertoire at or near the time of dispersal, the effect would be that individuals would have to improvise portions of their song. This improvisation could be based on three sources: (a) previously learned material, (b) alien song, (c) new improvisation.

Most young birds are tutored to a greater or lesser degree by singing individuals in their natal region. It requires only a few repetitions of a theme for many bird species to learn song themes (Kroodsma 1978, McNair and Forster 1983). Even juveniles hatched at the end of the breeding season hear some songs from neighborhood males. These songs could provide the stimulus needed for the young bird to learn conspecific song, at least partially (Peters et al. 1992).

In many instances on Cape Cod, entire populations of House Finches incorporated portions of the songs of other species into their own songs. My data include several instances of alien-derived song in House Finch repertoires (Yellowthroats in Osterville and Harwich, Purple Finch or Ovenbird at Crosby Landing, Yellow Warbler in Sandwich, Goldfinch at Herring Brook, Indigo Bunting at Plymouth Rock, Downy Woodpecker in Yarmouth, and Flicker in Brewster). Some colonies that learned these alien songs were presumably founded by groups (Mundinger 1975), and it is reasonable that at least some members of the founding groups were tutored by breeding males in their natal territories

or during migration. That these groups also adopted alien traditions suggests that post-dispersal learning is one means by which juvenile House Finches learn their songs.

Early investigators of cross species learning (Buffon 1791, Rennie 1833, Witschell 1896) suggested that some species were exceptionally good mimics while others improvised song from alien songs. Baylis (1982) used the term "primary mimicry" to describe the situation when an individual learned its song directly from an alien model. Recent investigators (Baptista 1977, Baylis 1982, McNair and Forster 1983, McNair 1985, Payne et al. 1988) found that individuals improvised on alien-derived song, calling this mis-copying. Mimicked songs often became more like the species-typical songs of the imitator. When subsequent generations learn alien-derived songs, from those that first learned them, i.e., "secondary mimicry" (Baylis 1982), the song may undergo further secondary improvisations, becoming altered to resemble species-typical song more closely. Secondary improvisation appeared to occur in all areas, where House Finches learned alien-derived patterns.

Rarely did alien-derived song comprise the majority of a population's repertoire. As did Payne et al. (1988), I found alien-derived song inserted into themes that also included typical House Finch syllables and routines. Thus, rather than blindly adopting alien song, Cape Cod House Finches appeared to improvise on or transform the material to conform to previously learned or genetically heritable preferences.

B. DISPERSAL

Mundinger and Hope (1982) described dispersal of the House Finch across the eastern United States. Their findings showed this species' range expanded because of two dispersal methods: diffusion and jump dispersal. The speed at which the House

Finch colonization of large areas was phenomenal. This precipitous rate of expansion continued on Cape Cod throughout the colonization period.

Distributions of songs, repertoire sizes of populations, pronunciation variants, and alien-derived traditions suggested a model of dispersal routes onto and across Cape Cod. Sight records (Hill 1965, Mundinger and Hope 1982) of House Finches were made in Chatham, at the elbow of the cape, in 1964; but they were not observed in Bourne, at the base of the cape, until 1968. Cape Cod's first colony of House Finches was, therefore, probably located in Chatham, at the elbow of the cape. Although the Chatham song institution was not the largest on Cape Cod in the 1980s, it was located in the vicinity of the first sightings of finches. Thus, the Chatham institution probably contained song patterns derived from traditions sung by the first colony.

A second colony was founded sometime later. Dispersal patterns (Mundinger and Hope 1982) and similarities between song patterns in North Falmouth and Mattapoiset, MA suggest that this second colony was probably founded in the Falmouth area by jump dispersal from coastal regions of Massachusetts to the west of Cape Cod (e.g., Mattapoiset).

The syllable and routine repertoires of the Chatham institution suggested possible cultural ties with New York song institutions (about 300 km away), while songs of the Falmouth colony were closely related to vocal traditions sung in Mattapoiset (about 15 km west of the colony). Several new colonies were subsequently formed from birds dispersing from these first colonies. In particular, the songs of the Barnstable institution were found to be closely related to both the Chatham and Falmouth institutions, and the Wellfleet tradition related to Barnstable and Chatham patterns. Provincetown themes, at

the outermost tip of the cape, were derived from themes associated with Barnstable, Falmouth, Wellfleet, and Chatham.

Other, colonies were founded in all areas of the cape. Some of these developed unique song patterns (suggesting dispersal from areas off Cape Cod) or sang patterns resembling other Cape Cod institutions. Where minor populations retained unique traditions, they were considered separate institutions. Minor institutions were found in Woods Hole (Falmouth), Salt Marsh (Sandwich), Crosby Landing (Brewster), and John's Pond (Mashpee). Where the unique patterns were hybridized with other, more widespread traditions, they were considered dialects of the more widespread tradition (e.g., the zones of stratification of the Barnstable institution in Brewster and Harwich).

As new colonies were being formed on Cape Cod, either by jump dispersal from older Cape Cod colonies or from elsewhere, the older colonies went through periods of growth and expansion. As these older colonies enlarged by diffusion, they often encountered and assimilated the song traditions of smaller colonies. Thus, the cultural traditions of many dialects of large institutions were often mixtures of two or more heritages.

Considering their explosive population growth, the differences in finch song institutions on Cape Cod did not surprise me. The large numbers of individuals that consistently sang themes of the Barnstable, Chatham, and Falmouth institutions were mind boggling, however. It does not seem possible this many birds could have been engendered in the colonies that were founded only 15 - 20 years earlier.

C. FURTHER QUESTIONS ARISING FROM THIS RESEARCH

I found song traditions with several different ancestries on Cape Cod. Reevaluation of some of these would provide important information about mechanisms of cultural evolution. (1) A satellite population in Truro was apparently founded by a single dispersal event from Falmouth. (2) The population in Provincetown was apparently founded by multiple dispersal events from four institutions. (3) Several dialects of the Barnstable institution included alien-derived songs in their repertoires.

The Truro dialect of the Falmouth institution was quite isolated from the parental population. I would expect that few, if any, individuals from the Falmouth institution dispersed again into this area in the decade since this study was made. Reexamining this dialect, therefore, may provide information on the speed of cultural evolution in an isolated population. The beauty of this dialect is that, since North Falmouth has been identified as the probable source population, evolutionary changes of both the source population and the satellite population can be examined.

The reticulate song patterns in Provincetown may provide information on whether migrants tend to collect at the ends of land masses. The patterns seen in Provincetown appeared to have resulted from repeated dispersal events into this town from other Cape Cod populations. If immigration no longer occurs, I would expect the song traditions of this population to become stable - although not necessarily with the same patterns that were present at the time of this study.

The complex zones of stratification in the Barnstable institution that included alien-derived song may provide information about the process of assimilation of alien-derived patterns into more species-typical patterns. At least five themes of local dialects were derived from alien song: copies of different Yellowthroat themes in Osterville (theme SP1)

and Harwich (theme H1), Downy Woodpecker in Yarmouth (theme Y1), Yellow-shafted Flicker in Harwich (theme DR1), and Goldfinch in Brewster (theme HK1). There were some areas where assimilation of the alien-derived theme was becoming assimilated into more typical House Finch song at the time of my data collection. The Yarmouth dialect included one form of theme Y1 with patterns that were probably derived from Downy Woodpecker and other forms of this theme that were intergrades between the woodpecker tradition and theme B1B of the Harwich dialect. The Yellowthroat-derived routine of theme H1 sung in the Harwich dialect intergraded with other themes sung in this dialect in western Dennis.

I intend to return to Cape Cod, therefore, to resample the songs in several areas of Barnstable, Provincetown, Truro, and Falmouth so that I can follow the course of cultural evolution in populations that derived their songs from varied circumstances. Questions I would be asking are: (1) How rapid is cultural evolution in a satellite population (Truro vs. North Falmouth)? (2) Given the unique geographic conditions at the ends of peninsulas (such as Provincetown), what happens to song traditions over time (do migrations occur rather continually, what are the sources of immigrants)? (3) How rapidly does reticulate evolution occur (Provincetown)? (4) Are alien-derived songs retained over time, or are they rapidly assimilated into themes more typical of the species (Barnstable alien-derived dialects)? Answers to these questions, if obtained, would be valuable when using song traditions to examine cultural relationships.

TABLES

Table 1: Means ($\pm$ S.D.) of Syllable Parameter Values by Song Segments.

Song segment (n is number of syllables)	segment duration x $\pm$ S.D.	syllable duration x $\pm$ S.D.	median frequency x $\pm$ S.D.	frequency sweep x $\pm$ S.D.	band width x $\pm$ S.D.	amplitude rank Tukey's q	syllables per segment	notes per syllable
Introduction n = 212	650 ms $\pm$ 322	109 ms $\pm$ 40.8	4040 kHz $\pm$ 593	1080 kHz $\pm$ 460	280 Hz $\pm$ 139	1.075 **	3.5 $\pm$ 1.53	1.7 $\pm$ 0.67
Core n = 500	1490 ms $\pm$ 482	110 ms $\pm$ 53.3	3540 kHz $\pm$ 597	1570 kHz $\pm$ 614	450 Hz $\pm$ 300	2.292 **	10.0 $\pm$ 5.19	2.2 $\pm$ 1.09
Ending Syllable								
Buzzy n = 135	670 ms $\pm$ 417	543 ms $\pm$ 143	3440 kHz $\pm$ 543	1580 kHz $\pm$ 685	880 Hz $\pm$ 255	3.031 **	3.1 $\pm$ 1.99	1.0 $\pm$ 0.19
Tonal n = 90	740 ms $\pm$ 347	137 ms $\pm$ 72.2	3480 kHz $\pm$ 564	1750 kHz $\pm$ 707	290 Hz $\pm$ 178	2.759 **	4.0 $\pm$ 2.35	2.2 $\pm$ 0.69
Complete Songs n = 100	2195 ms $\pm$ 349						16.8 $\pm$ 2.91	

Table 2: Variation in the number of routines, variants of routines, and frequency that routines and segments were sung in House Finch songs on Cape Cod.

Song Segment	# routines per song segment	# variants per routine	frequency a given routine is sung	frequency a song segment is sung
Introduction	1.3	2.5	0.59	0.64
Core	4.3	1.03	0.83	1.00
Ending	1.3	1.5	0.43	0.49

Table 3: Variation in sequencing routines within the two sub-themes of theme F1 sharing a common set of routines.

Sector:	Great Hollow			Aldrich Road			Pilgrim Lake					Snow St		Row Totals
Sub-theme A														
<i>J K L M N</i>							18		23		21			62
<i>J K L M n</i>		3	6	9	1	2					1			22
<i>J L M N</i>	11	7	7	12	3	14	2	13	1	12	3	6	6	97
<i>J L m n</i>								1						1
Sub-theme B														
<i>k L m n</i>	2	3	2	5	1	4	2	10	1	5		9	7	51
<i>k L M N</i>	2			1		1			3					7
Column Totals	15	13	15	27	5	21	22	24	28	17	25	15	13	240

Table 4: Number of syllables shared between the themes sung in the dialects of the Barnstable song institution.

Dialect	Number of syllables shared				
	A. with the Hyannis dialect			B. with other traditions	
	B1A	B1B		Theme	Derivation
A. Hyannis	6	13	9		
B. Doane Road	5†		8†	DR1‡	12 improvised
C. Harwich	4†	5*		H1‡	4 improvised
D. Osterville	5†		4†	SP1‡	6 from Mashpee 7 improvised
E. Yarmouth		11*	5*	Y1‡	2 from Barnstable
F. Phyllis Lane	3*	5*	3*		
G. Dennis	4*	11†	8*		
H. Herring Brook		9†	3*	HK1‡	4 from Barnstable
I. Long Pond		8†		LP1 C1	9 from Chatham from Chatham

* Most syllables sung in common with the Hyannis dialect have different alleles.

† Themes that shared the identified number of syllables with the Hyannis dialect with little or no modification.

‡ Themes that were partially derived from alien song.

Table 5: Reticulate evolution and bilingualism at Pimlico Pond and Spectacle Pond: Identity of the institutions from which birds at Spectacle Pond and Pimlico Pond select their songs.

Number of Birds	Barn only	Mashp only	Other	Falm & Mashp	Falm &	Mashp &	Falm Mashp &
Spectacle			Spect		Spect	Spect	Spect
23	1	2	1	8	3	3	5
Pimlico Pond			Pimlico		Pimlico	Pimlico	Pimlico
25			6		3	11	5
Totals	1	2	7	8	6	14	10

Table 6: Sequences of song routines found in ten songs sung by bird 1 at Pimlico Pond.

Song Numbers	routines	themes
1	A B B C D	i1 M3 M3 M2 M1
2	H I J K B	M1 M1 M1 M2 M3
4	A B E	i1 M3 M3
6	A B B C D	i1 M3 M3 M2 M1
7	H I J	M1 M1 M1
8	A B B C D	i1 M3 M3 M2 M1
9	F A B B C D E	i2 i1 M3 M3 M2 M1 M3
10	F A B B C D	i2 i1 M3 M3 M2 M1
14	H I J K	M1 M1 M1 M2
15	H J B	M1 M1 M3

Upper case routine identifiers refer to the same routines sung by bird 2 at this location. Upper and lower case routine identifiers with the same letter refer to different routines. Theme identifiers refer to themes of described song institutions: e.g. M1 refers to Mashpee theme 1. Lower case letter "i" refers to an introductory routine.

Table 7: Sequences of song routines found in ten songs sung by bird 2 at Pimlico Pond.

1	a b c d	P1 P1 P1 P1
2	a b c d e	P1 P1 P1 P1 e1
3	H I J d e	M1 M1 M1 P1 e1
5	a b c d	P1 P1 P1 P1
6	a b c d e	P1 P1 P1 P1 e1
7	L M I J d e	i1 i2 M1 M1 P1 e1
8	L O I J d	i1 i3 M1 M1 P1
21	N N J	M3 M3 M1
22	c d m N	P1 P1 ? M2
23	m I J d	? M1 M1 P1

Upper case routine identifiers refer to the same routines sung by bird 1 at this location. Upper and lower case routine identifiers with the same letter refer to different routines. Theme identifiers refer to themes of described song institutions: e.g. M1 refers to Mashpee theme 1, P1 refers to Pimlico Pond theme 1. Lower case letter "e" refers to an ending routine. Lower case letter "i" refers to an introductory routine. Although these birds did not sing Falmouth themes, other individuals in this colony did include Falmouth themes in their repertoires.

Table 8: Sequences of song routines found in twenty songs sung by one bird at Spectacle Pond.

Song Numbers	routines	themes
1	A B C D	M1 F1 F1 e1
2	E F G H	SP2 SP2 SP2 SP2
3	I J K	M4 M4 M4
4	A B C D L	M1 F1 F1 e1 i1
5	A B C	M1 F1 F1
6	A B C D	M1 F1 F1 e1
7	L A B	i1 M1 F1
8	E F G	SP2 SP2 SP2
9	E F G' H	SP2 SP2 SP2 SP2
10	A B C D	M1 F1 F1 e1
11	I J K	M4 M4 M4
12	I J K	M4 M4 M4
13	I B C	M4 F1 F1
14	A B C D	M1 F1 F1 e1
15	E F G'	SP2 SP2 SP2
16	E F G' H	SP2 SP2 SP2 SP2
17	I J K H L A B	M4 M4 M4 SP2 i1 M1 F1
18	A B C D	M1 F1 F1 e1
19	E F G'	SP2 SP2 SP2
20	A B C D	M1 F1 F1 e1

Upper case routine identifiers refer to different routines than at Pimlico Pond. Apostrophes indicate a routine is a derivative of the routine with the same identifier. Theme identifiers refer to described

Table 9: Demarcation at the Falmouth/Mashpee boundary: The institutions from which birds at the Falmouth/Mashpee boundary select their songs.

Map Sector	Number of Birds	Falm only	Mashp only	Other only	Falm & Mashp	Falm & Other	Mashp & Other	Falm Mashp Other
2605	4	4						
2706	2	2						
2707	3	3						
2813	2	1		1				
3409	2		1	1				
3418	2		2					
3511	1		1					
3514	6		6					
3608	4	2	2					
3609	1		1					
3610	1		1					
3611	1	1						
3709	12	11	1					
3810	1		1					
3819	2		1				1	
3912	1		1					
4220	1			1				
Totals	46	24	18	3			1	

Table 10: Intergradation at the Falmouth/Sandwich boundary: The institutions from which birds at the Falmouth/Sandwich boundary select their songs.

Map Sector	Number of Birds	Falm only	Sandw only	Other	Falm & Sandw	Falm & Other	Sandw & Other	Falm Sandw Other
2936	6		1		5			
3033	1	1						
3036	9	1	1		7			
3133	3	1			2			
3231	3	1			2			
3331	7	4		1		2		
3333	3	3						
3731	2				2			
3732	6			6				
Totals	40	11	2	7	18	2		

Table 11: Stratification at the Falmouth/Barnstable boundary: The institutions from which birds at the Falmouth/Barnstable boundary select their songs.

Map Sector	Number of Birds	Falm only	Barns only	Other	Falm & Barns	Falm & Other	Barns & Other	Falm Barns Other
4230	6		6					
4429	3		3					
4328	2		1		1			
4428	5		3		2			
4415	1			1				
4513	2				2			
4514	2					2		
4617	1				1			
4620	3		1		2			
4621	3				3			
4719	3				3			
4722	1				1			
Totals	32		14	1	15	2		

Table 12: A comparison of repertoires of probable source populations and their satellite populations.

Primary institutions and their satellites		common themes			shared syllables	
primary	satellite	# syllables source	# syllables satellite	% change	# syllables	% of primary repertoire
Falmouth	Truro	30	26	-13.3	18	40.0
Falmouth	Provincetown	21	18	-14.3	15	28.6
Barnstable	Spectacle Pond	23	18	-21.7	18	21.7
Barnstable	Provincetown	13	12	- 7.7	7	46.2
Mashpee	Harwich	10	11	10.0	9	10.0
Mashpee	Eastham	10	9	-10.0	9	10.0
Chatham	Dennis	20	17	-15.0	9	55.0
Chatham	Sandwich	11	14	27.3	9	18.2
Wellfleet	Provincetown	10	12	20.0	6	40.0
Spectacle Pond	Osterville	9	13	44.4	8	11.1
Mean % changes				2.0		28.1

Table 13: A comparison of repertoires of probable source populations and their dialect populations.

Dialect populations		common themes			shared syllables	
primary	secondary	# syllables		% change	# syllables	% primary repertoire
		primary	secondary			
Wellfleet	Truro	17	11	-35.3	10	41.2
Hyannis	Yarmouth	27	31	14.8	18	33.3
Hyannis	Phyllis Lane	27	17	-37.0	11	59.3
Hyannis	Harwich	19	14	-26.3	9	52.6
Hyannis	Long Pond	13	15	15.4	8	38.5
Hyannis	Herring Brook	22	24	9.1	12	45.5
Hyannis	Doane Road	15	16	6.7	13	13.3
Hyannis	Osterville	15	20	33.3	9	40.0
Hyannis	Dennis	27	26	- 3.7	23	14.8
Falmouth	North Falmouth	30	29	- 3.3	16	46.7
Falmouth	Sandwich	30	32	6.7	17	43.3
Falmouth	Wareham	21	26	23.8	19	9.5
Mean % changes				- 1.8		39.0

Table 14: A comparison of repertoires of Cape Cod song institutions with possible source institutions located both at some distance from Cape Cod, and near or on Cape Cod.

Source institution distant		common themes			core syllables	
source	secondary	# syllables source	secondary	% change	# shared	% of source repertoire
East Lyme, CT	Wareham	12	14	16.7	7	41.7
Larchmont, NY	Chatham	12	11	- 8.3	8	33.3
Harrison, NY	Chatham	11	8	-27.3	7	36.4
Mean % changes				- 6.3		37.1
Source population local						
source	secondary					
Plymouth Rock	Salt Marsh	16	18	12.5	13	18.8
Mattapoiset	Falmouth	5	9	80.0	5	0.0
Falmouth	Barnstable	7	7	0.0	4	42.9
Chatham	Barnstable	11	13	18.2	11	0.0
Chatham	Wellfleet	8	8	0.0	2	75.0
Barnstable	Wellfleet	13	11	-15.4	10	23.1
Mean % changes				15.9		26.6

Table 15: A comparison of repertoires of sub-themes of Cape Cod song institutions.

Song institution Theme	# syllables in sub-theme		% increase in song A to B	# shared core syllables	% change from core	
	A	B			A	B
Falmouth F1	7	9	28.6	6	16.7	50.0
Barnstable B1	8	12	50.0	8	0.0	50.0
Chatham C1	6	6	0.0	6	0.0	0.0
Mean % changes			26.2		5.6	33.3

FIGURES

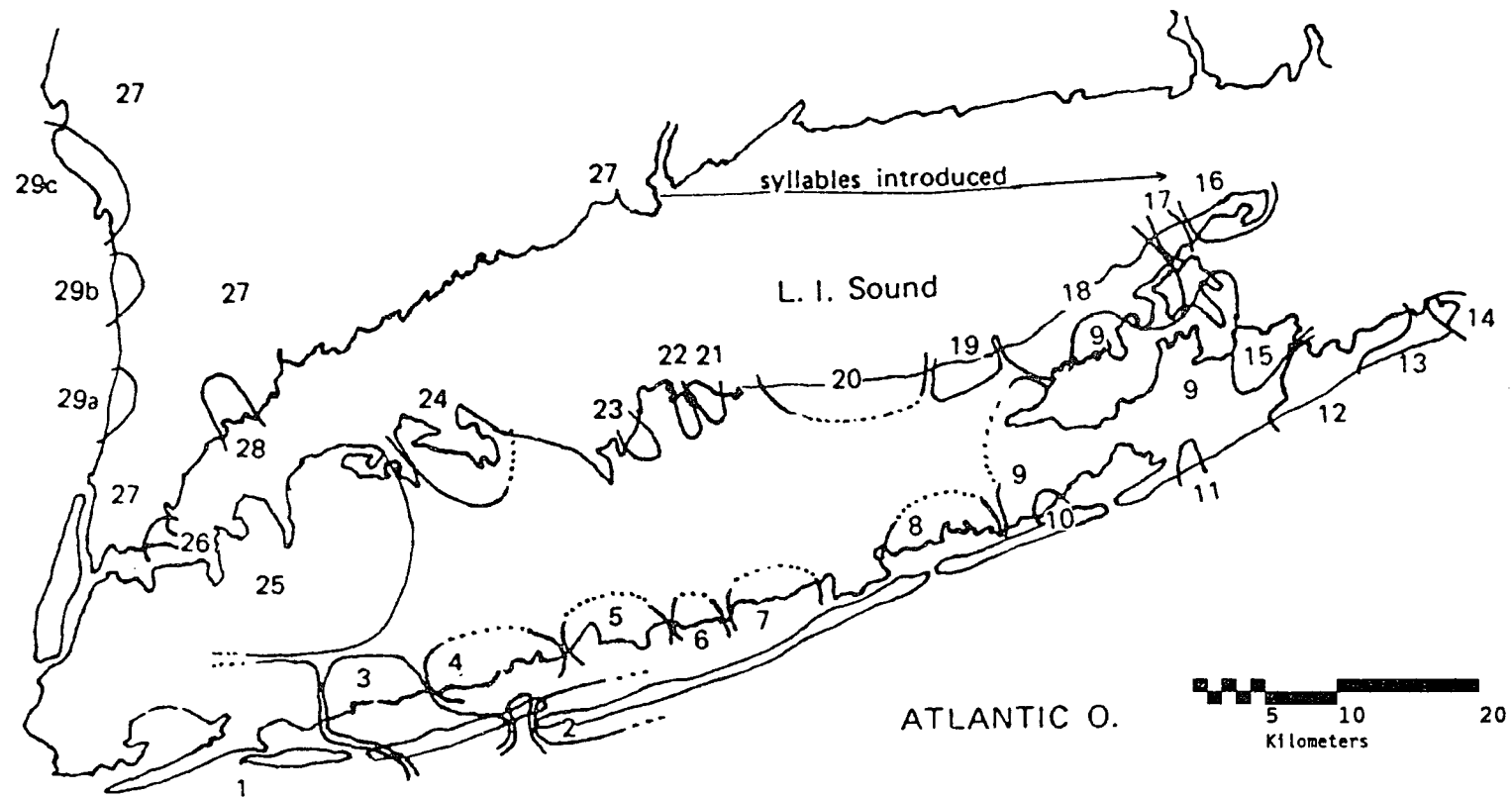


Figure 1: House Finch song institutions on Long Island, New York, and in Westchester County, New York. Solid lines are song institution boundaries; dotted lines are boundary estimates. There are 29 institutions. Institutions No. 1, No. 4, and No. 25 mark the sites of three of the original breeding colonies of this species. The songs of institution No. 16 include syllables also sung in institution No. 27.

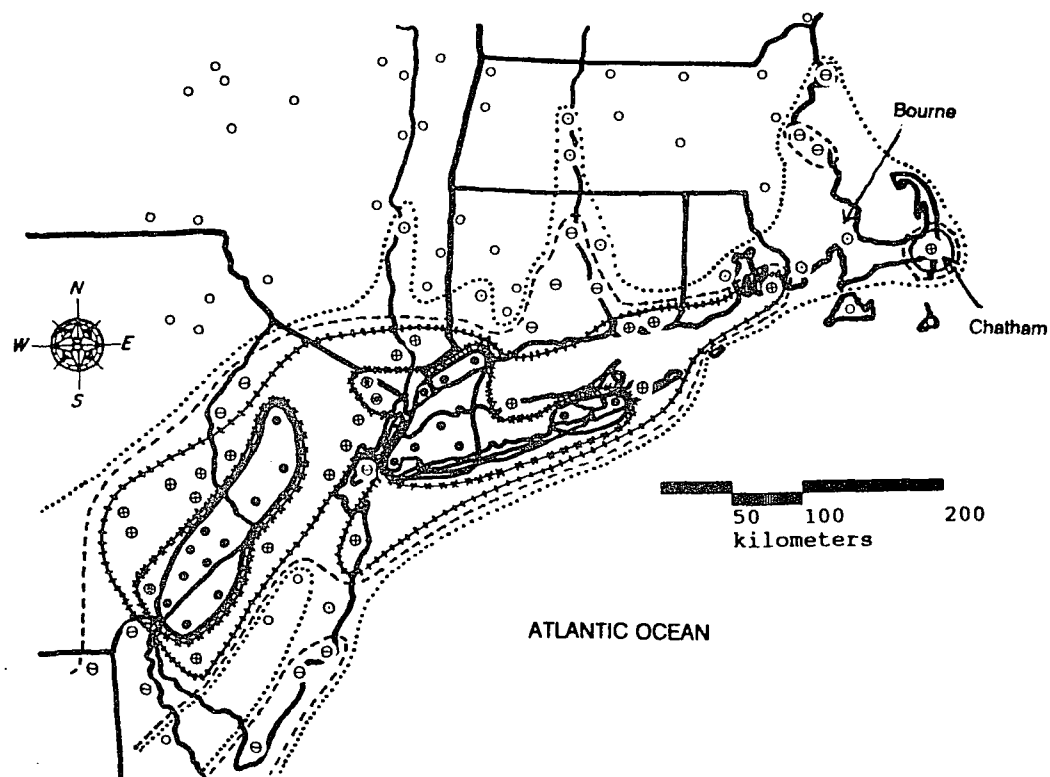


Figure 2: Range expansion of the House Finch in the eastern United States from the period 1960 through 1968.

Circles represent the sites of reporting Christmas Bird Counts (CBCs) through this period. Lines enclose all CBCs recording House Finches for the years indicated. The 1960 range limits are represented by the solid lines and closed circles (●); the increased limits in 1962 are shown by lines with "x"s and circles with asterisks (⊗); limits in 1964 are shown by crossed lines and circles with "+"s (⊕); limits in 1966 are shown by dashed lines and circles with "-"s (⊖); and limits in 1968 are shown by the dotted lines and circles with dots (⊙). All CBCs shown on this map recorded House Finches by 1975. (based on Mundinger and Hope 1982.)

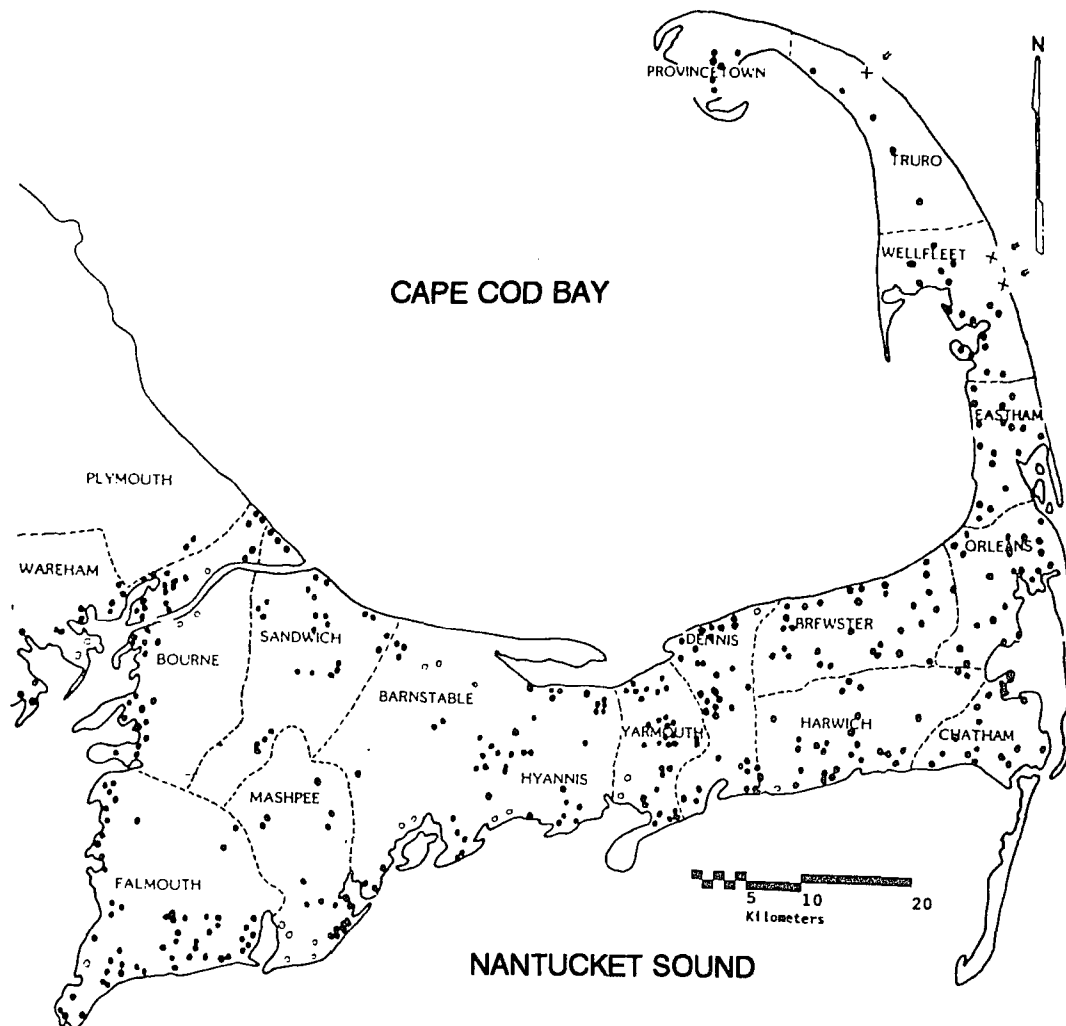


Figure 3: Locations of House Finches on Cape Cod in 1985 and 1986.

Closed circles represent the locations of populations from which songs were recorded. Open circles represent the locations of populations that were seen, but from which no songs were obtained. "X"s represent residential areas where this species was neither seen nor heard.

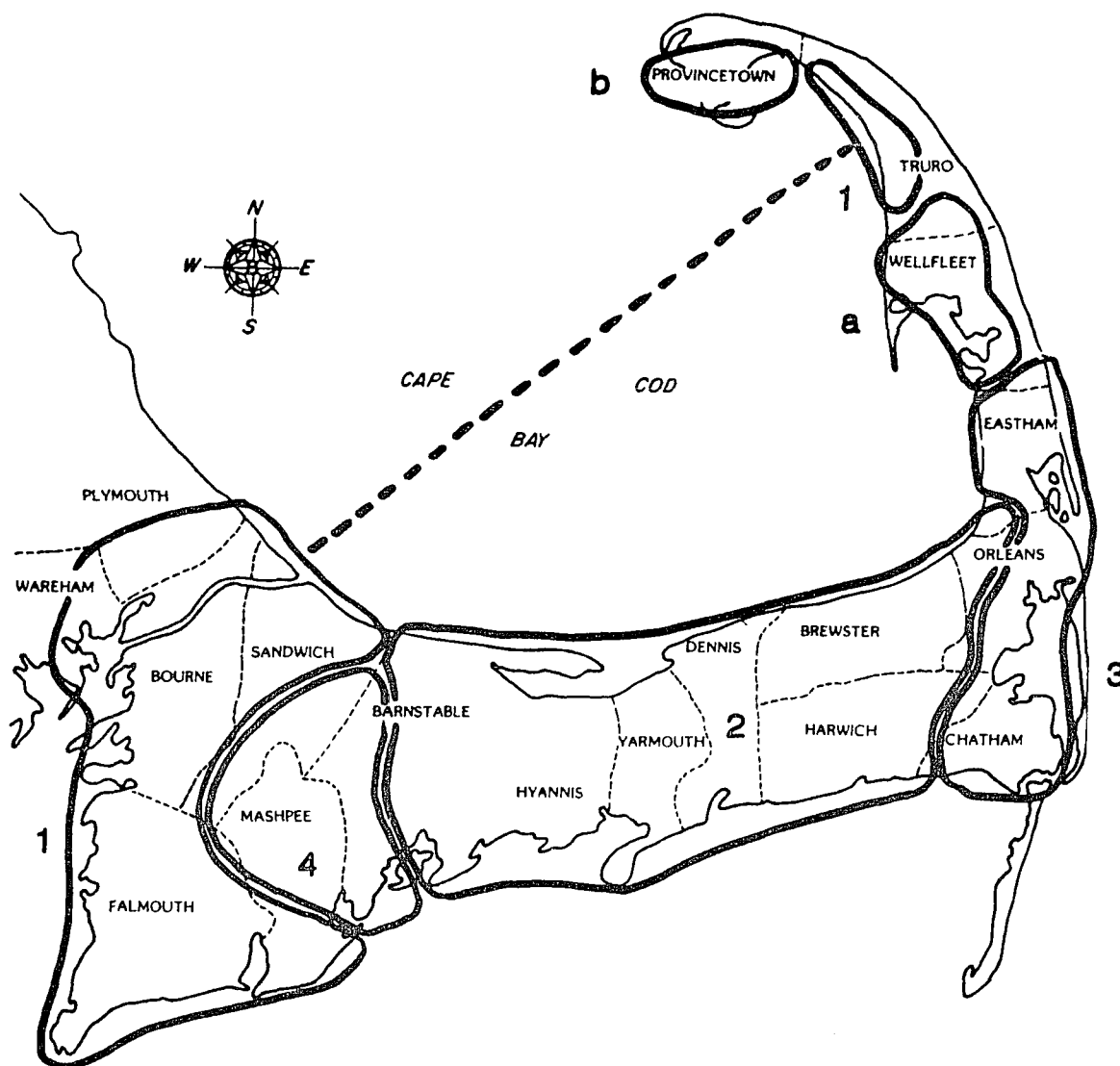


Figure 4: Locations of four major song institutions recorded on Cape Cod (1 - 4), and two minor institutions (a and b).

- | | |
|---------------|------------------|
| 1 - Falmouth | 2 - Barnstable |
| 3 - Chatham | 4 - Mashpee |
| a - Wellfleet | b - Provincetown |

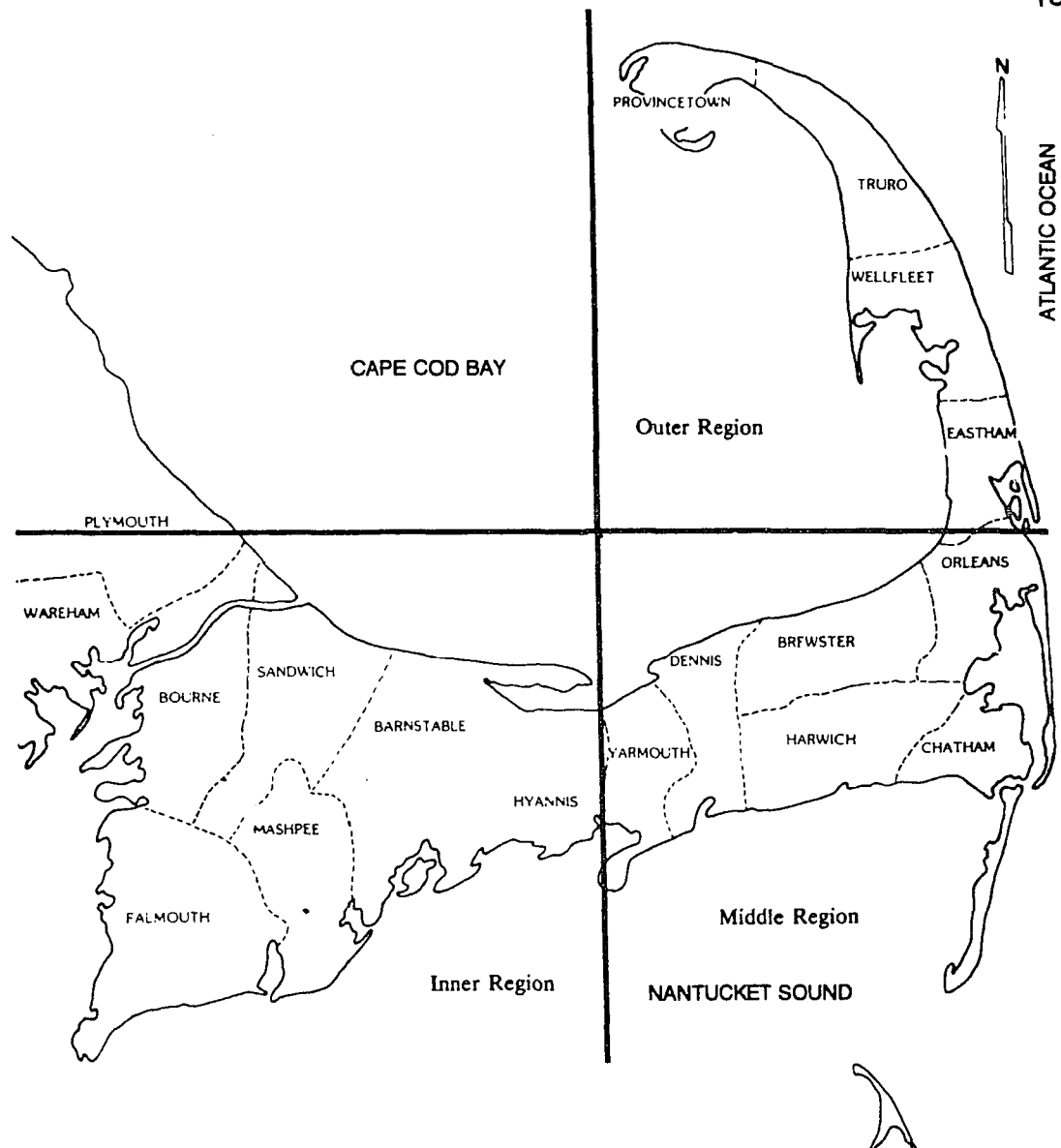


Figure 5: Map of Cape Cod showing the three study regions in this thesis.

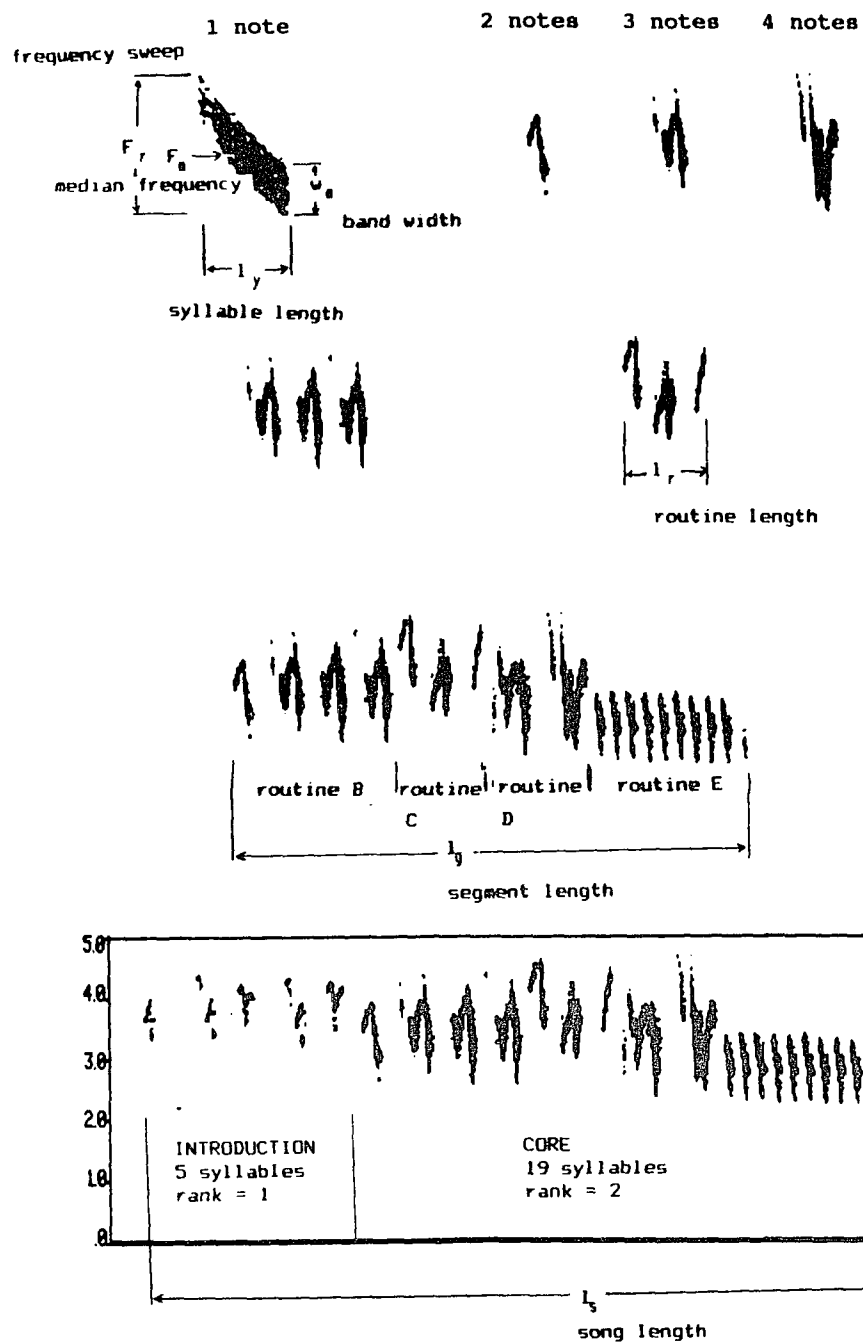


Figure 6: A sample sonogram showing ten song parameters used to describe House Finch song structure.

See text for description of parameters.

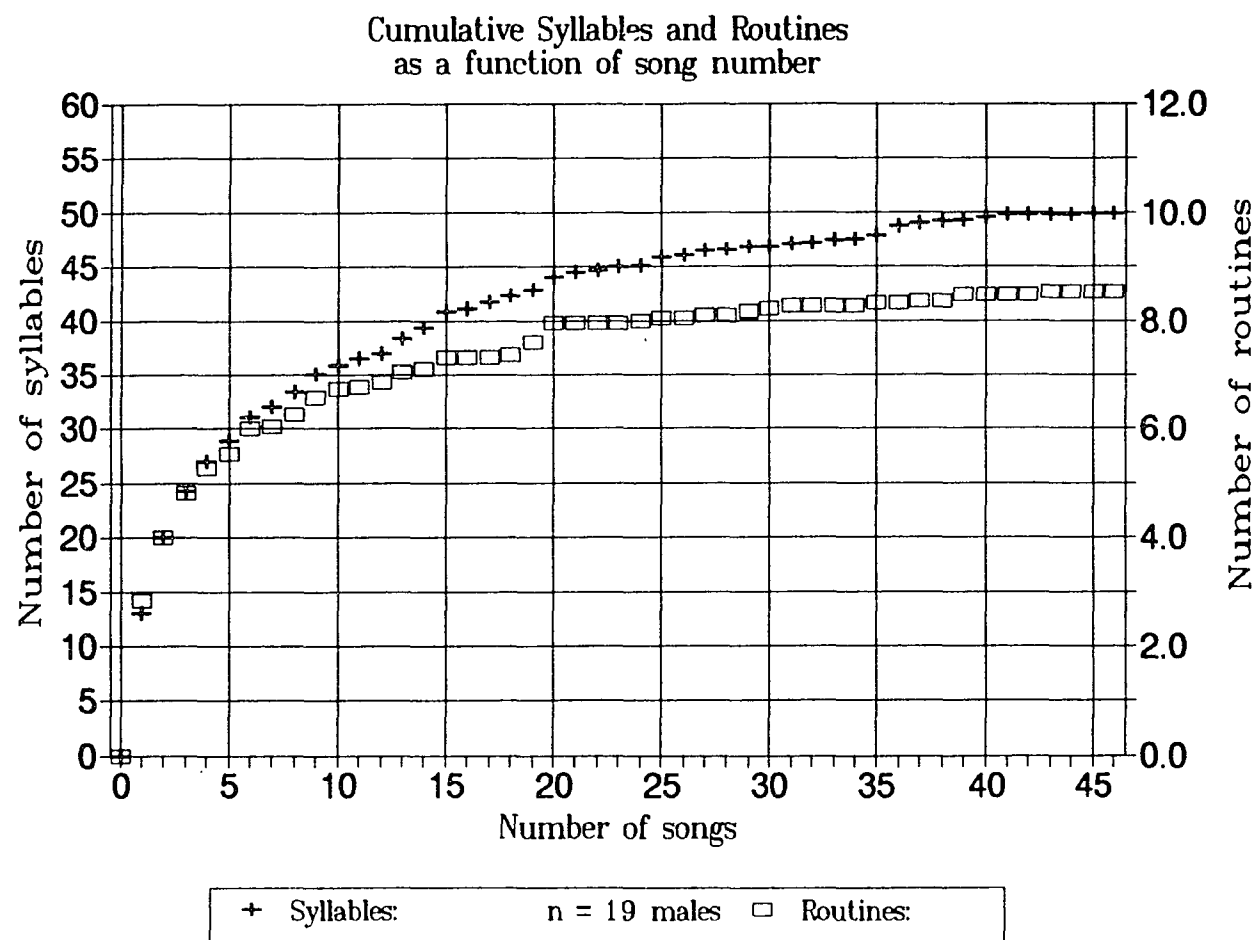


Figure 7: The cumulative number of syllables and routines sung (in bouts of at least 45 songs) as a function of the number of songs sung by the birds.

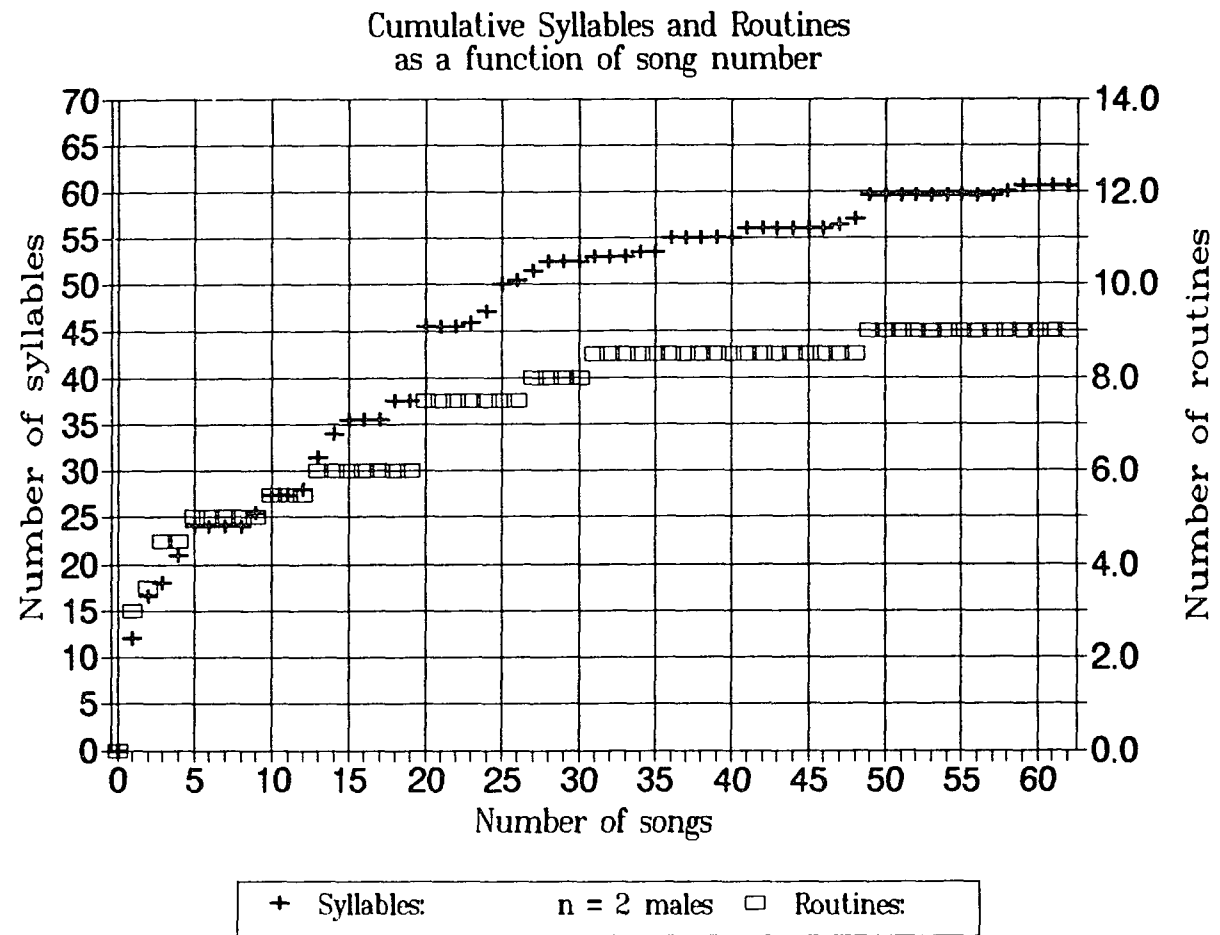


Figure 8: The cumulative number of syllables and routines sung (in bouts of at least 60 songs) as a function of the number of songs sung by the birds.

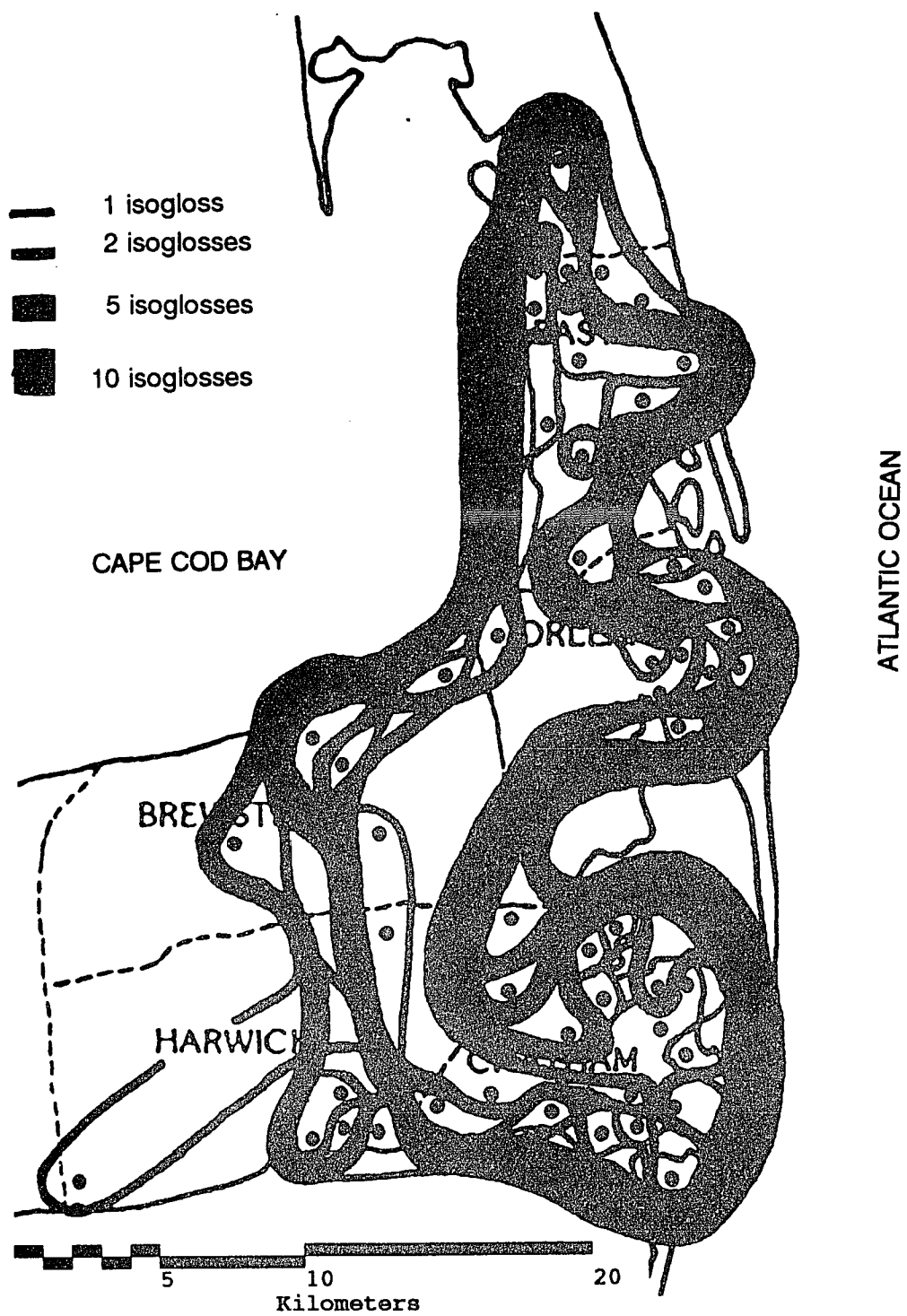


Figure 9: Isogloss plot of the distribution of song syllables in the outer cape.

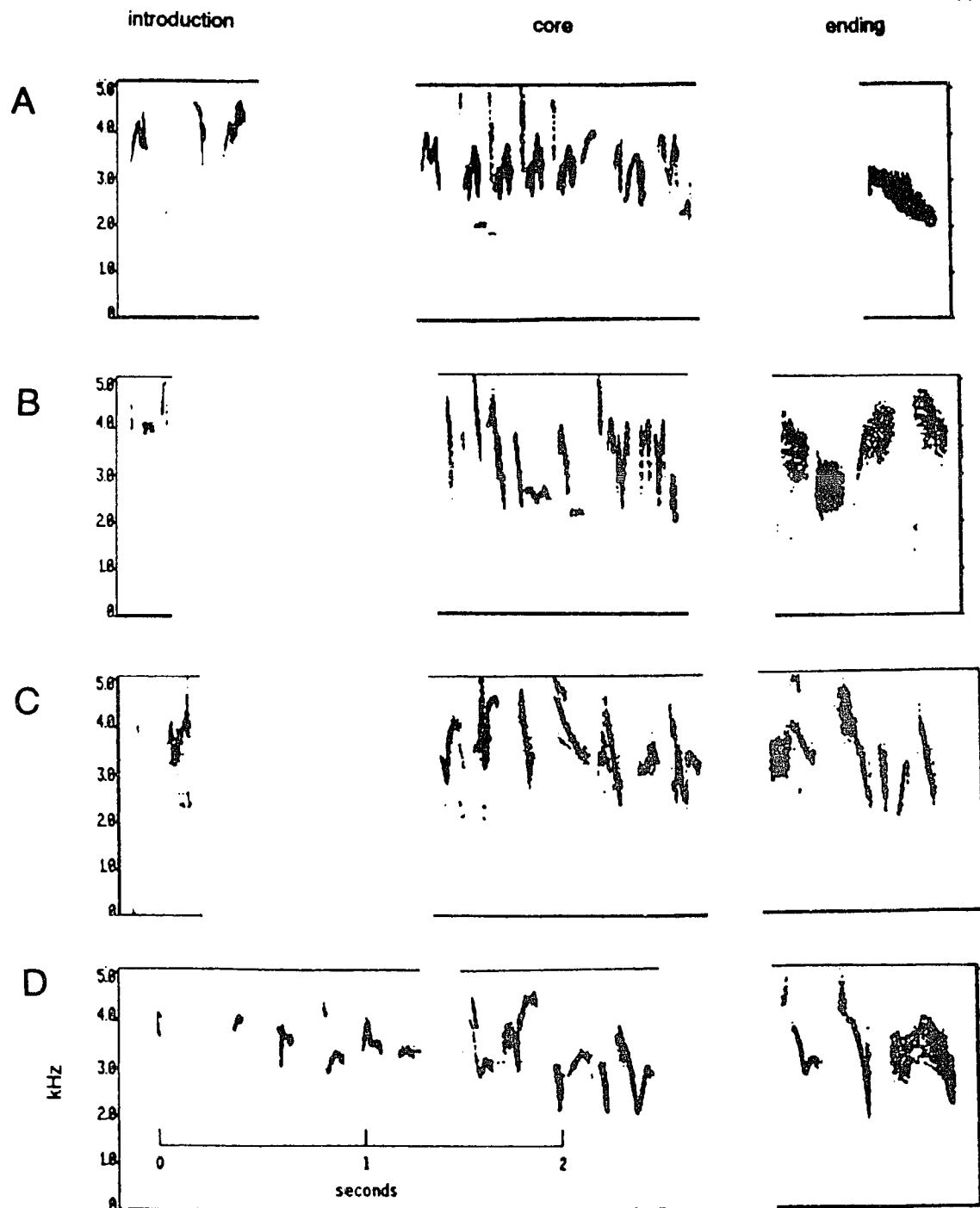


Figure 10: Representative songs sung by House Finches on Cape Cod in 1985 and 1986.

The songs are divided into three segments: introduction, core, and ending. Syllables differ in these segments (see text).

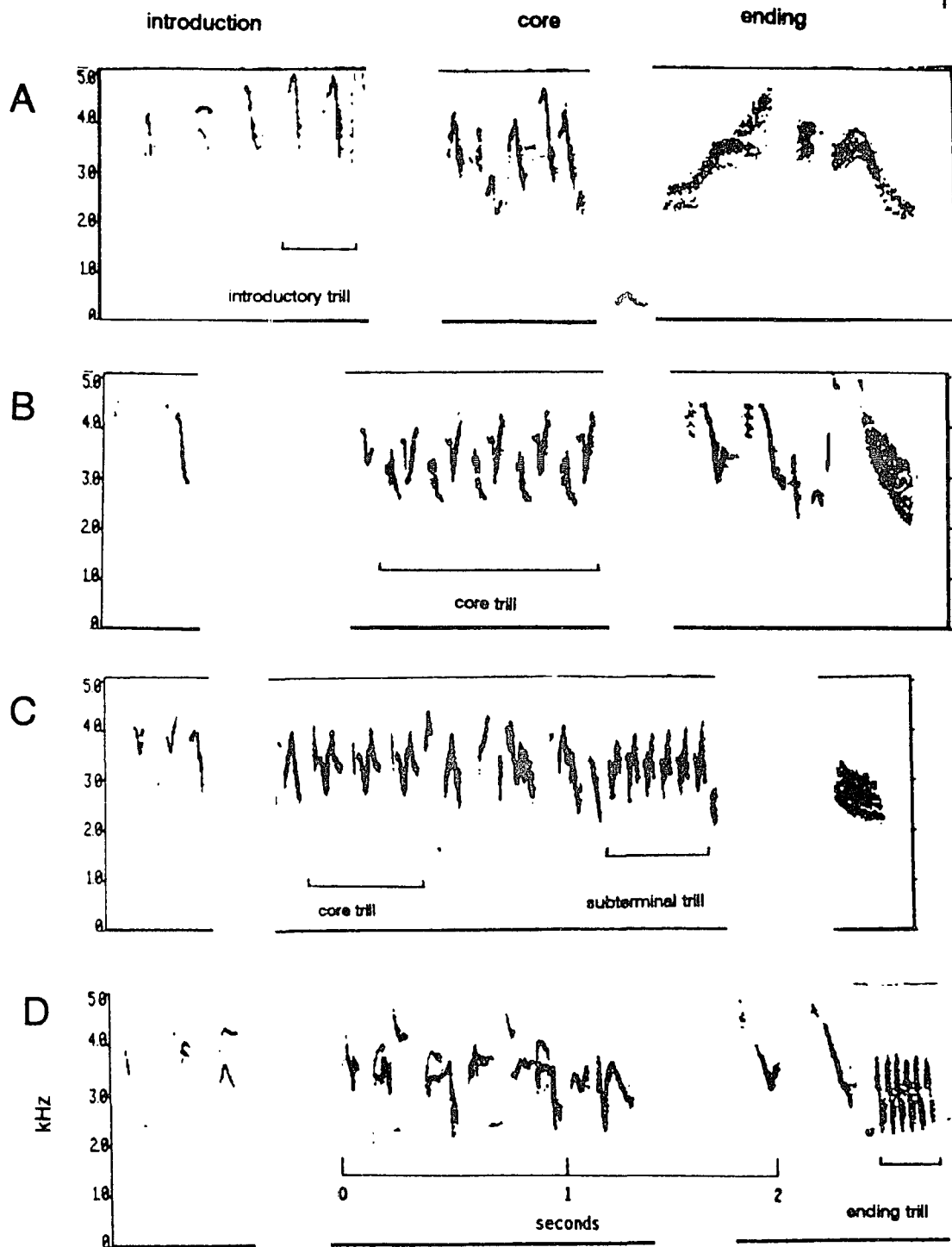


Figure 11: Representative songs containing trills sung by House Finches on Cape Cod.

The songs are divided into three segments: introduction, core, and ending. Trills appear in different segments of the songs (see text).

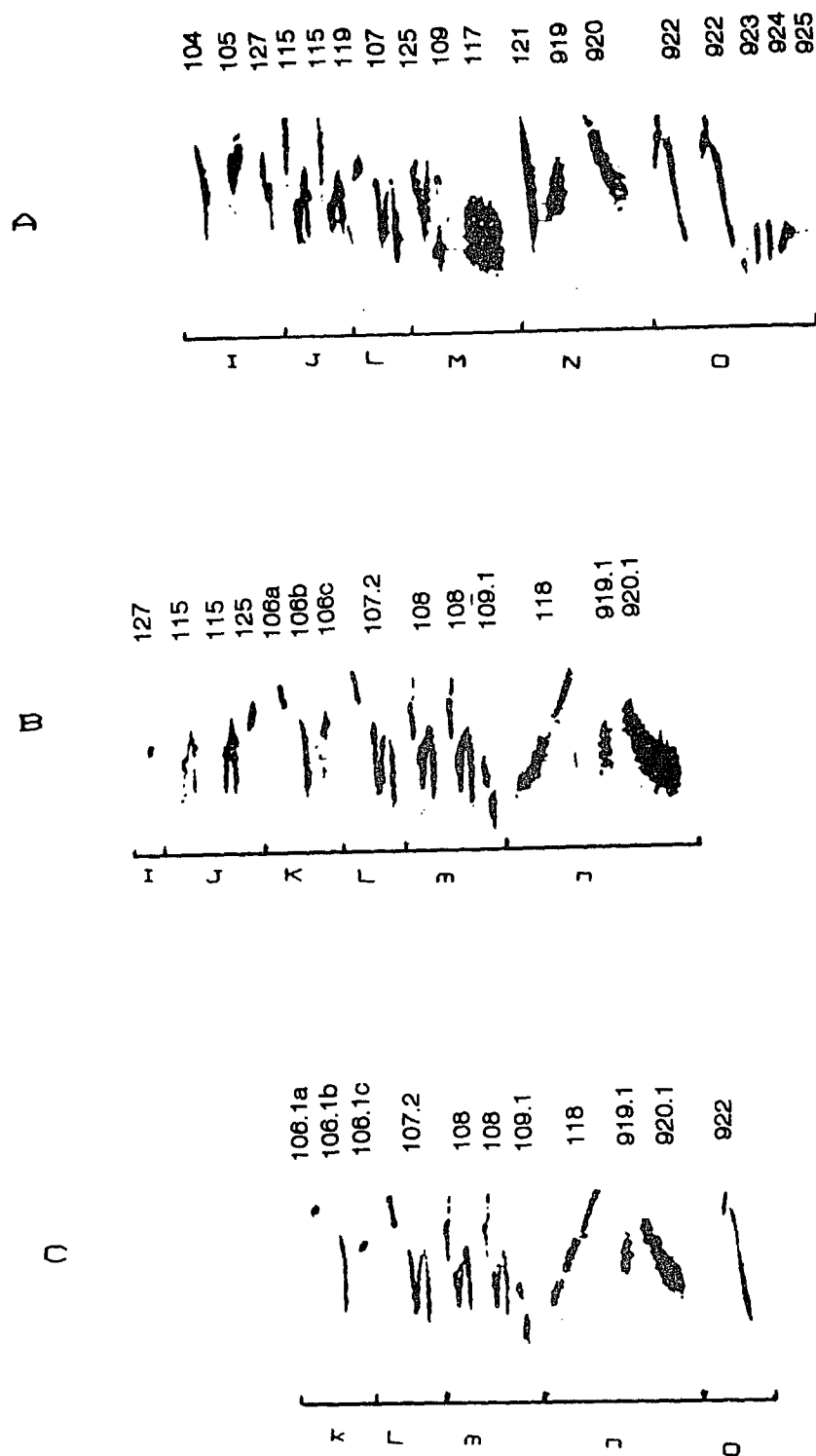
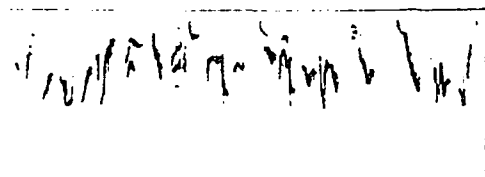


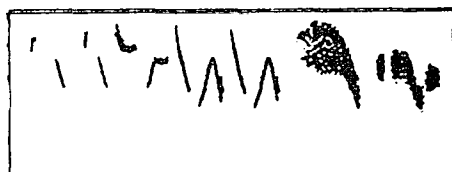
Figure 12: Representative songs sung in Truro demonstrating variation in songs within a dialect.

The range of variation within these songs represents the variation found in the songs of a single male.

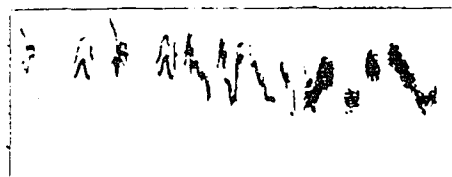
Population A



Theme 1

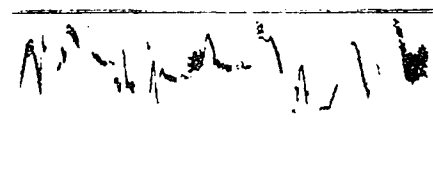


Theme 2

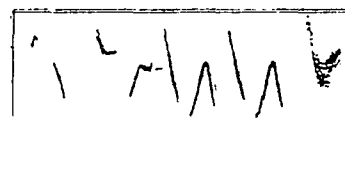


Theme 3

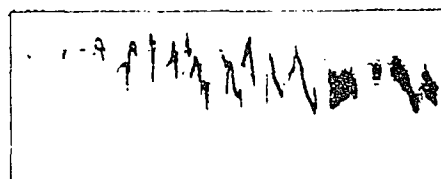
Population B



Theme 4

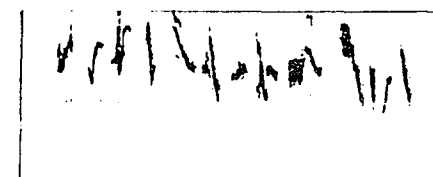


Theme 2

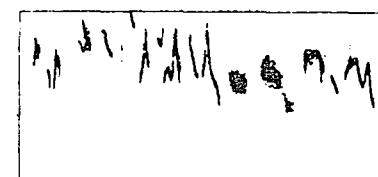


Theme 3

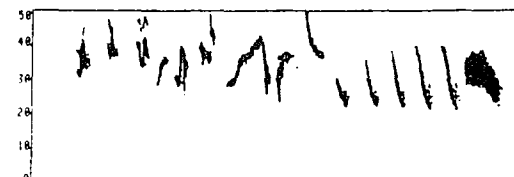
Population C



Theme 4



Theme 5



Theme 6

Figure 13: Theme replacements across a stratification zone.

Themes 1 through 3 are sung by population A. Theme 1 is replaced by theme 4 in population B. Themes 2 and 3 are replaced by themes 5 and 6 in population C.

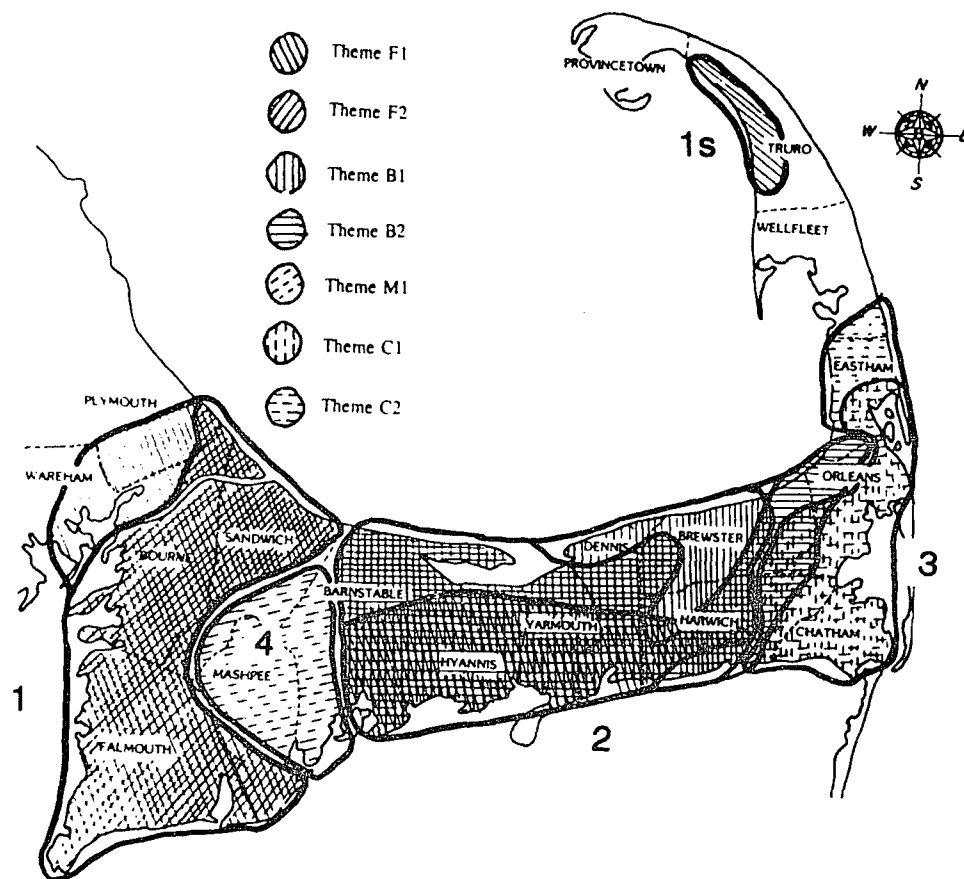


Figure 14: Primary locations where the seven themes of the four major institutions were sung on Cape Cod.

The four regional institutions are numbered: (1) Falmouth, (2) Barnstable, (3) Chatham, and (4) Mashpee. The population marked 1s is the Truro satellite of the Falmouth institution.

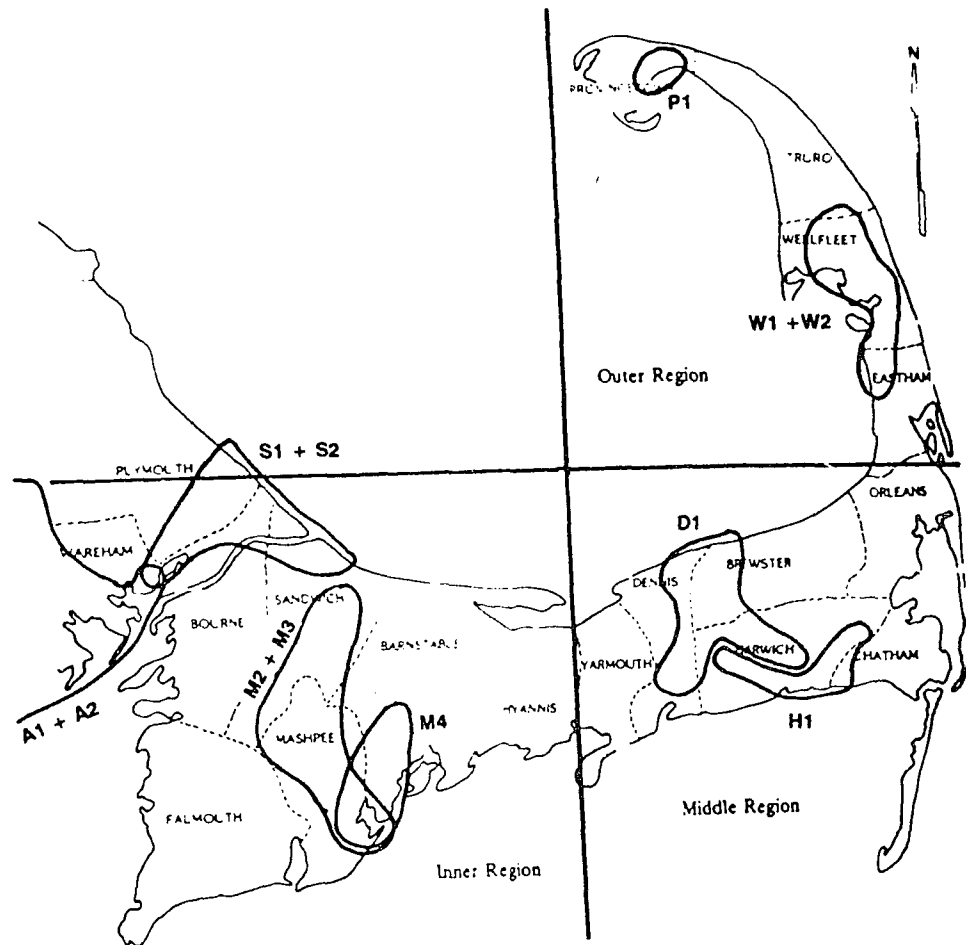


Figure 15: Locations of twelve minor song themes on Cape Cod.

Solid lines enclose areas within which themes were sung. Theme identifications are described in the text.

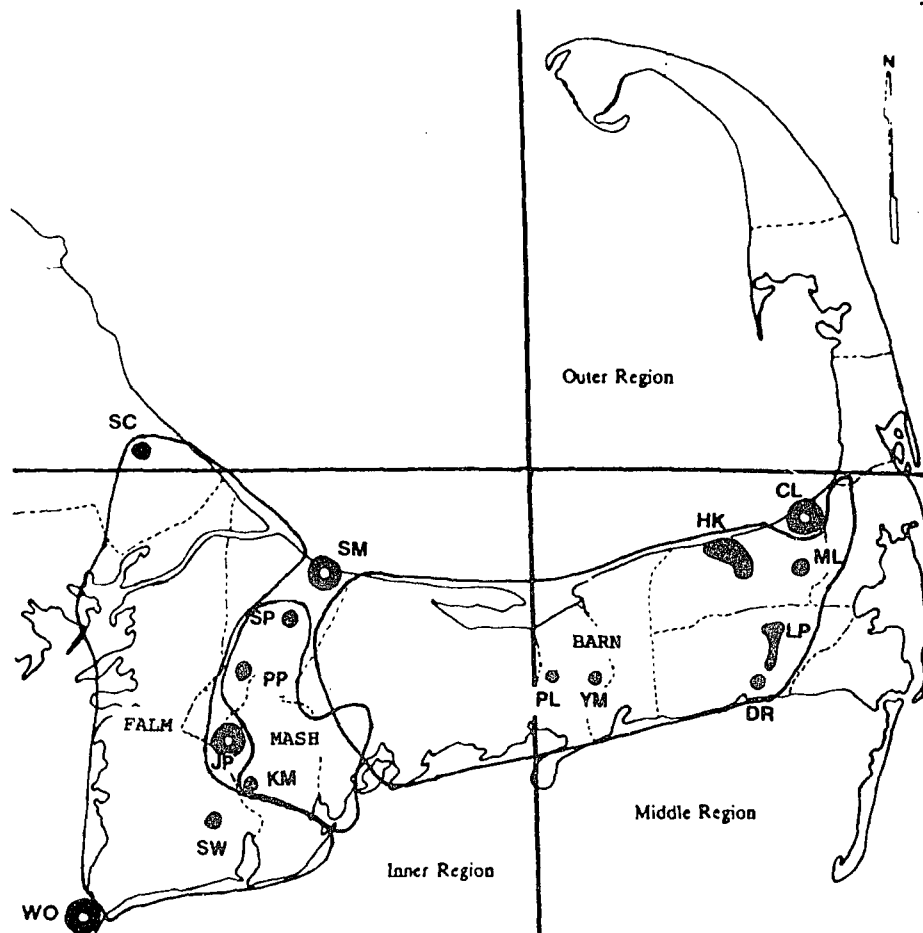


Figure 16: Map of Cape Cod showing locations of local song themes.

Open circles enclose areas within which local song institutions were sung. Solid circles enclose areas within which local themes were sung as part of the Falmouth (FALM), Mashpee (MASH), and Barnstable (BARN) song institutions. See text for theme identifications.

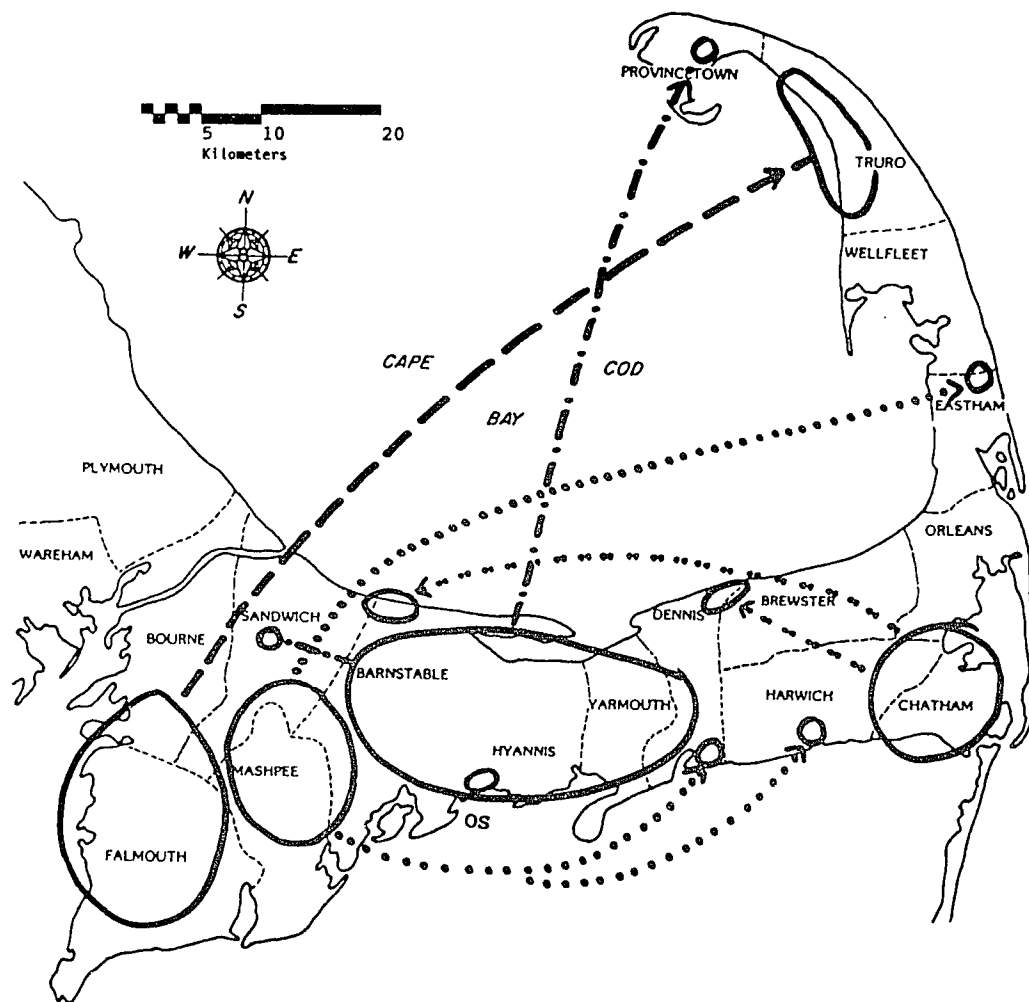


Figure 17: Locations of satellite populations of song institutions found in other areas of Cape Cod.

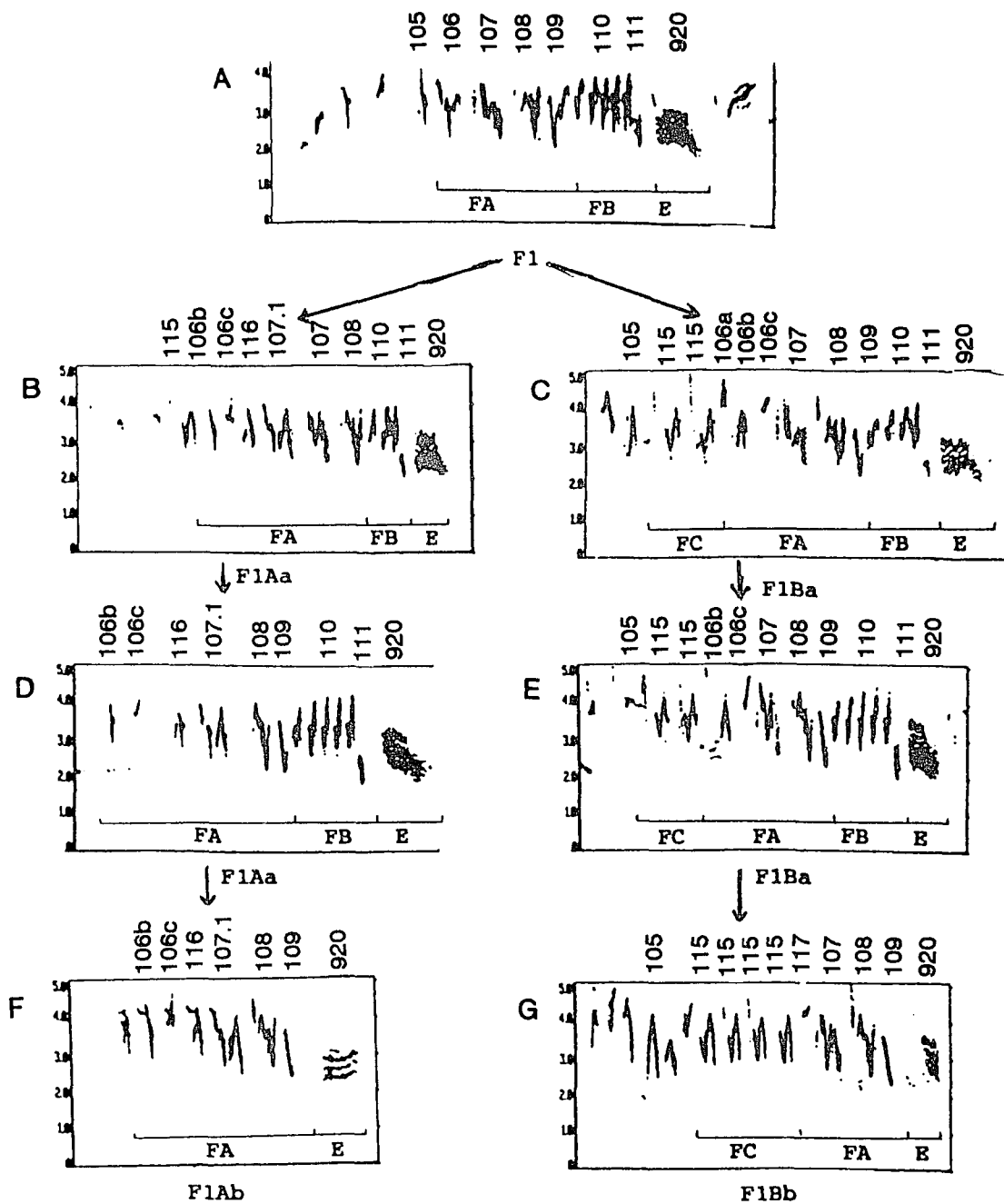


Figure 18: Sonograms showing divergence of theme F1, sung in Falmouth, MA, (sonogram A) into four sub-themes.

F1Aa (sonograms B and D), F1Ab (sonogram F),

F1Ba (sonograms C and E), and F1Bb (sonogram G)

The core routines of each sub-theme are underlined and identified.

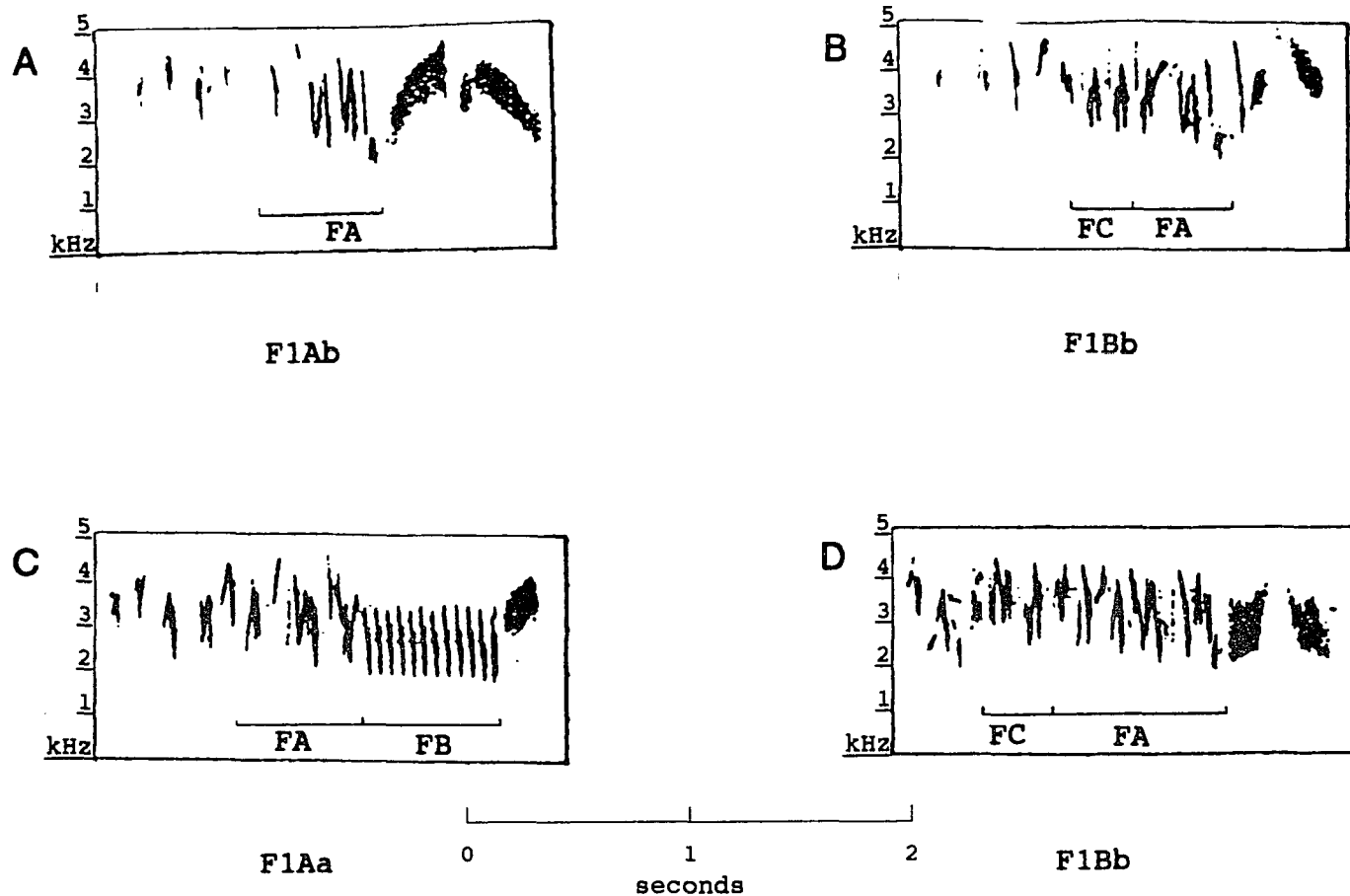


Figure 19: Sonograms of sub-themes F1A and F1B as sung in two dialects of the Falmouth institution.

Sonograms A and B were sung in Truro. Sonograms C and D were sung in Buttermilk Bay, Wareham.

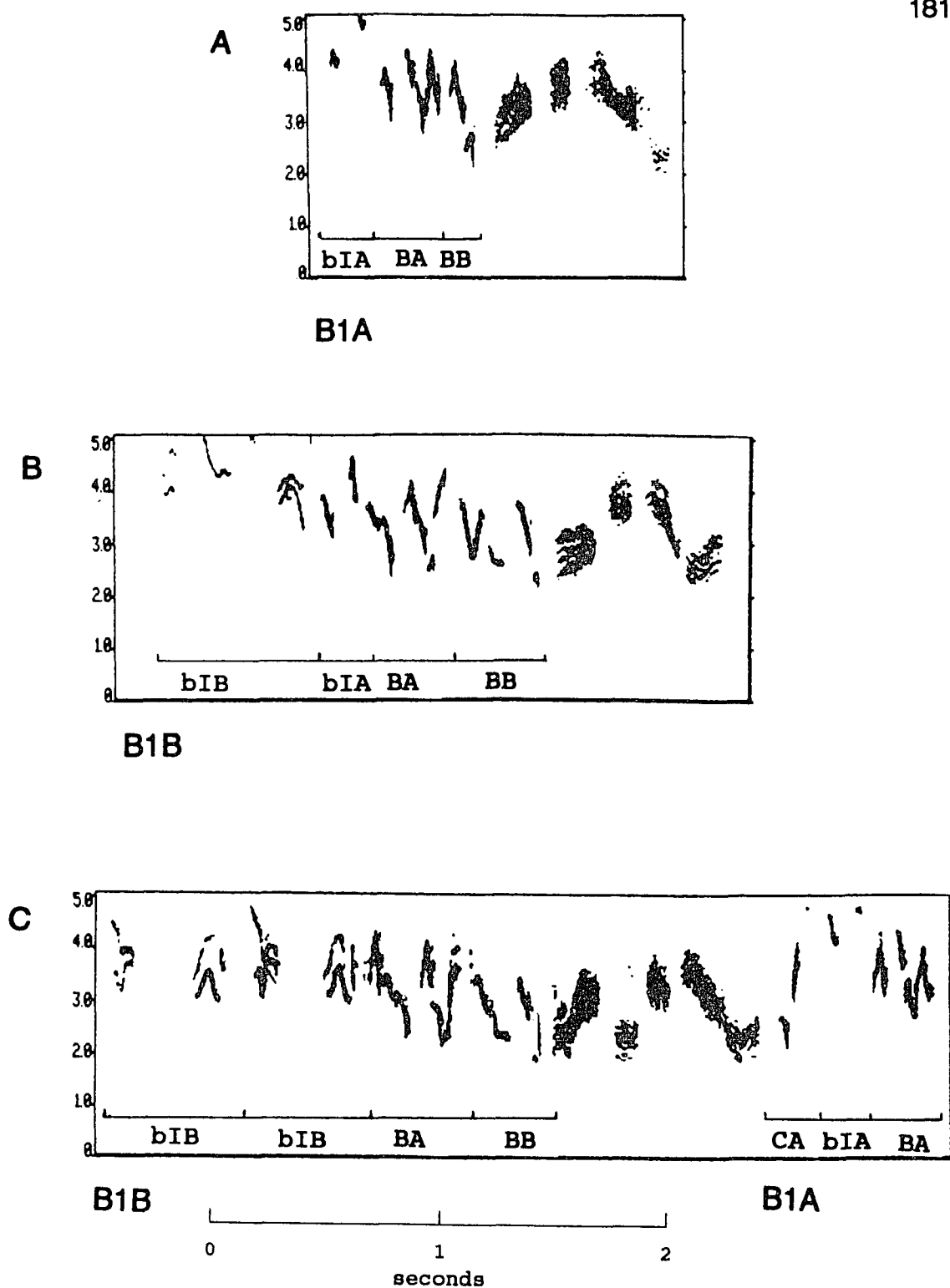


Figure 20: Sub-themes of theme B1, sung in the Barnstable institution.
Routines are discussed in the text.

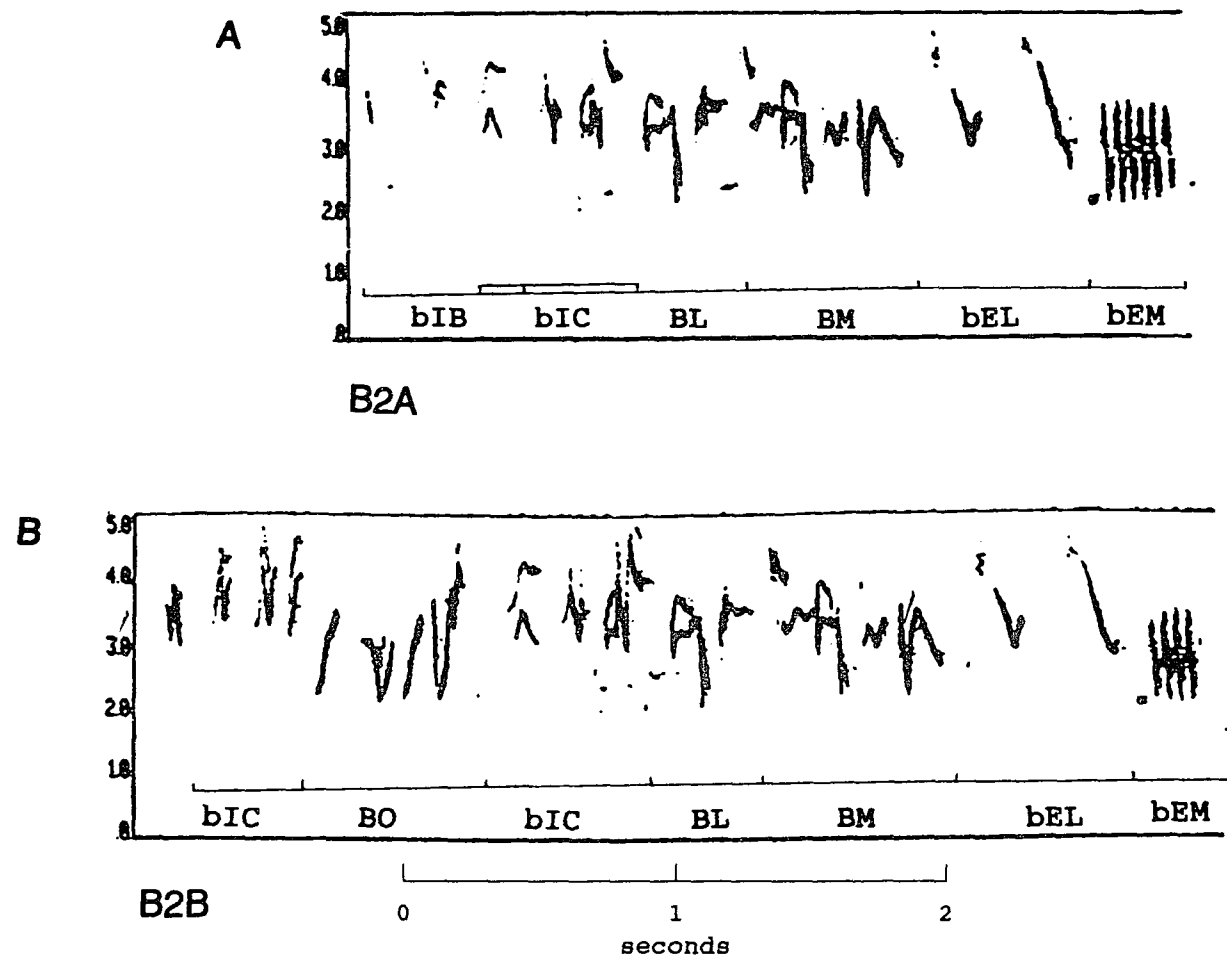


Figure 21: Sub-themes of theme B2, sung in the Barnstable institution.
Routines are discussed in the text.

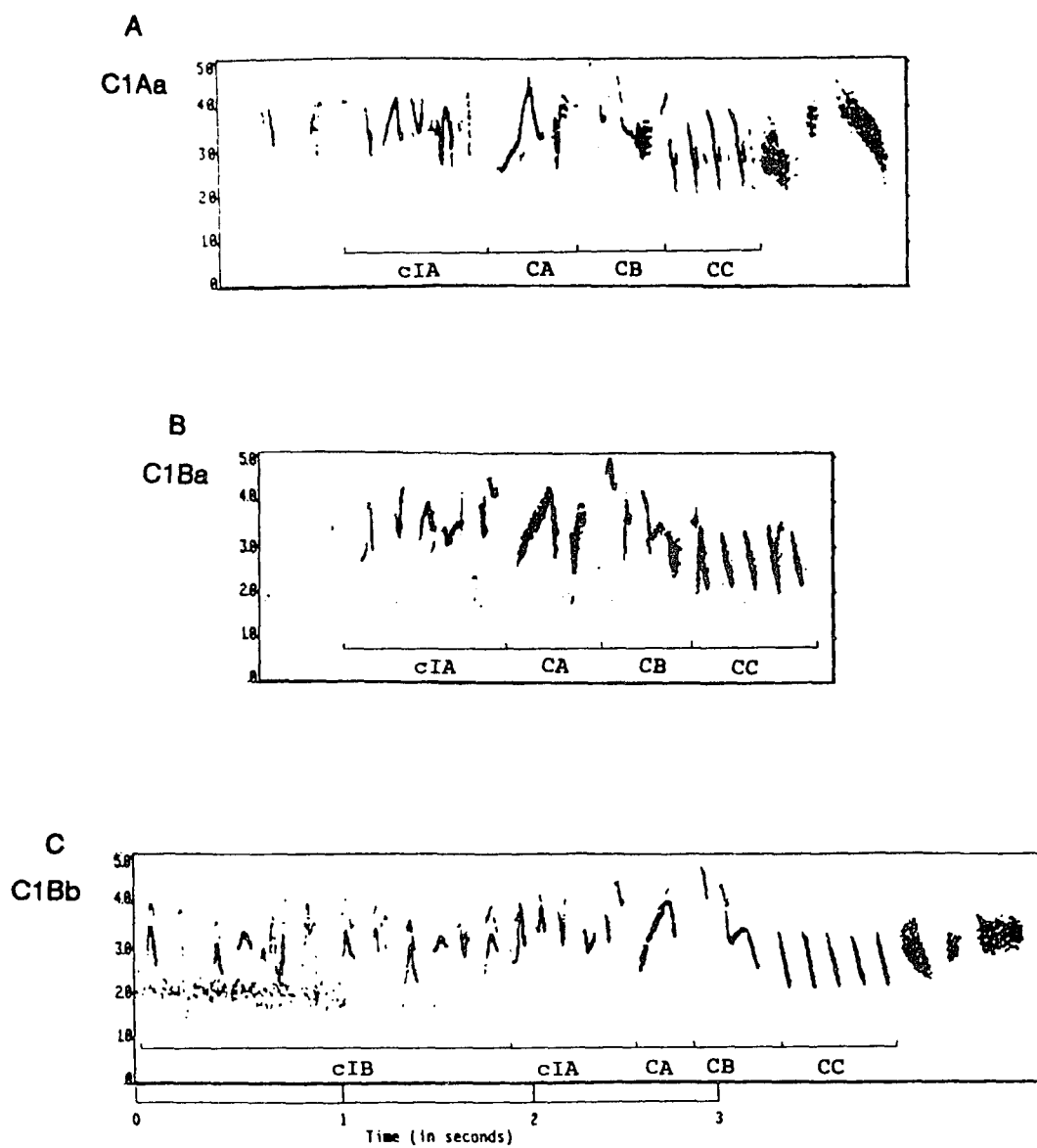


Figure 22: Sub-themes of theme C1, sung by one finch in the Chatham institution. Routines are discussed in the text.

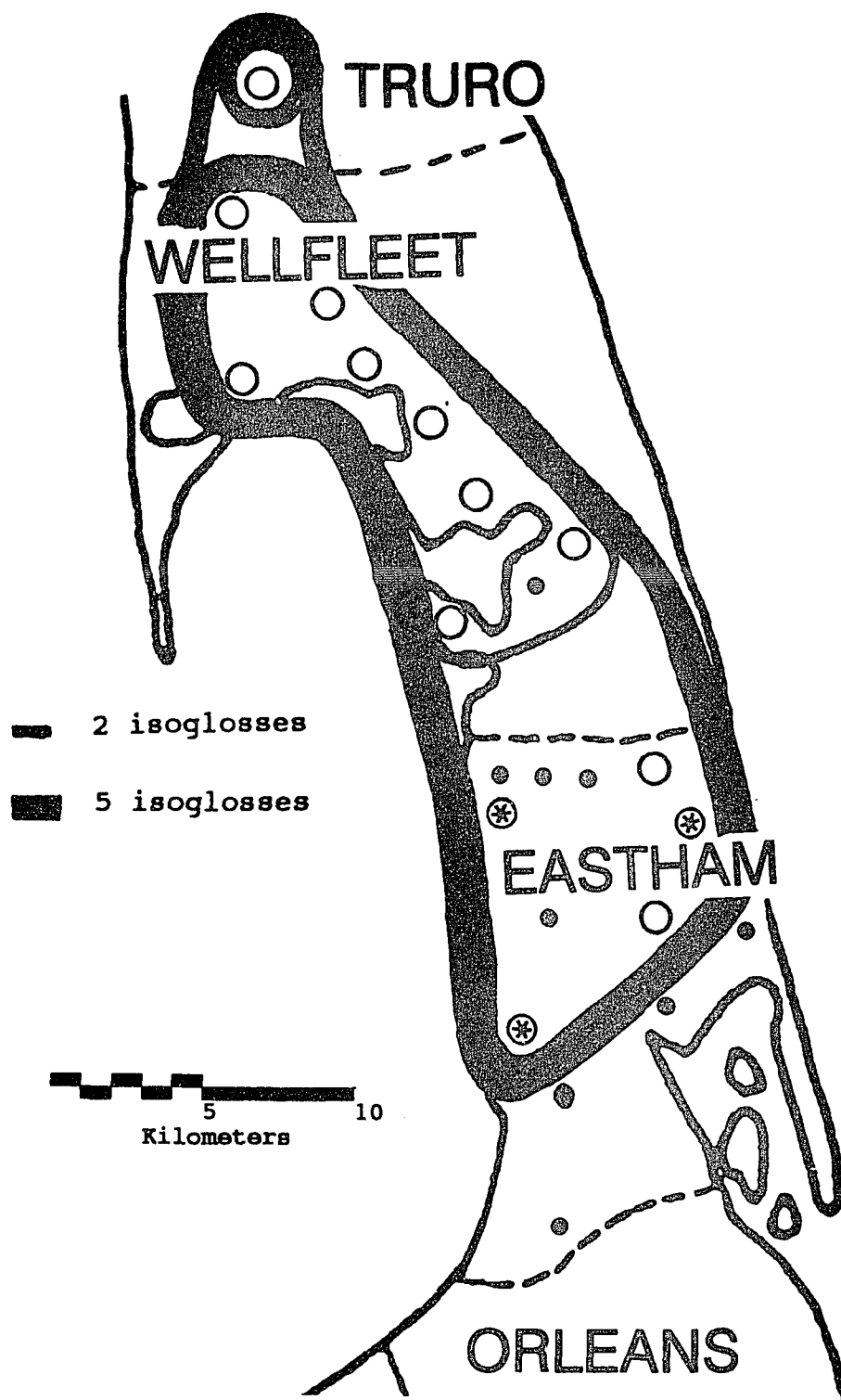


Figure 23: Isogloss analysis of the Wellfleet song institution.

Open circles (○) represent populations that sang only the Wellfleet institution. Circles with an asterisk (⊛) represent populations that sang both the Wellfleet and the Chatham institutions. Small filled circles (●) represent populations that sang only the Chatham institution.

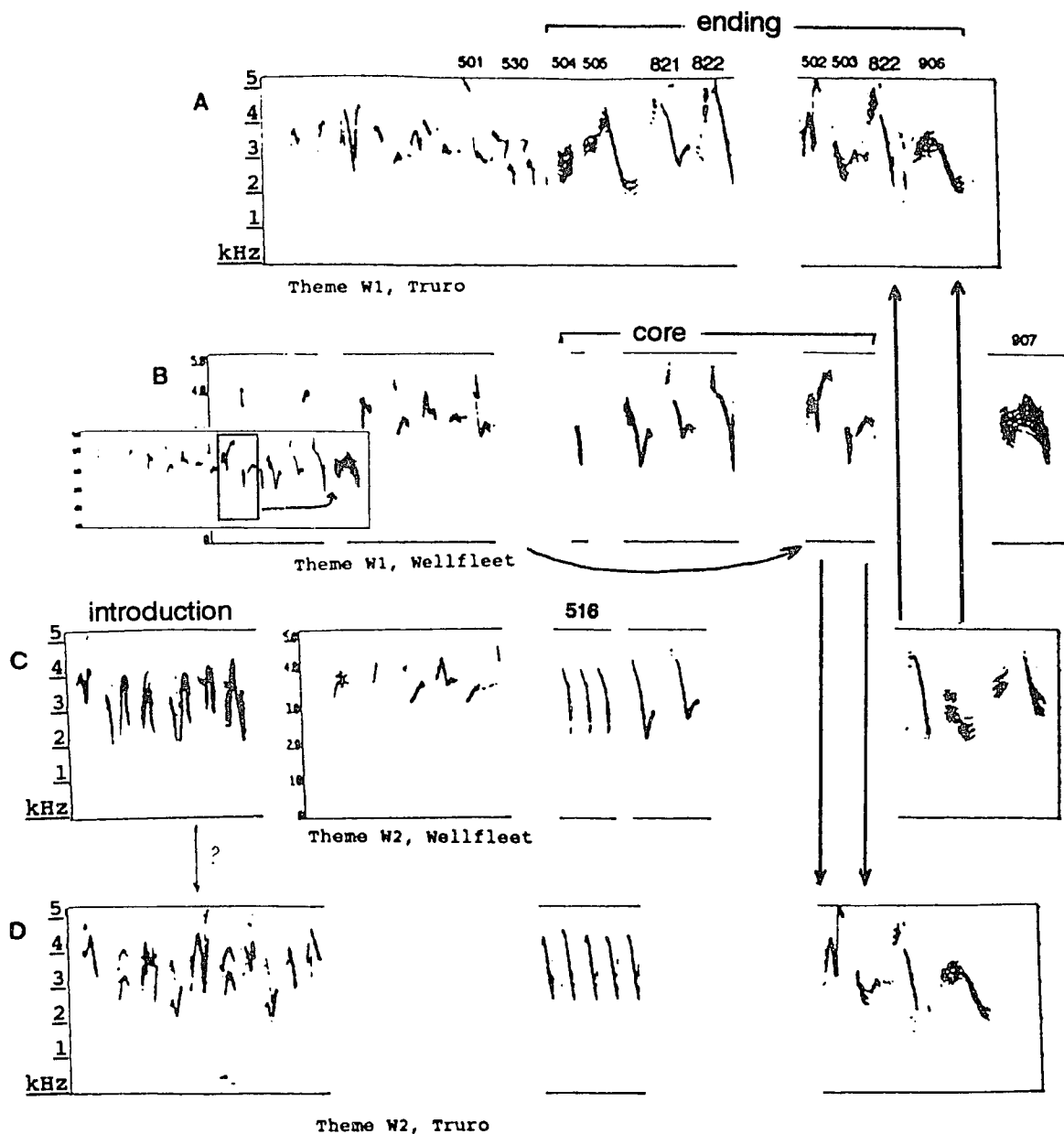


Figure 24: Sonograms showing variation in themes W1 and W2 as sung in the Wellfleet and Truro dialects of the Wellfleet institution.

Sonograms A and B are of theme W1 as sung in Truro and Wellfleet, respectively. Sonograms C and D are of theme W2 as sung in Wellfleet and Truro, respectively. Syllables of sonograms A, C, and D are in the sequences they were sung. In sonogram B, syllables 502 and 503 were moved by me to the right as indicated by the curved arrow (see inset for their original position in song) so they would align with their variants sung in Truro. Vertical arrows indicate where routines sung in one theme in Wellfleet were inserted into the alternate theme in Truro.

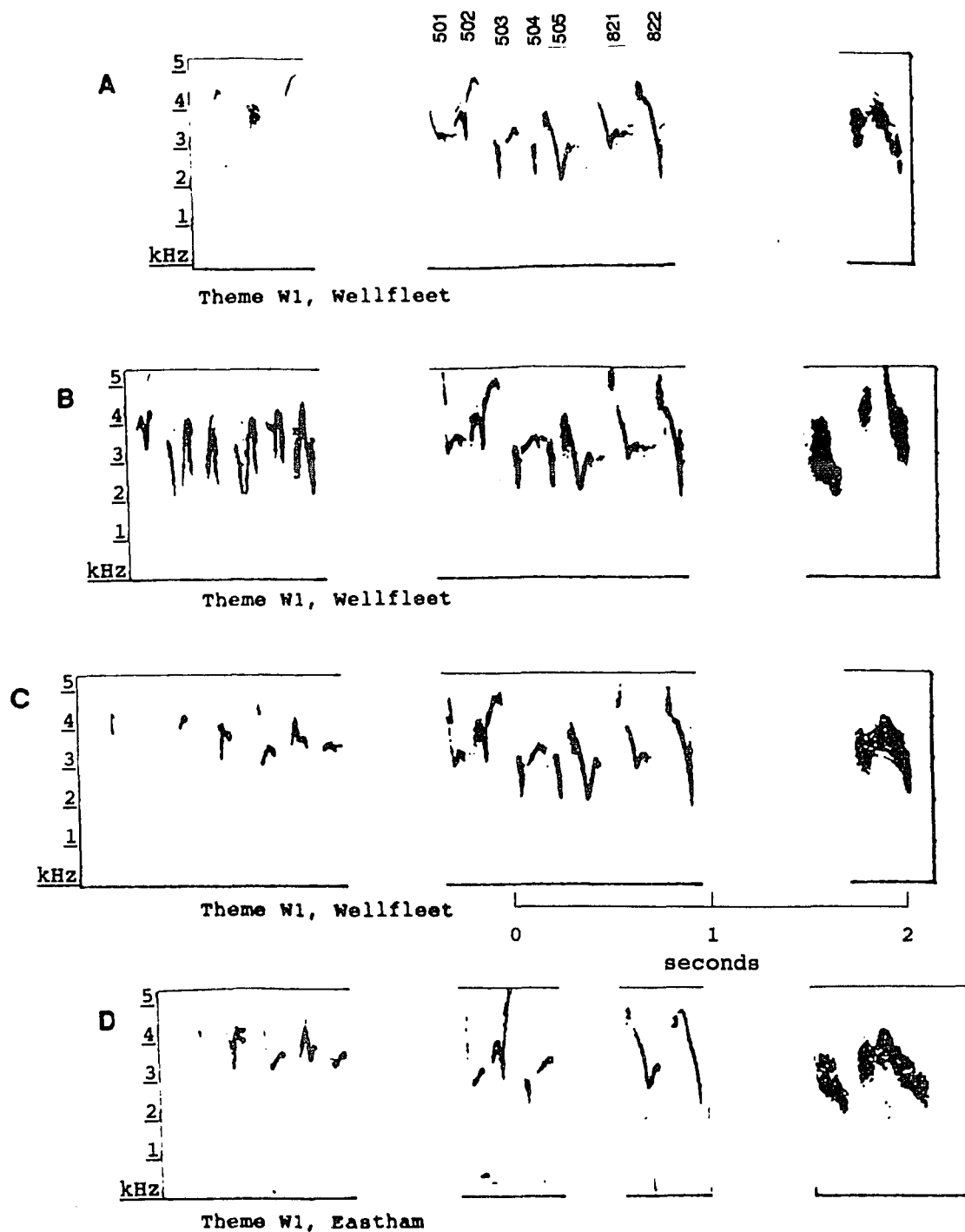


Figure 25: Theme W1 as sung in Wellfleet and Eastham.

Sonograms A, B, and C were sung in Wellfleet. Sonogram D was sung in Eastham. Homologous core and ending syllables are numbered and their routines are positioned in columns. Differences in introductory routines are discussed in the text.

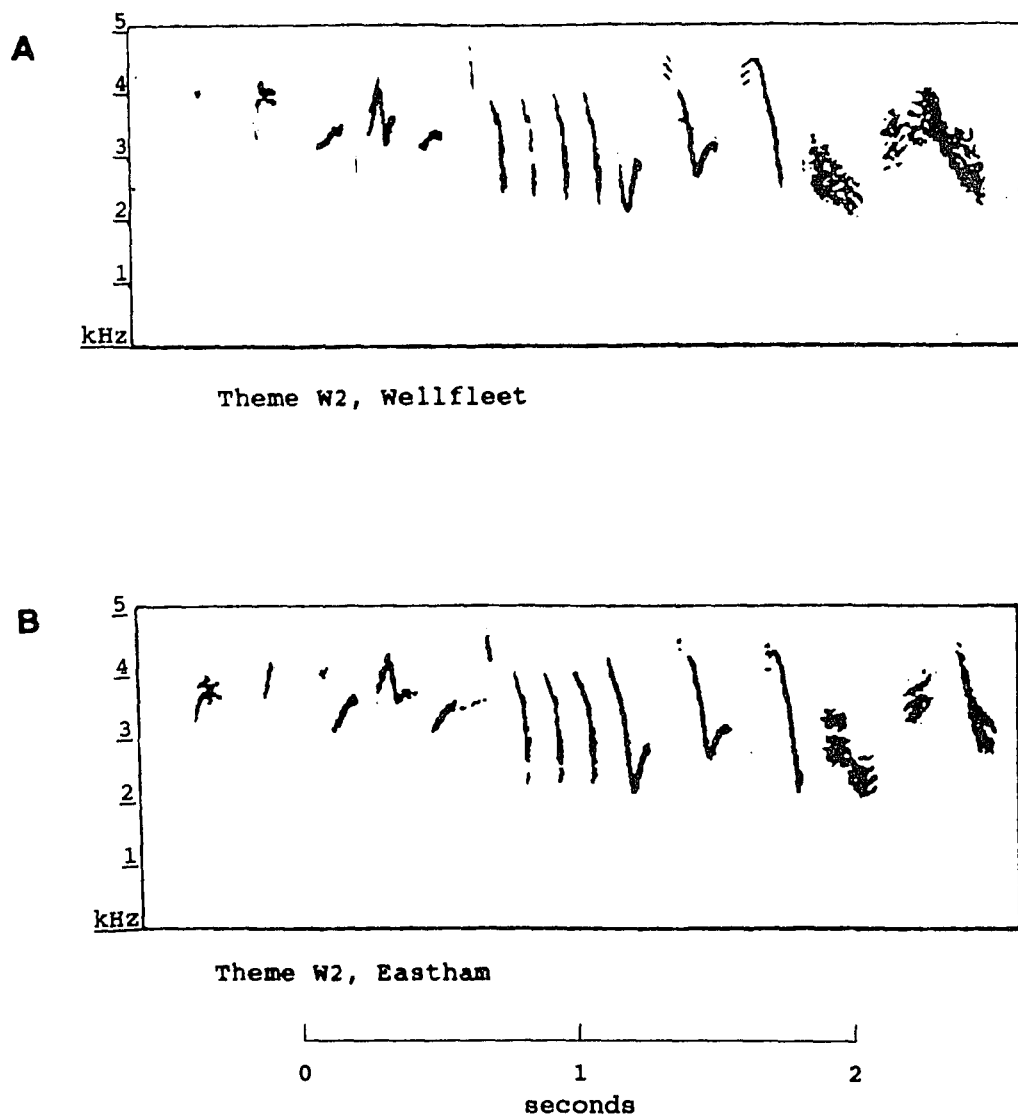


Figure 26: Theme W2 as sung in Wellfleet and Eastham.
Sonogram A was sung in Wellfleet. Sonogram B was sung in Eastham.

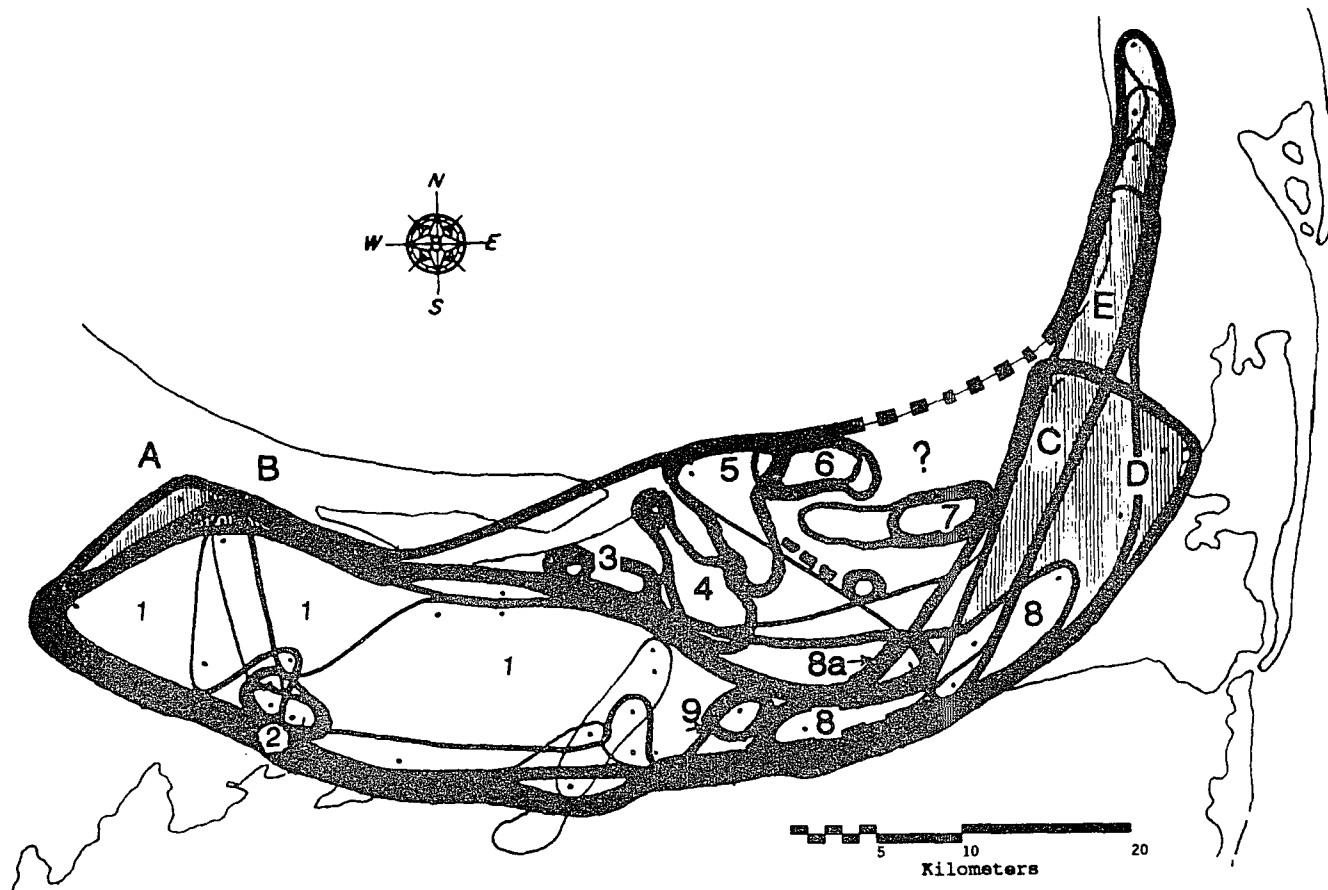


Figure 27: Isogloss analysis of the Barnstable song institution.

The nine dialects are numbered. The themes sung in each dialect are identified in the text.

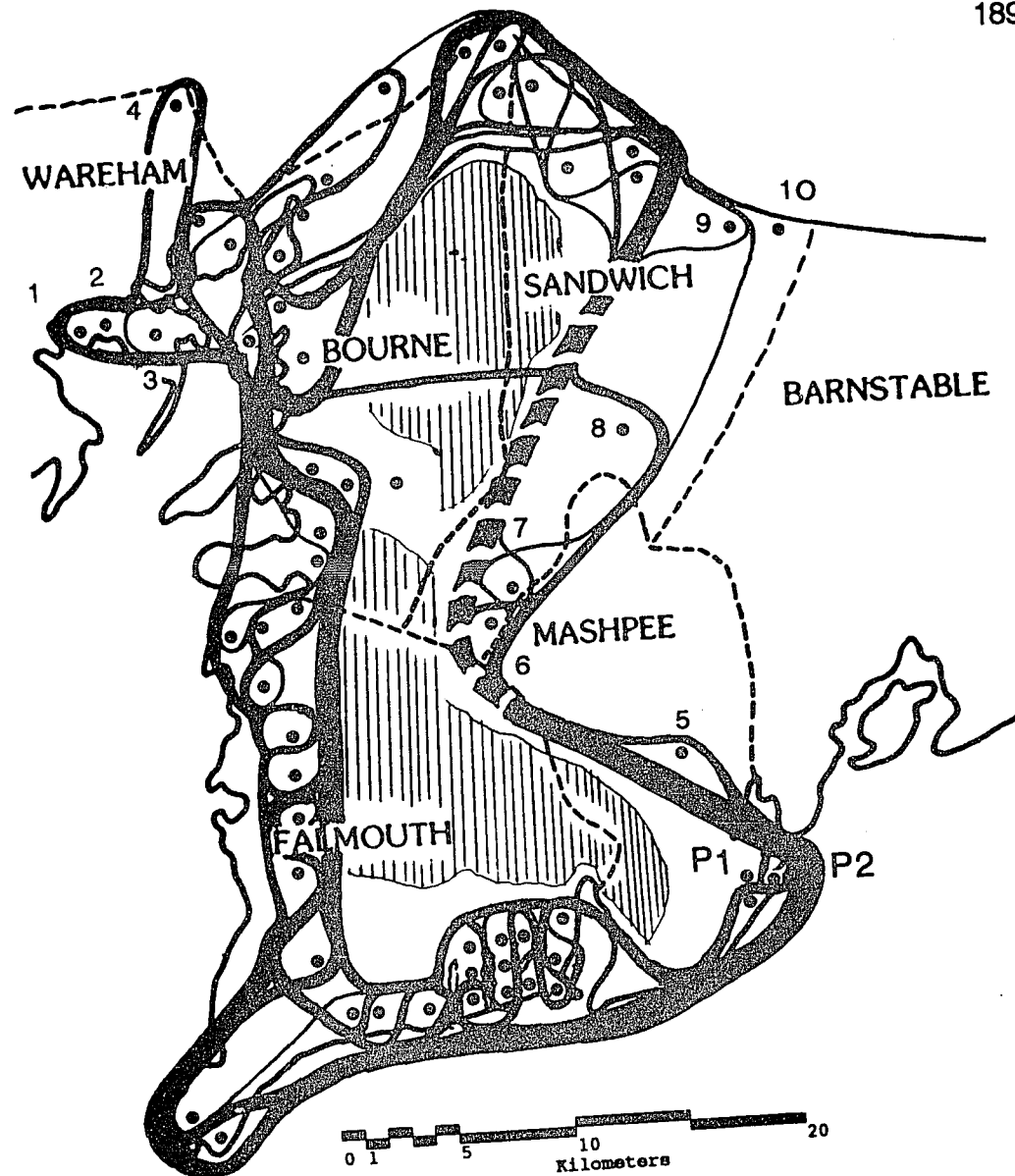


Figure 28: Isogloss analysis of the Falmouth song institution based on distribution of twenty five common song routines.

P1 and P2 are the two Popponesset populations (see text). Populations 1 through 10 belong to the Wareham, Mashpee, and Salt Marsh institutions (see text). The shaded area represents inhospitable terrain or military bases (see text) so no house finches were sampled there.

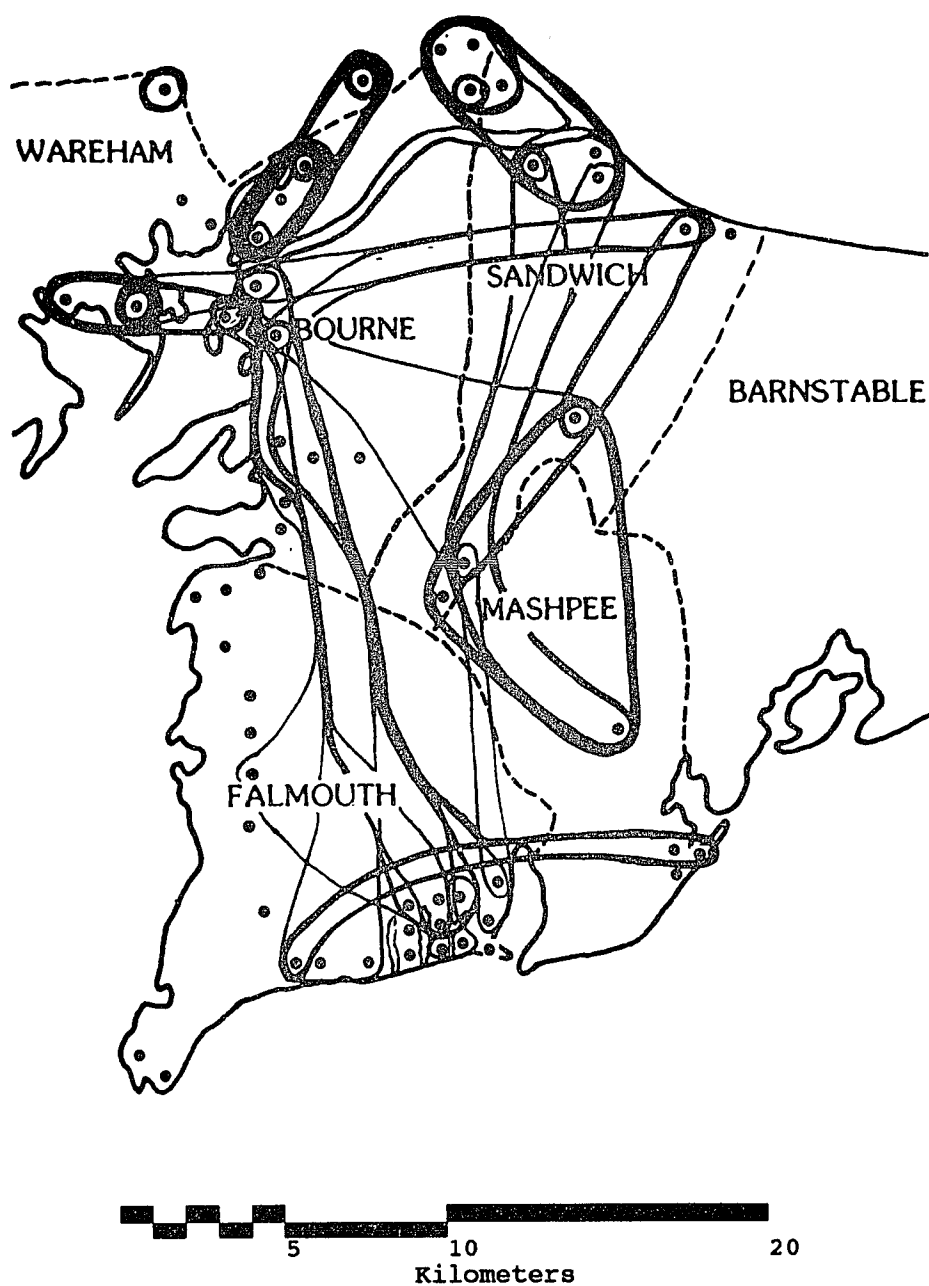


Figure 29: Isogloss analysis of the Falmouth song institution based on distribution of twenty nine rare song routines.

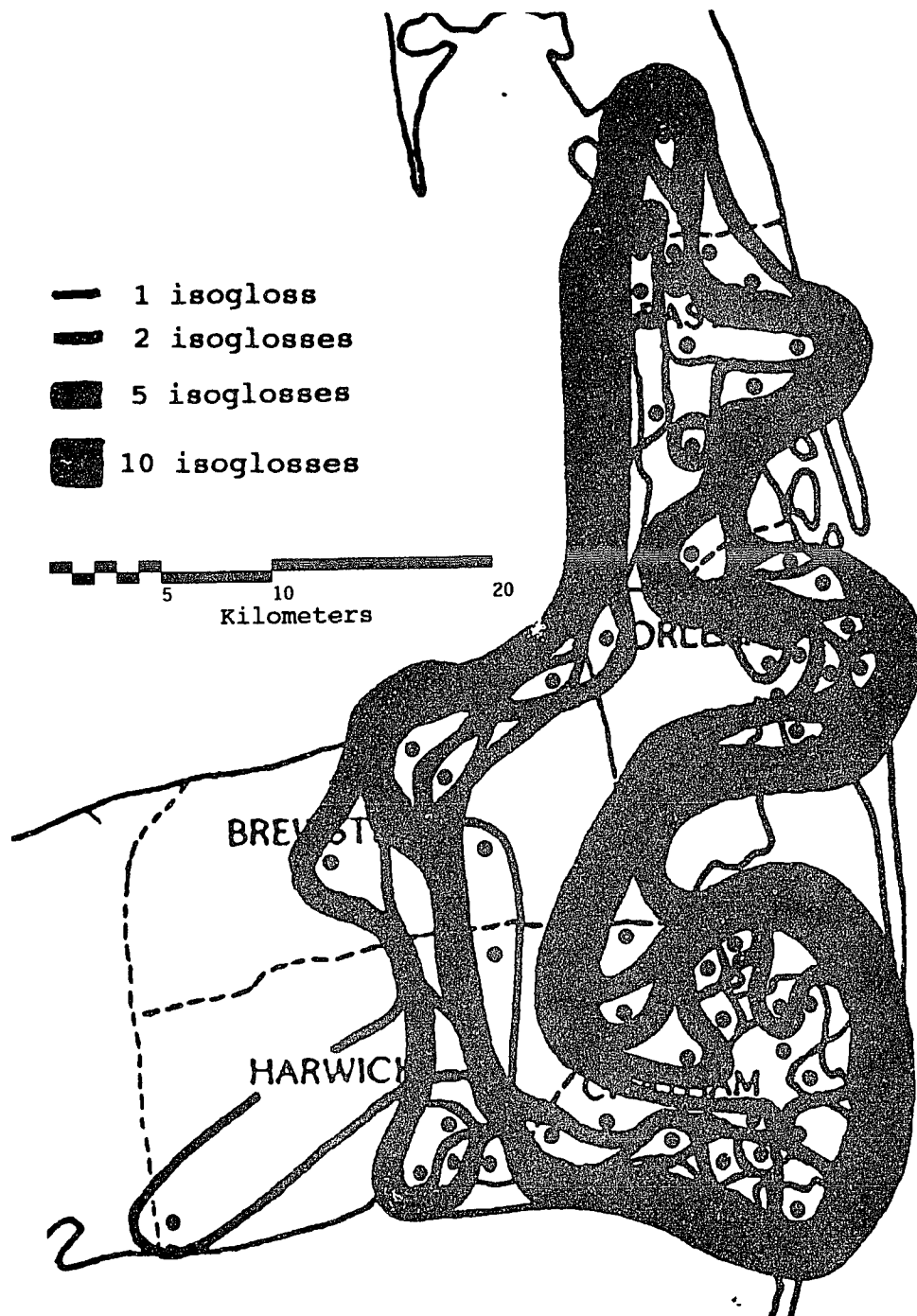


Figure 30: Isogloss analysis of the Chatham song institution sung in the middle cape and Eastham.

Black dots mark bird locations at which one or more House Finches were recorded.

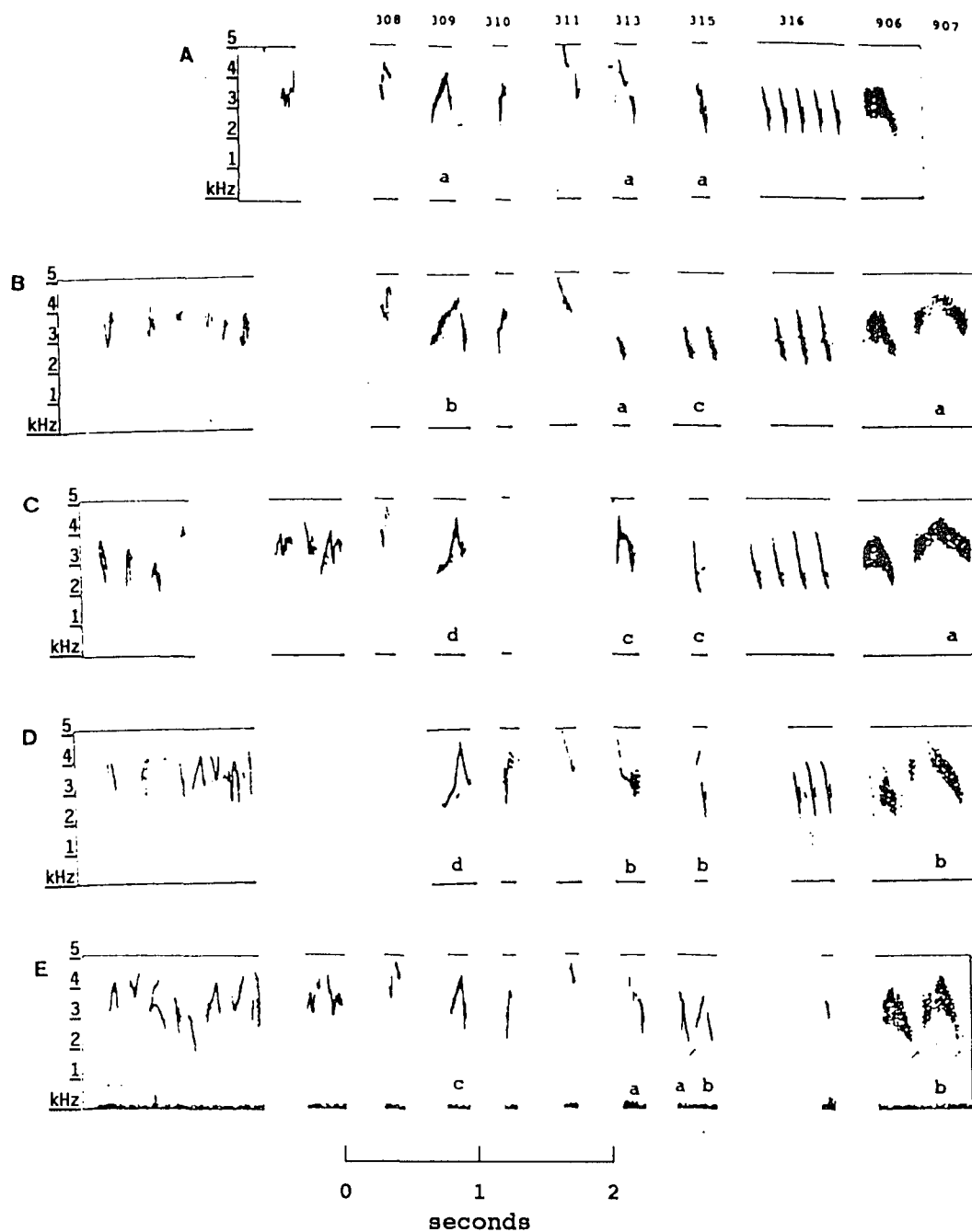


Figure 31: Pronunciation variants of syllables of theme C1 sung in the Chatham song institution.

Homologous syllables are positioned in columns. Variants of syllables 309, 313, 315, and 907 (lower case letters) are discussed in the text.

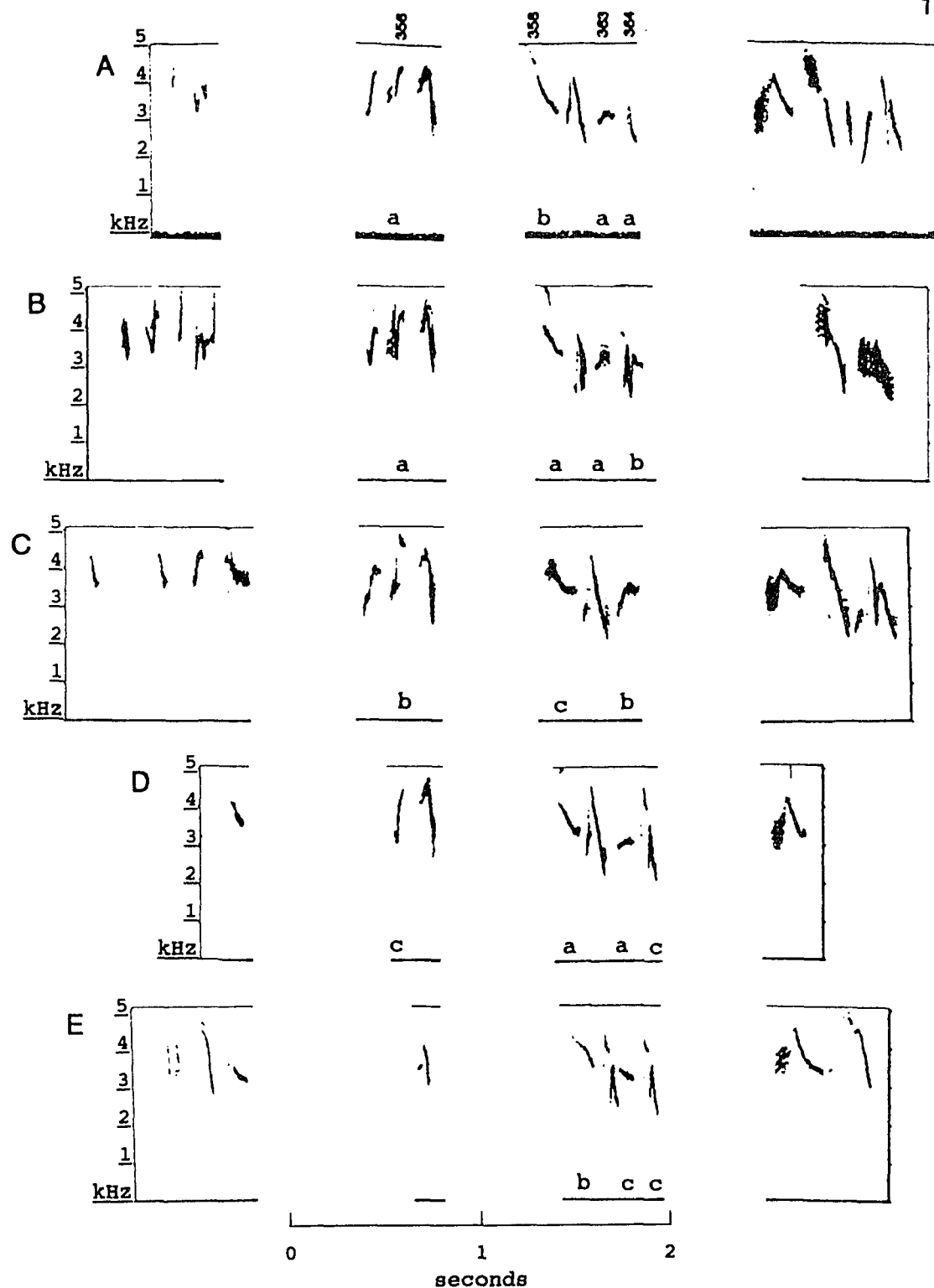


Figure 32: Pronunciation variants of syllables of theme C2 sung in the Chatham song institution.

Homologous syllables are positioned in columns. Variants of syllables 356, 358, 363, and 364 (lower case letters) are discussed in the text.

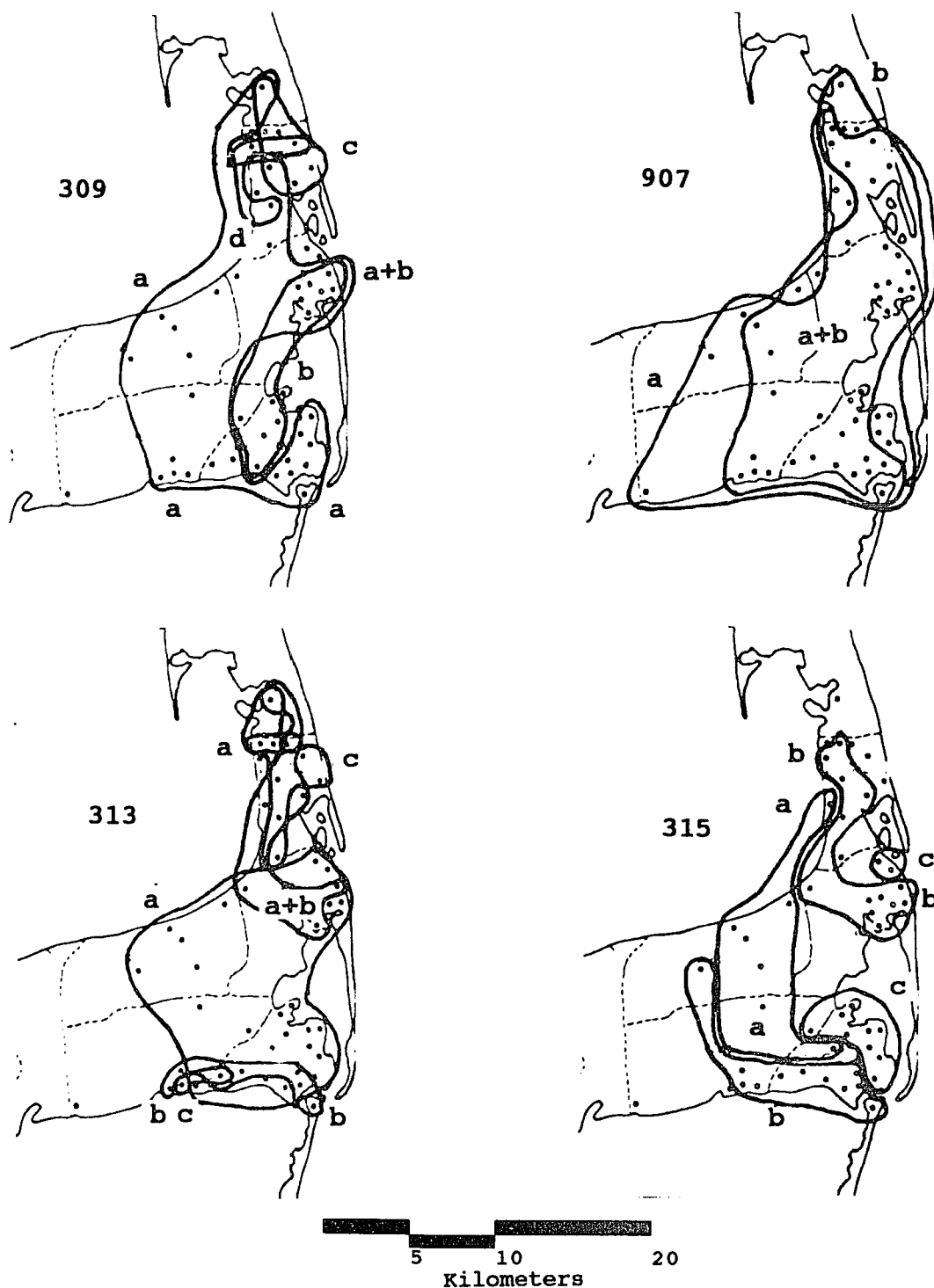


Figure 33. Standard maps of the middle and lower outer cape showing locations of populations singing the several variants of syllables 309, 907, 313, and 315 sung in theme C1 of the Chatham song institution.

Black dots mark locations at which one or more House Finches were recorded.

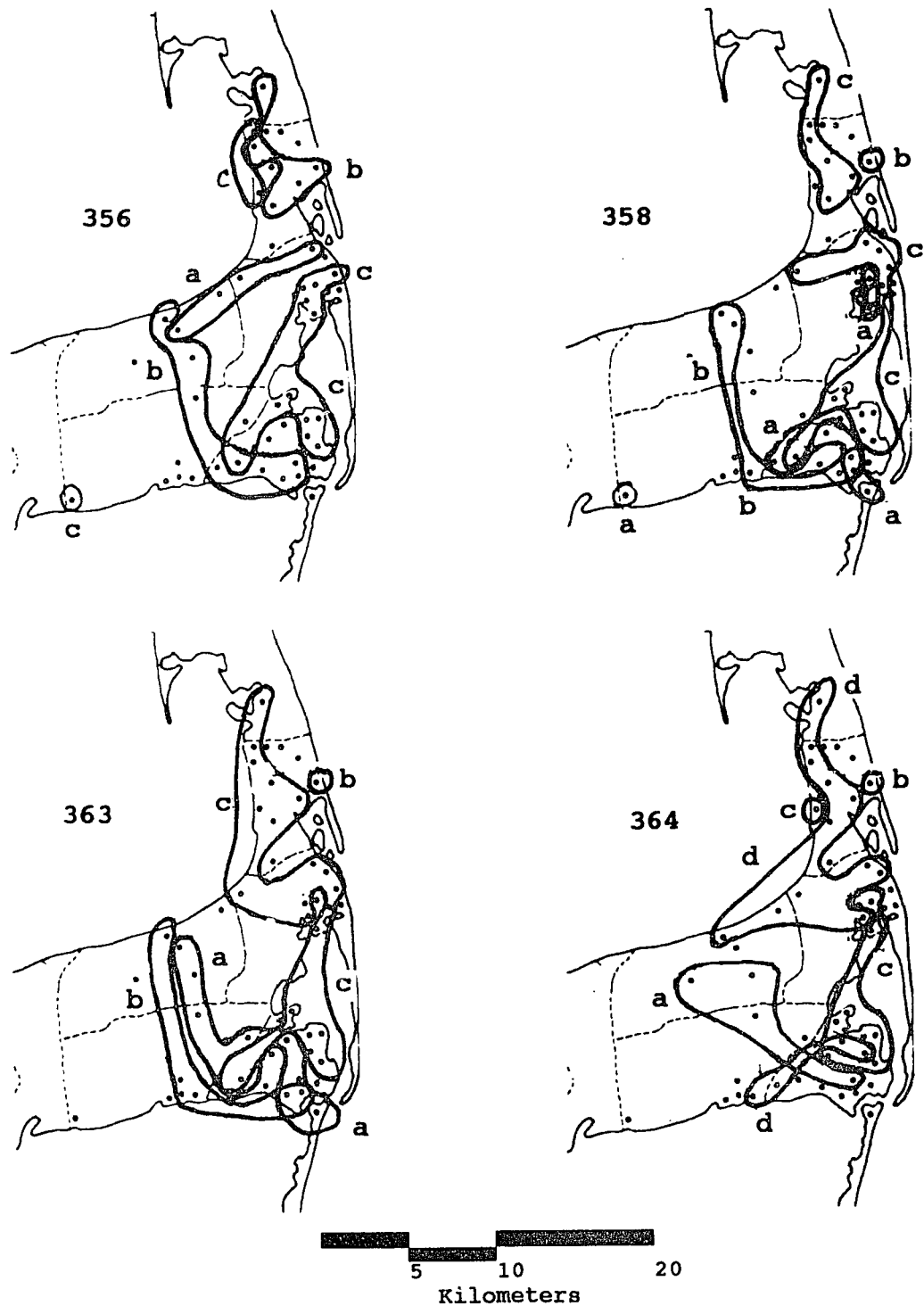


Figure 34. Standard maps of the middle and lower outer cape showing locations of populations singing the several variants of syllables 356, 358, 363, and 364 sung in theme C2 of the Chatham song institution.

Black dots mark locations at which one or more House Finches were recorded.

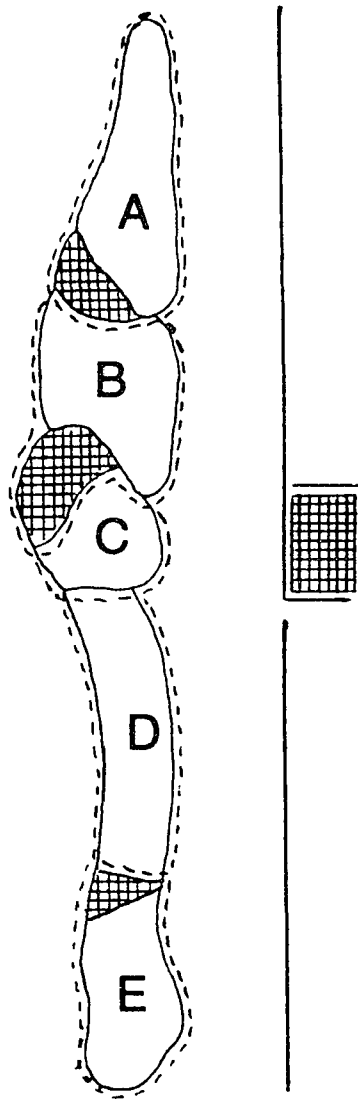


Figure 35: Patterns of geographic variation in four parts of White-crowned Sparrow song in a series of contiguous dialects of the Point Reyes National Seashore.

Solid lines enclose populations sharing complex syllables, dashed lines, those sharing simple syllables. Cross-hatched areas indicate males singing the complex syllable of one population and the simple syllables of the adjacent population ("hybrid songs"). Vertical lines on the right indicate sharing of ending and introductory syllables. Dialects A, B, and C shared a common ending that differed from the ending shared by dialects D and E. Dialects A and B shared a common introduction that differed from the introduction shared by dialects C, D, and E. Intergradation between these groups is noted by the cross hatching on the right. After Baker and Thompson (1985).

Song Stratum	Dialect population				
	A	B	C	D	E
Introduction	Northern form		Southern form		
Complex	C(a)	C(b)	C(c)	C(d)	C(e)
Simple	S(a)	S(b)	S(c)	S(d)	S(e)
Ending	Northern form		Southern form		

Figure 36: Stratification analysis of zones of overlap between dialect populations of White-crowned Sparrows in the Point Reyes National Seashore.

Complex syllables are identified as C(a), C(b), etc. Simple syllables are identified as S(a), S(b), etc. Vertical lines indicate dialect boundaries of the syllables. Shading indicates regions of stepwise hybridization (stratification). The double lines at dialect C indicate the transition zone between northern and southern forms of the several syllable types.

Sector	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Themes																Stratum	
	B1		D1		B1	D1	B1							-		I	
	B2A							C2	-	C2	B2A	-	B2A	-		C2	II
	B1B	-	B1d	-	B1B	B1d	H1			-	H1	-	H1		C1B	III	
	-								LP1		-	C1A					IV

Figure 37: The pattern of stratified theme replacement in 16 populations of House Finches recorded in a transect in the southern portions of the towns of Dennis, Harwich, and Chatham on Cape Cod.

There are four strata (levels in the repertoire) identified by roman numerals. Symbols in the boxes identify the themes sung by populations under which the boxes extend (see text). The symbol B1d represents the Dennis dialect of theme B1B. Dashes indicate no theme is sung by a population in a particular stratum. The double vertical lines indicate the culturally hybrid region between the Barnstable and Chatham song institutions (see text).

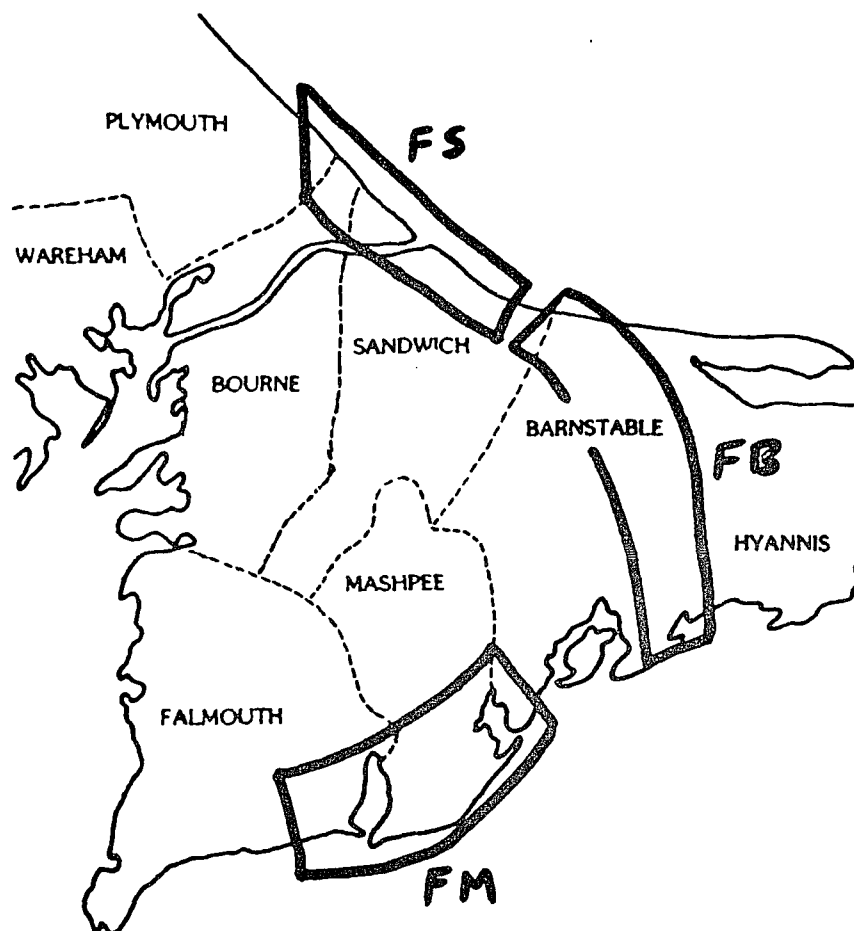


Figure 38: Three transects through boundary regions of the Falmouth song institution which demonstrated song intergradation (FS), reticulate evolution (FM), and song stratification (FB, see text).

FM = the Falmouth/Mashpee boundary; FB = the Falmouth/Barnstable boundary; FS = the Falmouth/Sandwich boundary.

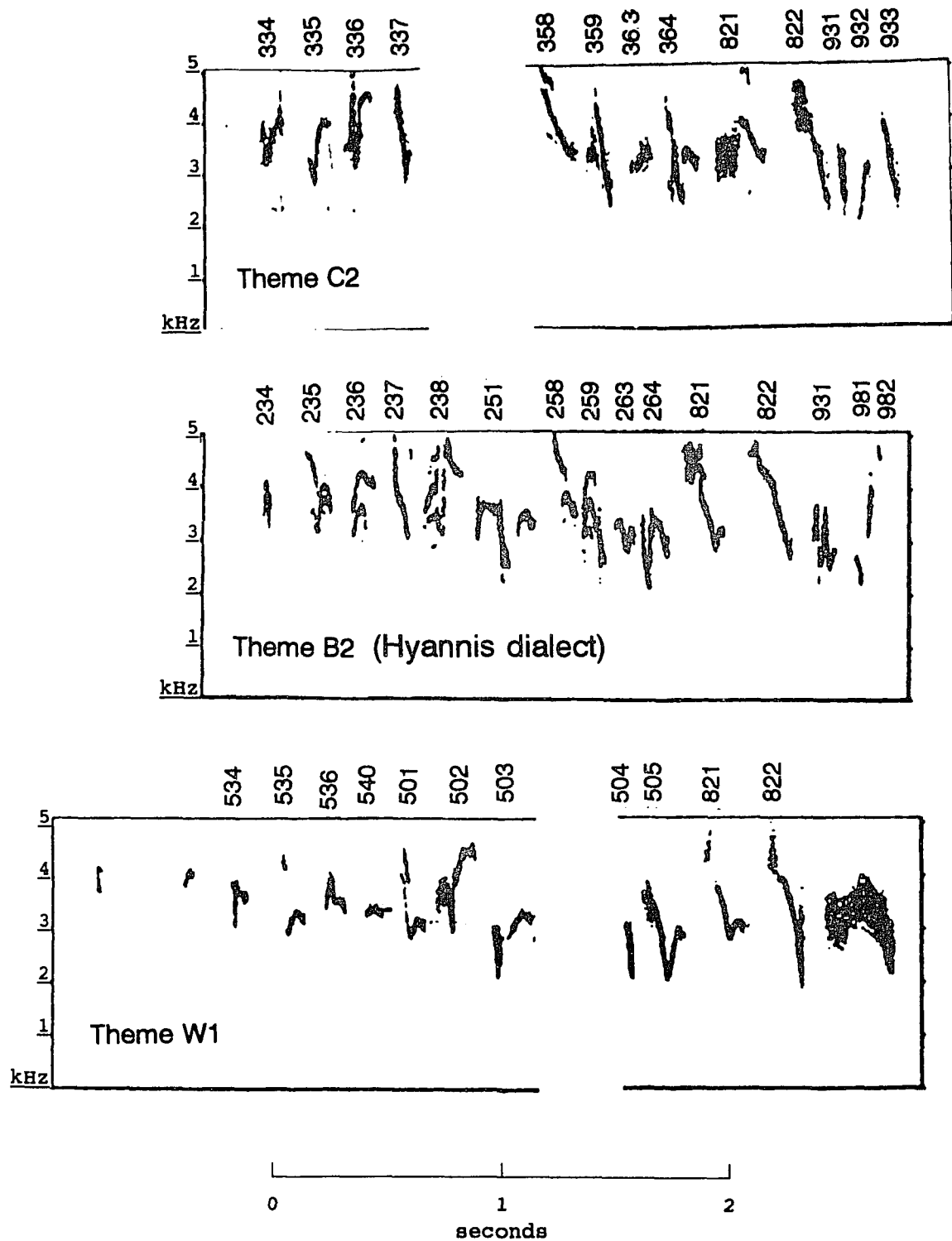


Figure 39: Sonograms of the culturally related themes B2, C2, and W1.
See text for details and the 3-digit code for culturally related syllables.

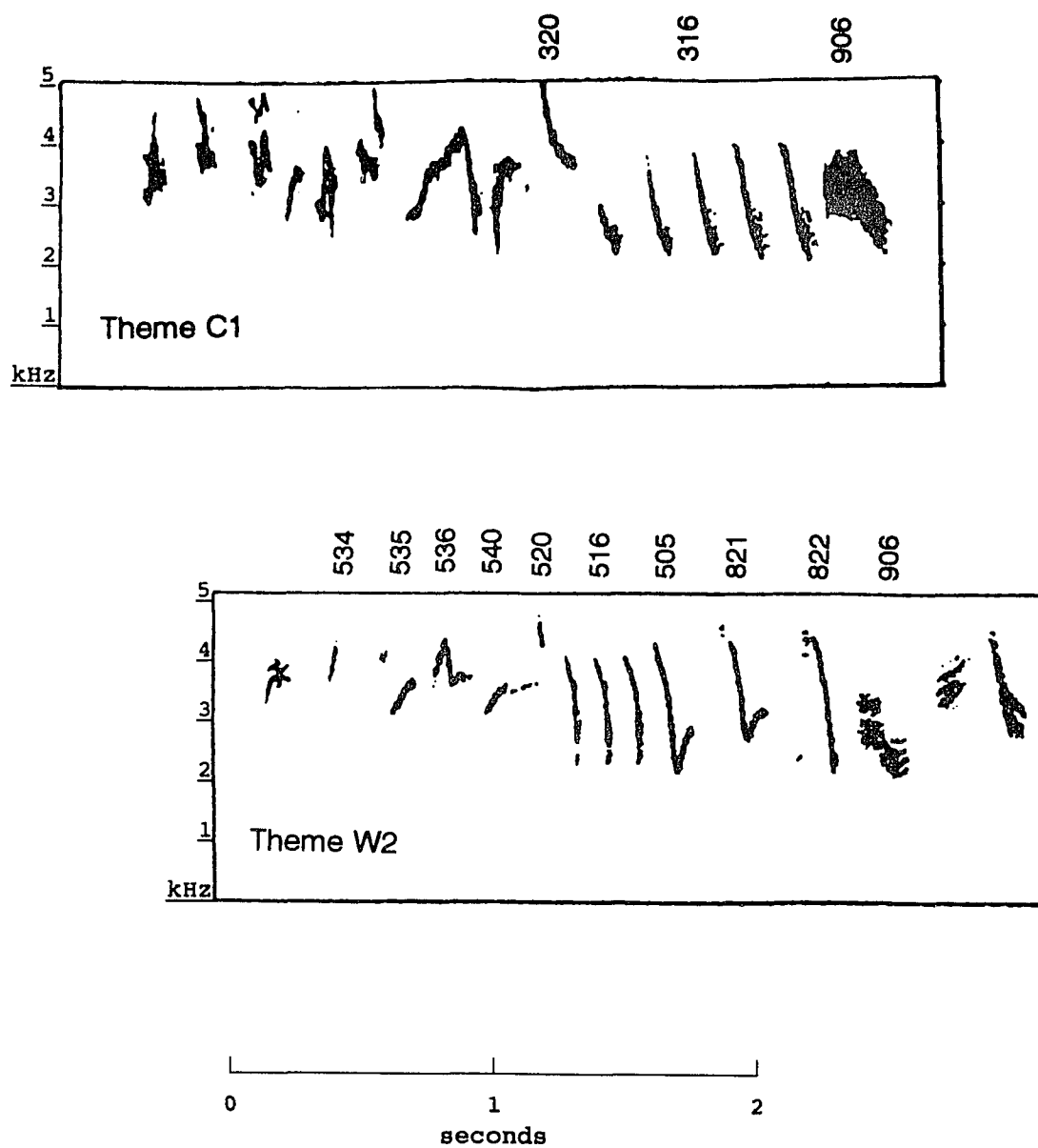


Figure 40: Sonograms of the culturally related themes C1 and W2.
See text for details and the 3-digit code for culturally related syllables.



Figure 41: Probable locations of the earliest established colonies on Cape Cod.

The Chatham colony's repertoire was derived from New York traditions (more than 200 km away). The North Falmouth (NF) colony's repertoire was derived from Mattapoiset traditions (15 km away).

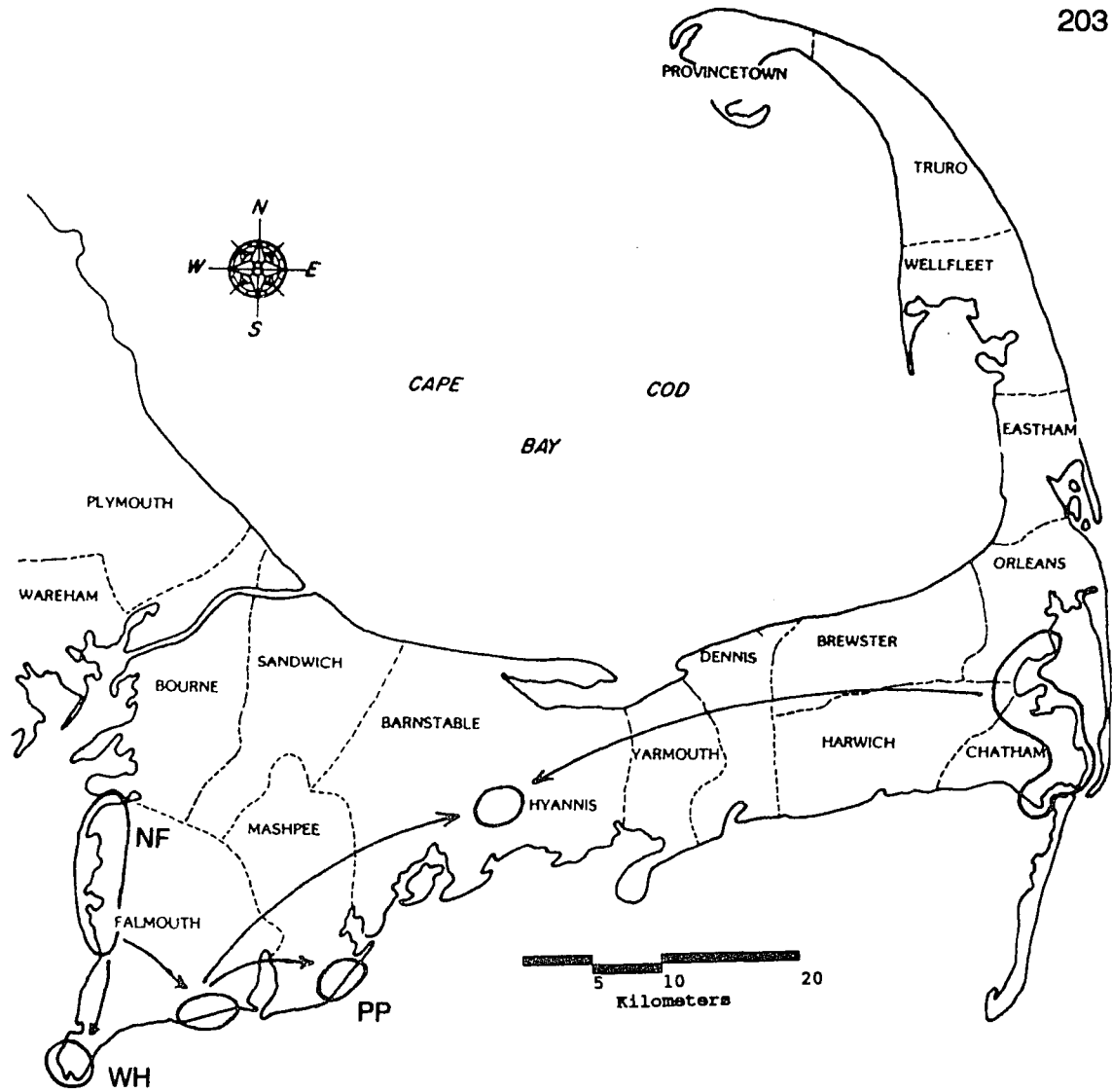


Figure 42: Primary expansion of the Chatham and Falmouth song institutions. Both colonies were restricted to coastal areas by forests in the interior. Dispersers from both colonies met near Hyannis where their traditions hybridized (see text). NF = North Falmouth; PP = Popponesset peninsula; WH = Woods Hole

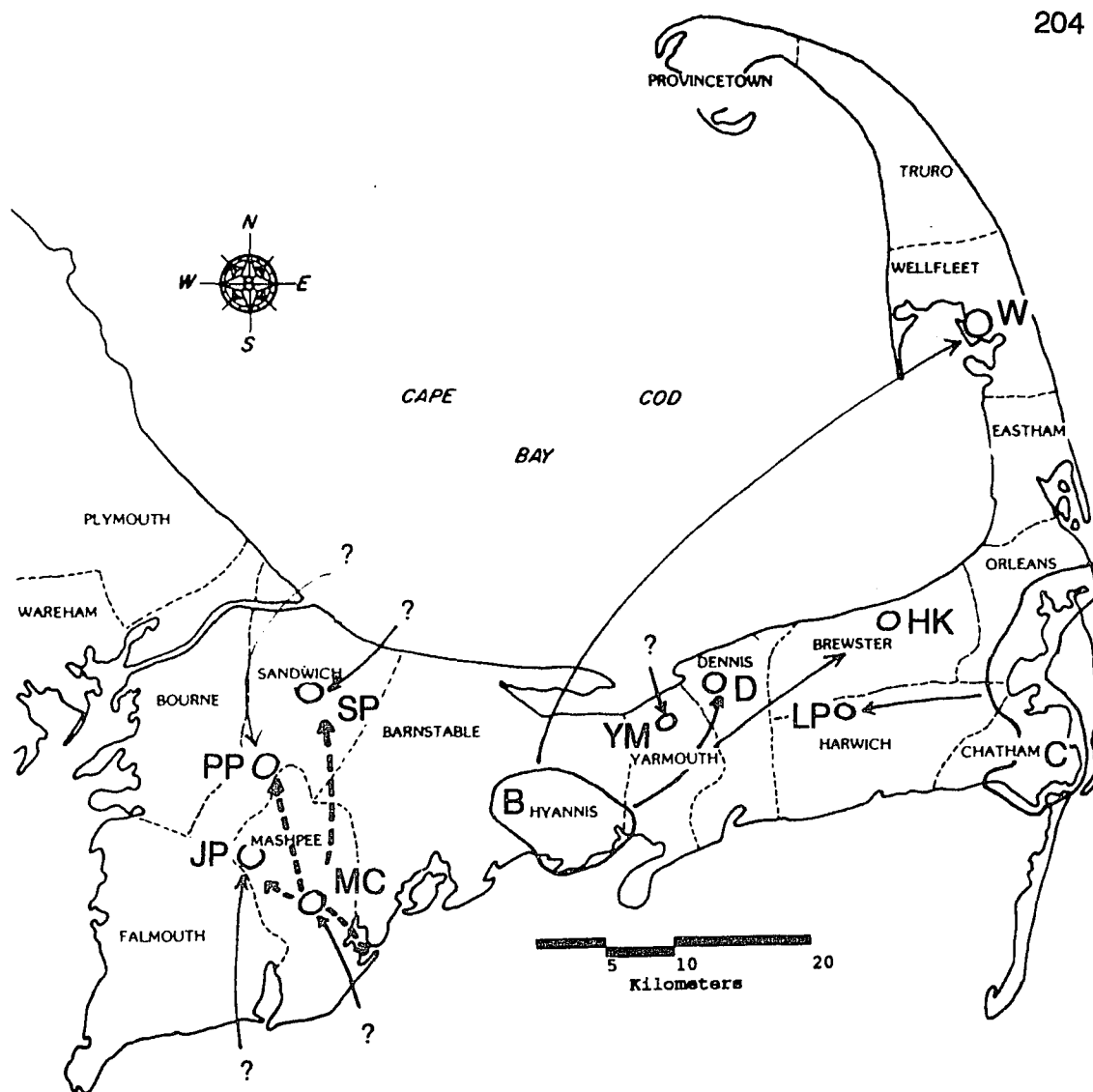


Figure 43: Primary expansion of the Barnstable institution to Wellfleet, Dennis and Brewster; and locations of colonies in Harwich, Mashpee, Sandwich, and Yarmouth generally established by populations of unknown cultural ancestry.

See text for description of expansion and colonization. Dashed arrows indicate diffusion of Mashpee center traditions into John's Pond, Pimlico Pond, Spectacle Pond, and Popponesset.

B = Barnstable institution, C = Chatham institution, D = Dennis dialect of Barnstable, HK = Herring Brook dialect of Barnstable, JP = John's Pond institution, LP = Long Pond dialect of Barnstable (derived from Chatham), MC = Mashpee center population, PP = Pimlico Pond population, SP = Spectacle Pond population, W = Wellfleet institution (derived from Barnstable), YM = Yarmouth dialect of Barnstable

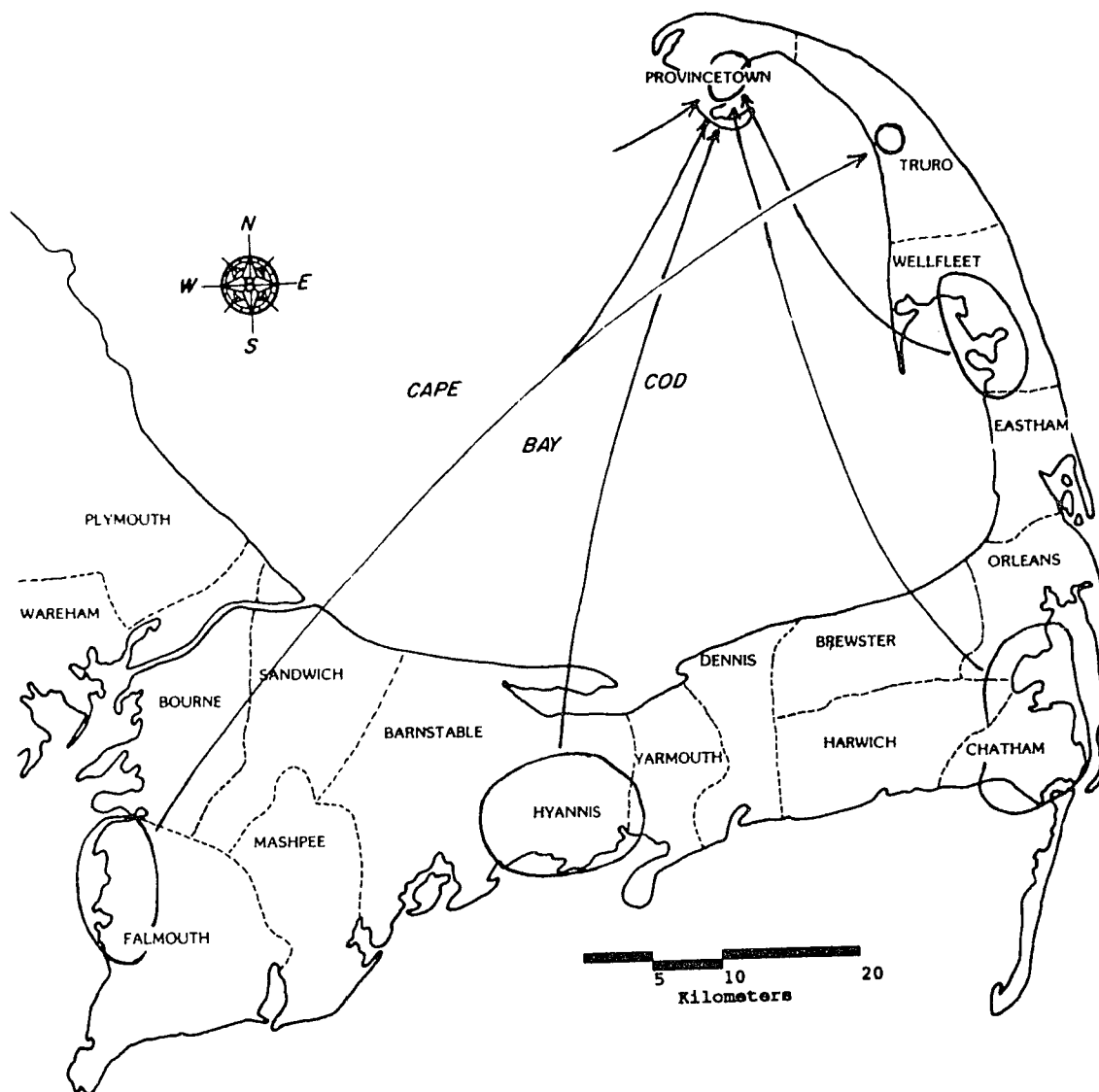


Figure 44: Colonization of the Truro and Provincetown populations (see text).

The Truro population was established from a single dispersal event and the themes comprised a dialect of the Falmouth institution. The Provincetown population received repeated immigrations from a variety of sources and its cultural traditions were complex.

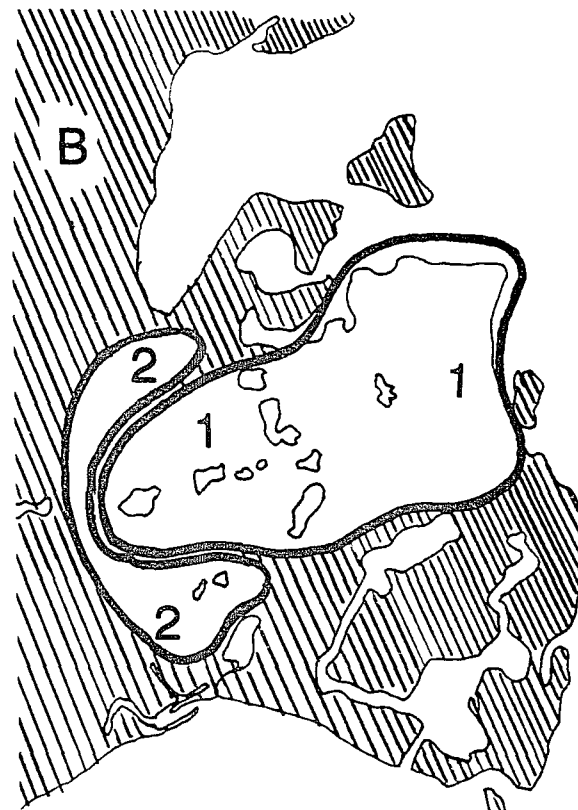
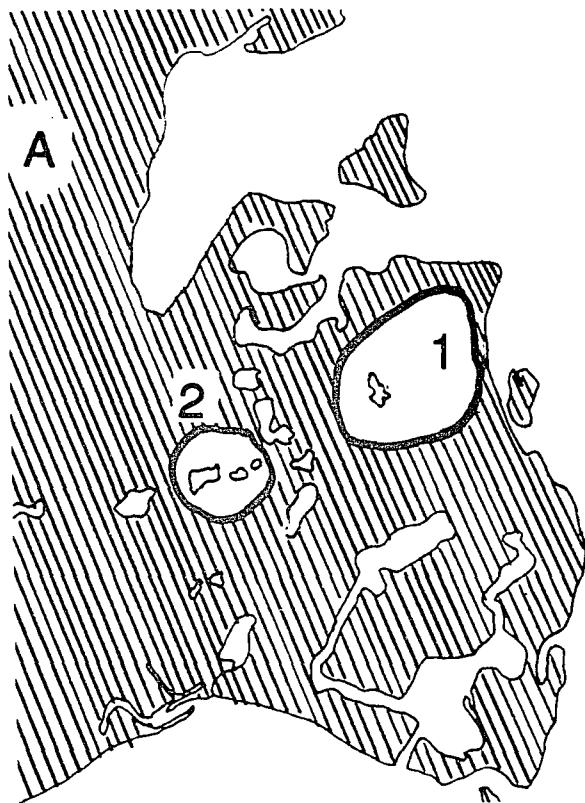


Figure 45: A - Divergence of a postulated primary Chatham population into two sub-populations.

B - Expansion of one Chatham sub-population (1) causing the second sub-population (2) to be pushed to either side of the expanding population. Shaded areas represent postulated unoccupied territory.

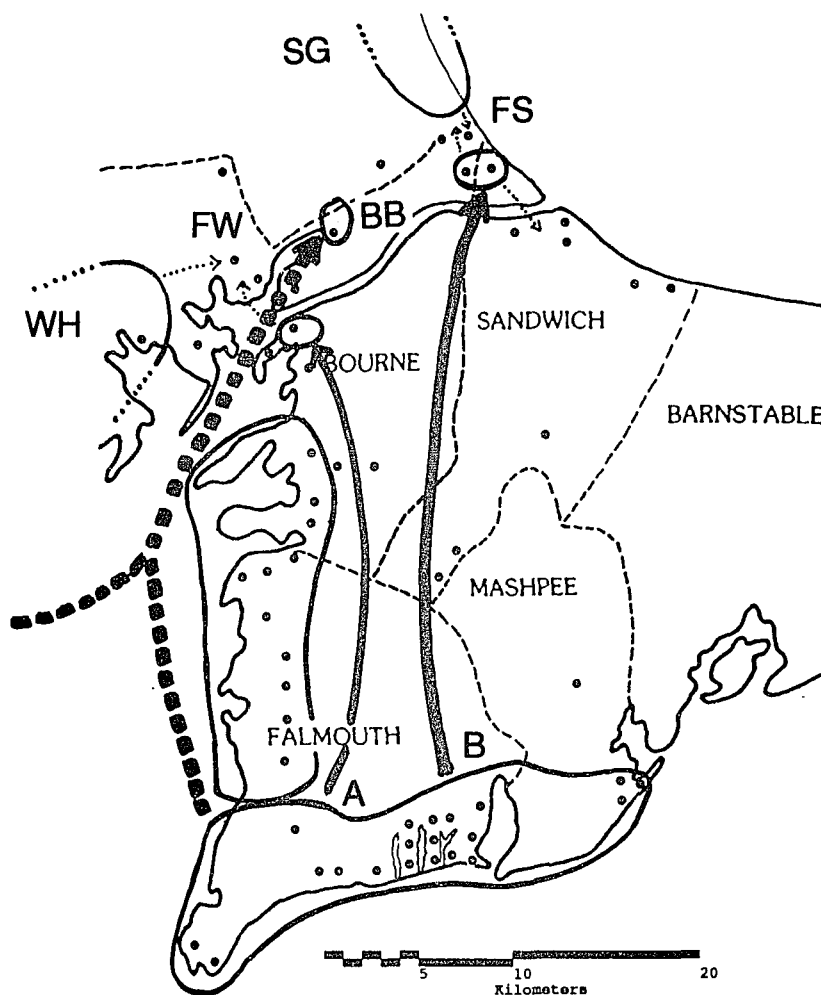


Figure 46: Late jump dispersal events in the Falmouth institution.

Separate populations at A and B colonized the Bourne and Sandwich dialects respectively. Dashed lines indicate that the Buttermilk Bay dialect (BB) may have been colonized from either the Falmouth or Mattapoiset institutions. Dotted lines indicate postulated boundaries of the Wareham and Sandwich institutions. Dotted arrows indicate dispersion of Bourne and Sandwich dialects of Falmouth into areas of hybridization (FW and FS).

FS = area of hybridization of the Falmouth and Sandwich traditions,
 FW = area of hybridization of the Falmouth and Wareham traditions,
 SG = Sandwich institution, WH = Wareham institution

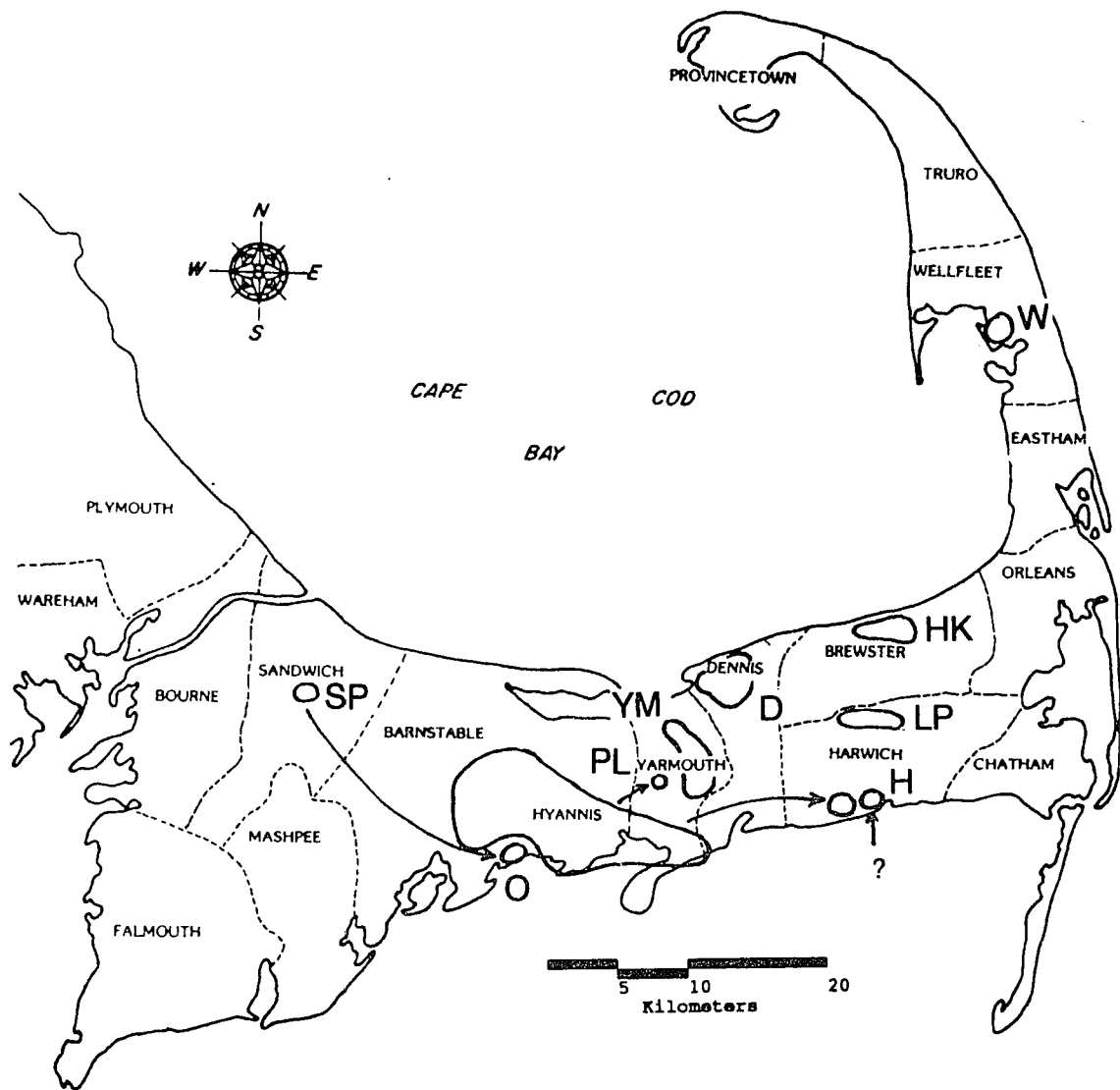


Figure 47: Early expansion of the Hyannis dialect of the Barnstable song institution.

The Phyllis Lane colony (PL) was founded by jump dispersal from the Hyannis dialect. The Osterville colony (O) was founded by finches dispersing from Spectacle Pond (SP). The Harwich colony (H) may have been founded by finches dispersing from Hyannis or from some other source (?).

D = Dennis dialect of Barnstable, HK = Herring Brook dialect of Barnstable, JP = John's Pond institution, LP = Long Pond dialect of Barnstable (derived from Chatham), W = Wellfleet institution (derived from Barnstable), YM = Yarmouth dialect of Barnstable

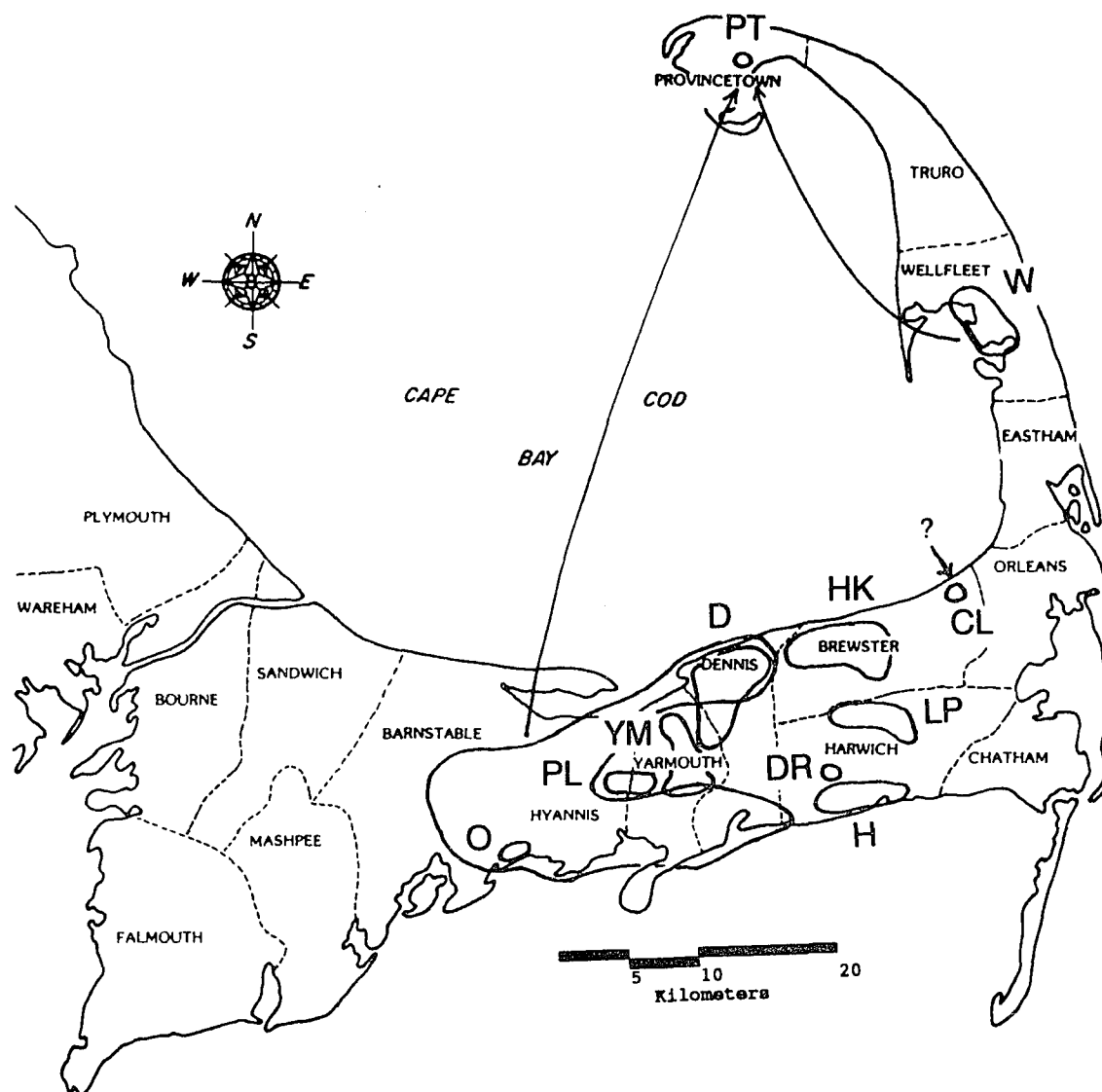


Figure 48: Intermediate spread of the Barnstable song institution.

Showing secondary contact between the Hyannis dialect and previously established dialects at Dennis (D), Harwich (H), Osterville (O), and Yarmouth (YM). Cohorts dispersed to Provincetown from both Barnstable and Wellfleet (W). The Crosby Lane (CL) and Doane Road (DR) colonies were from unknown sources. Other abbreviations as in Figure 47.

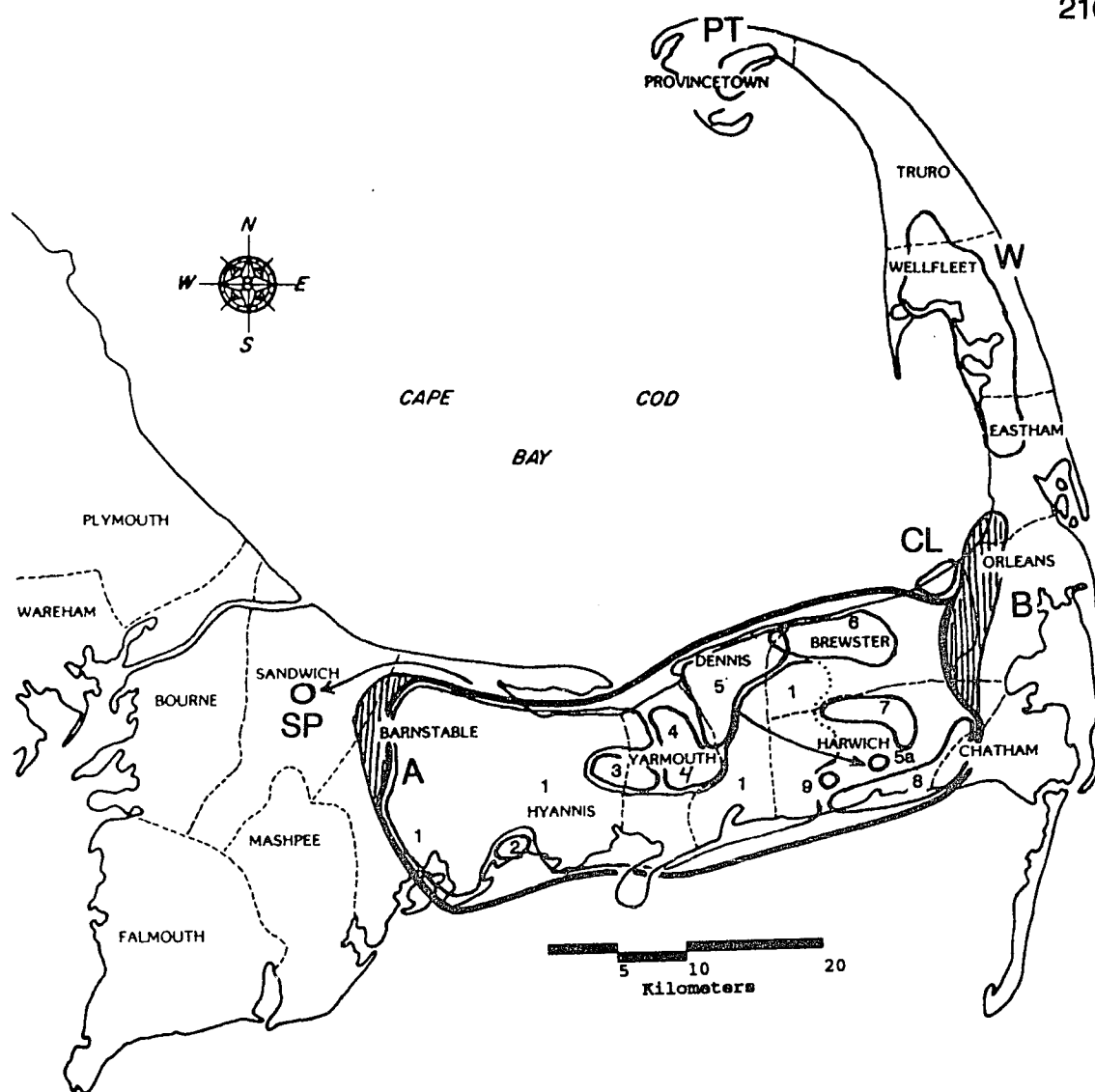
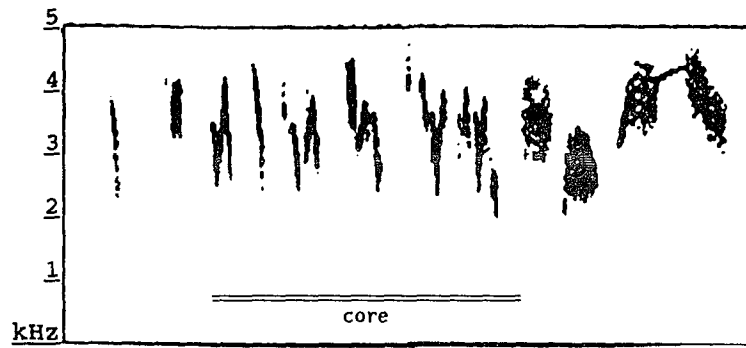


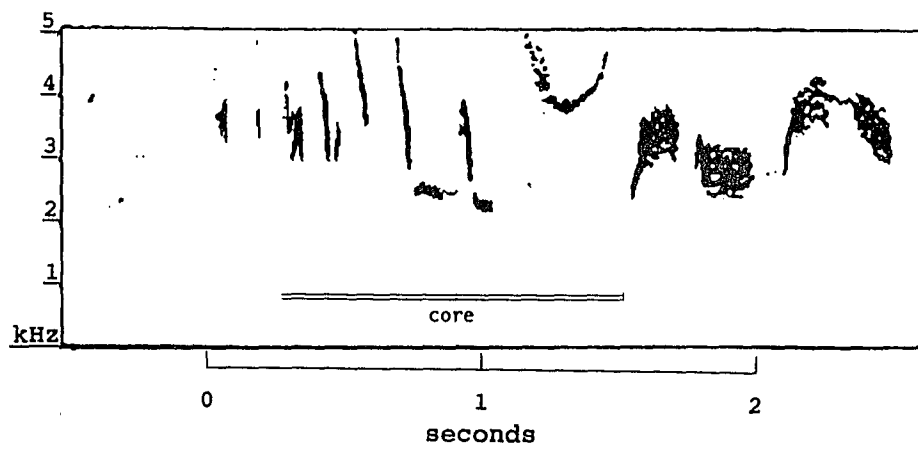
Figure 49: Limits of the Barnstable song institution in 1986.

The dialects are numbered 1 to 9. The dotted lines indicate estimated boundaries. Shaded regions indicate hybrid areas between the Barnstable institution and the Mashpee (A) and Chatham (B) institutions. The Provincetown (PT) and Spectacle Pond (SP) populations were culturally heterogeneous and partially derived from the Barnstable institution. The Wellfleet (W) population sang a separate institution that was derived from the Barnstable institution. The Crosby Landing (CL) populations sang a separate institution that was of unknown ancestry.

APPENDIX A
SONOGRAMS OF HOUSE FINCH THEMES
SUNG ON CAPE COD

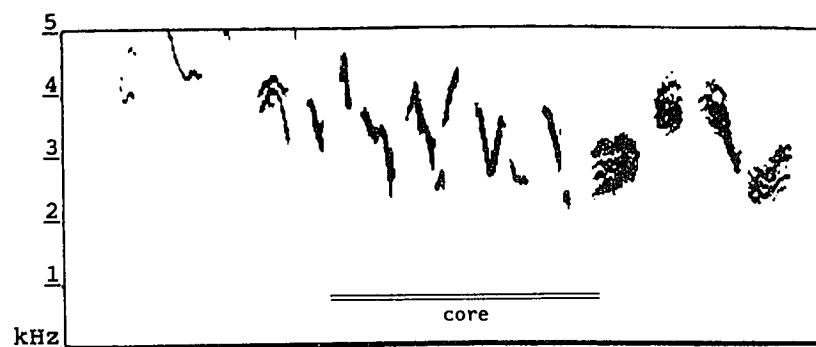


A. Theme F1

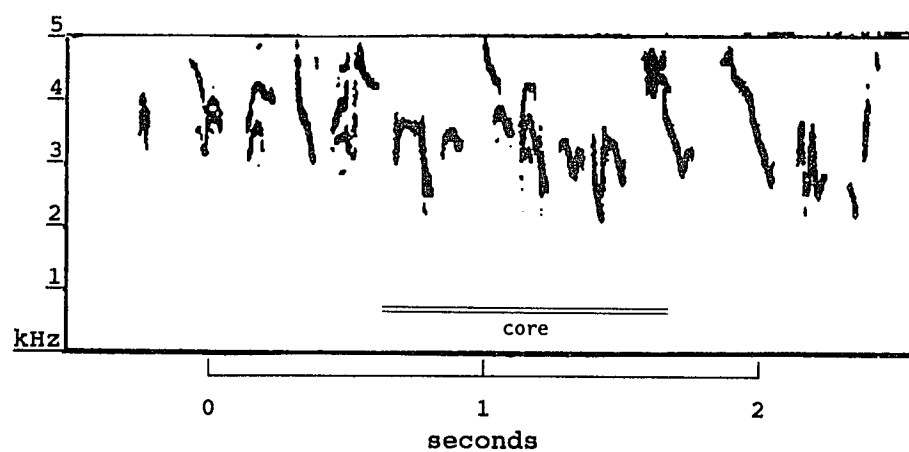


B. Theme F2

Figure A.1: Sonograms of Falmouth themes F1 and F2.

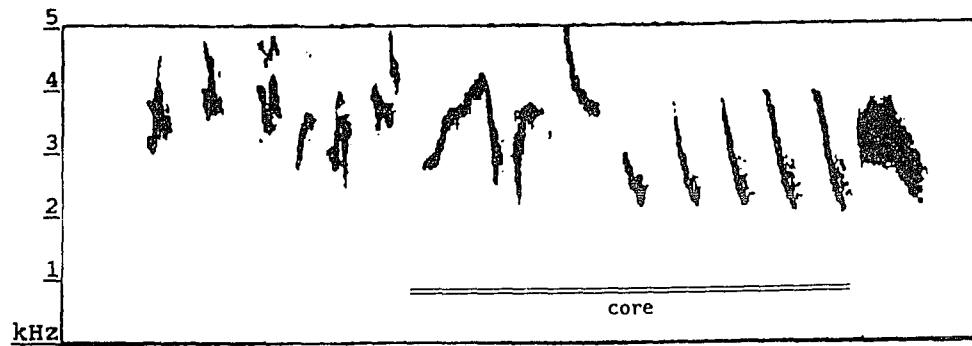


A. Theme B1

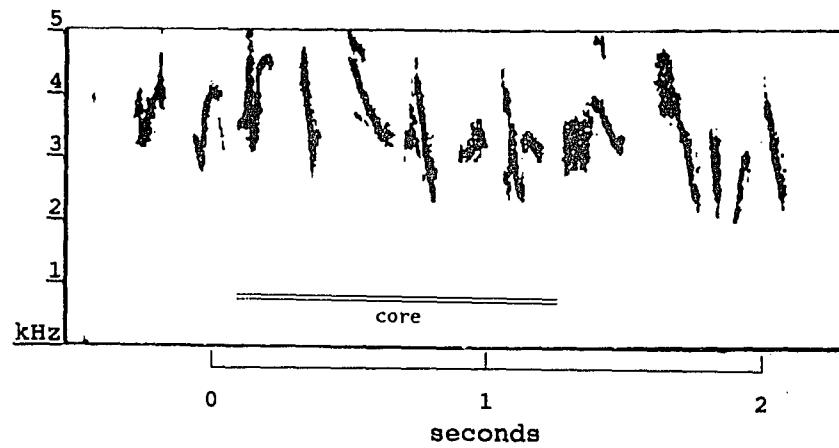


B. Theme B2

Figure A.2: Sonograms of Barnstable themes B1 and B2.

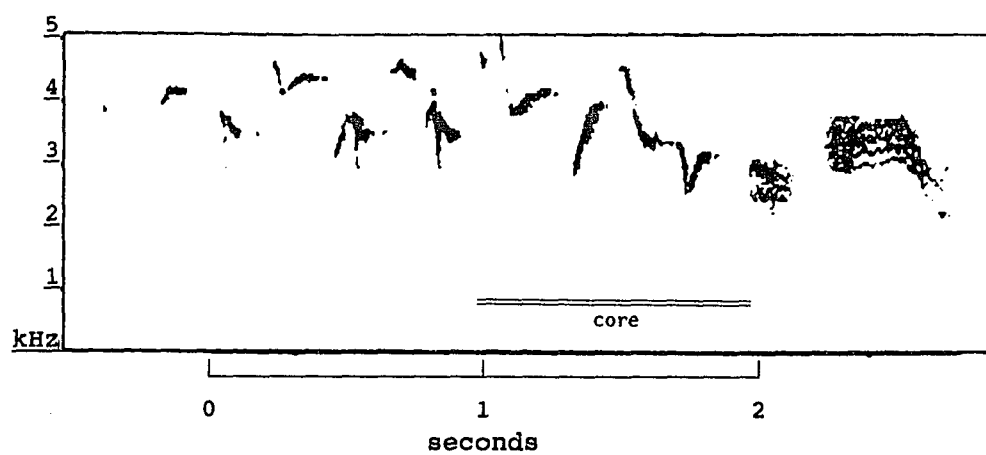


A. Theme C1



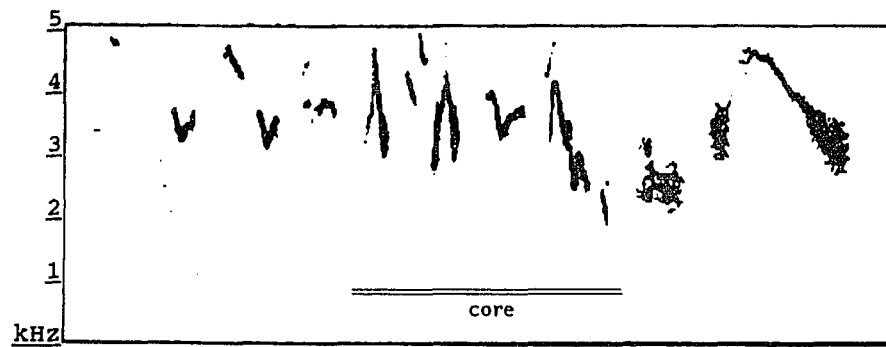
B. Theme C2

Figure A.3: Sonograms of Chatham themes C1 and C2.

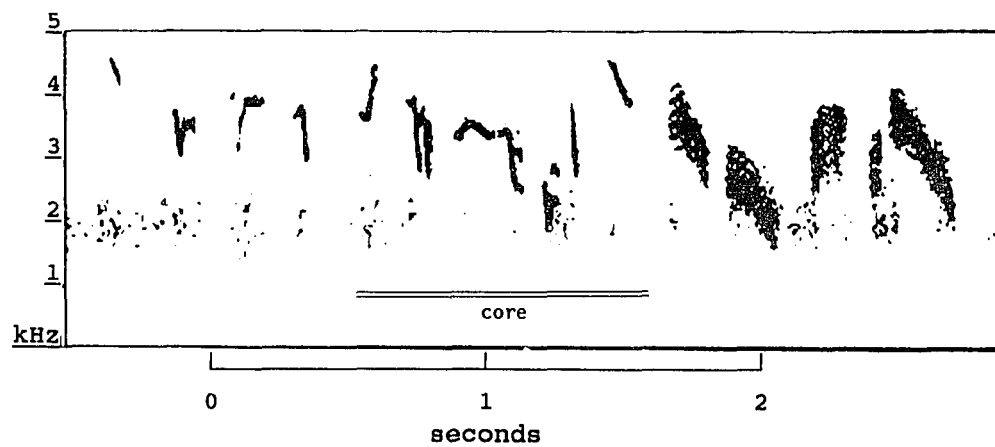


A. Theme M1

Figure A.4: Sonogram of Mashpee theme M1.

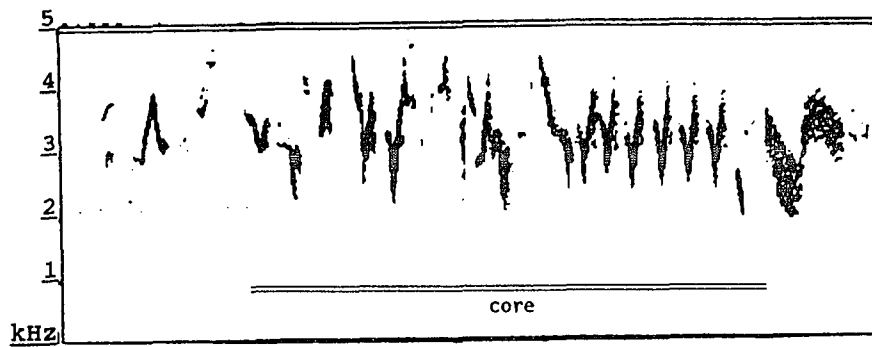


A. Theme A1

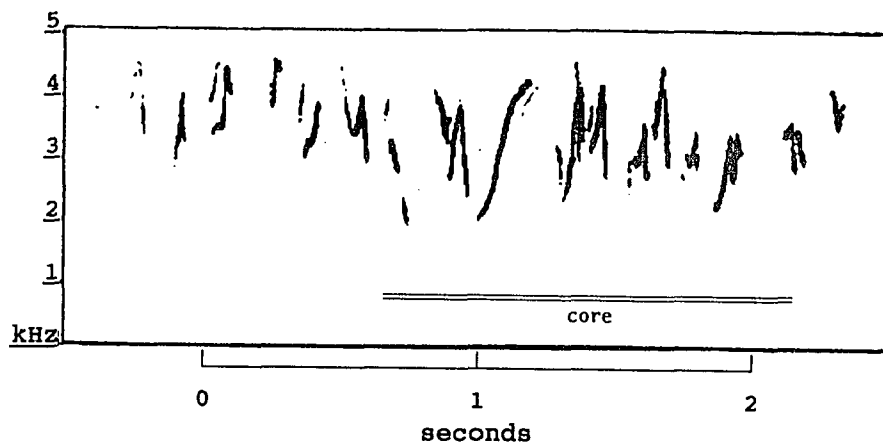


B. Theme A2

Figure A.5: Sonograms of Wareham themes A1 and A2.

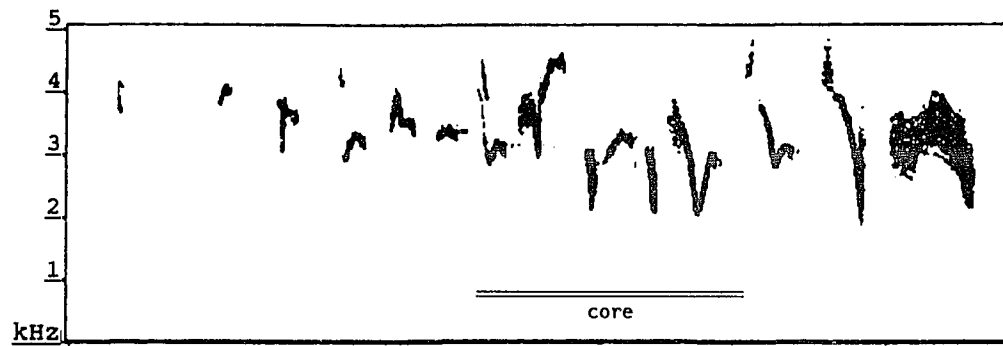


A. Theme S1

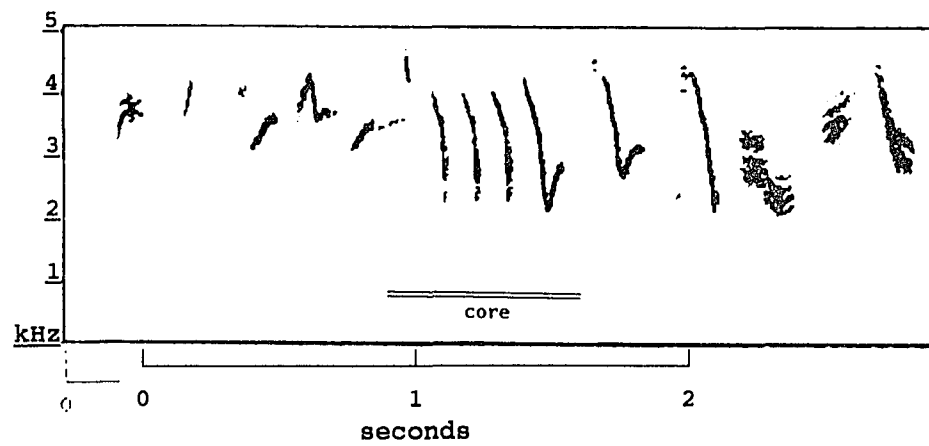


B. Theme S2

Figure A.6: Sonograms of Sandwich themes S1 and S2.

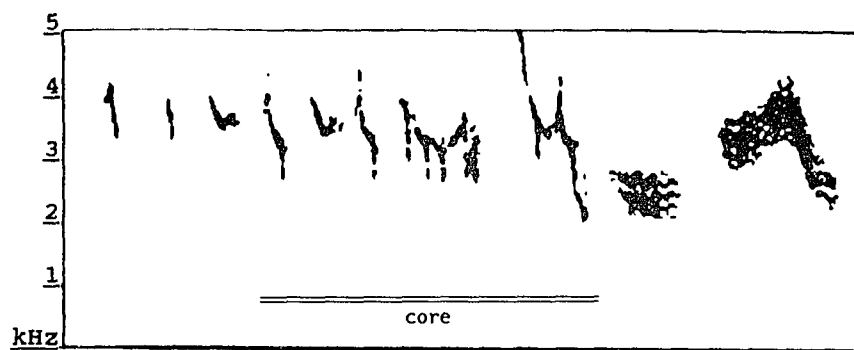


A. Theme W1

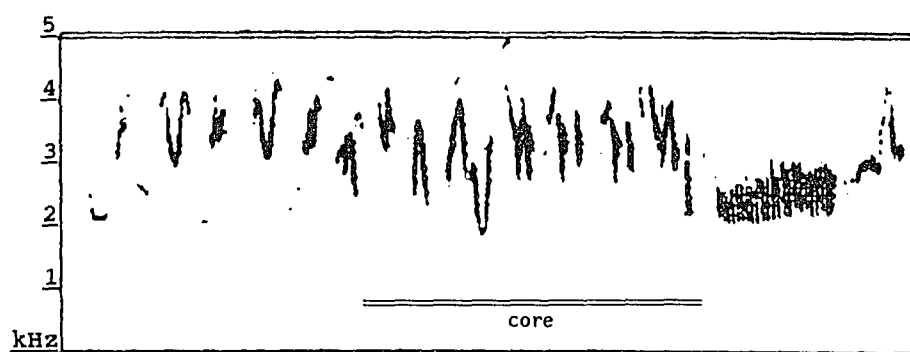


B. Theme W2

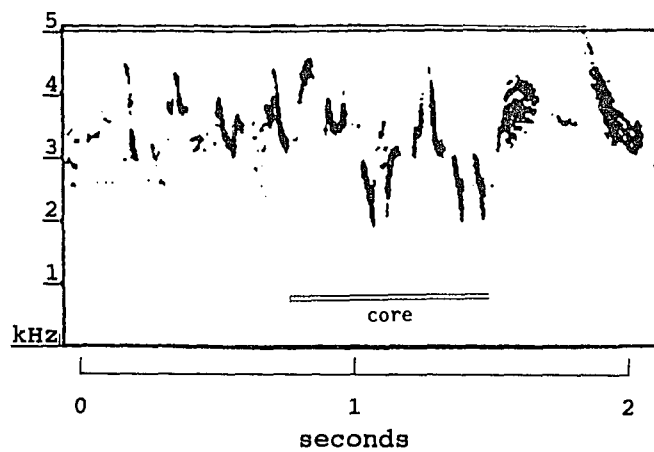
Figure A.7: Sonograms of Wellfleet themes W1 and W2.



A. Theme M2

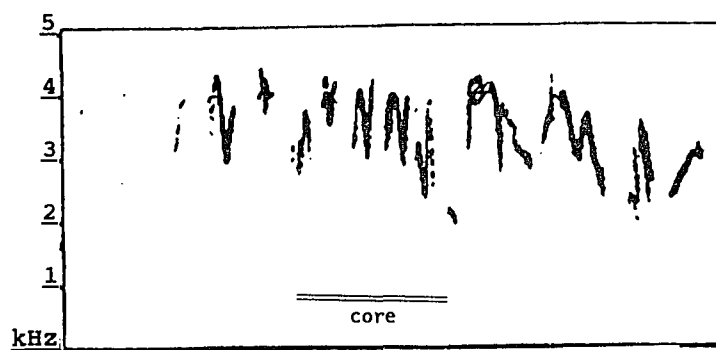


B. Theme M3

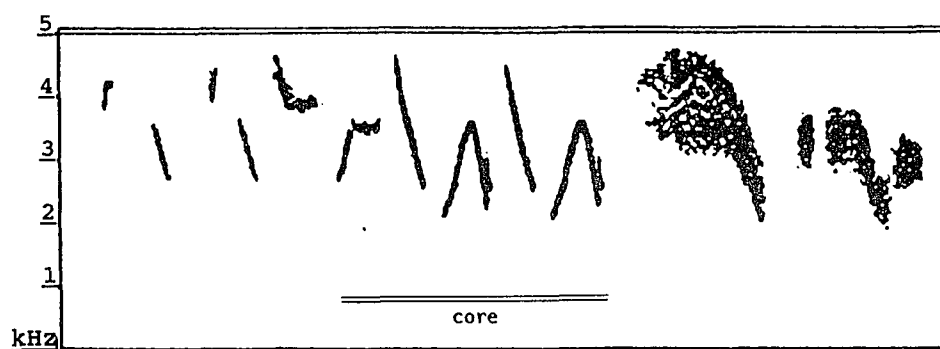


C. Theme M4

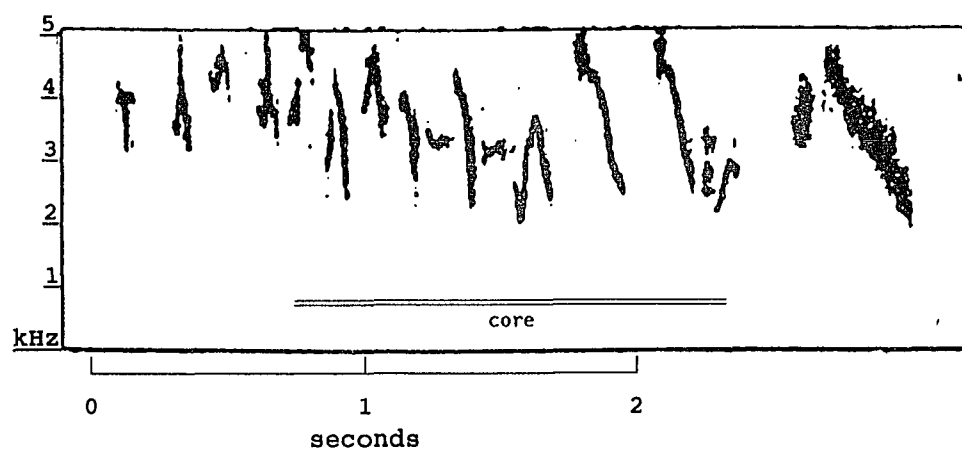
Figure A.8: Sonograms of Mashpee themes M2, M3, and M4.



A. Theme D1

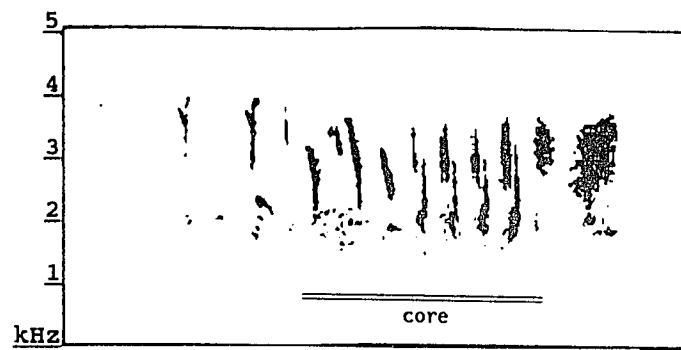


B. Theme H1

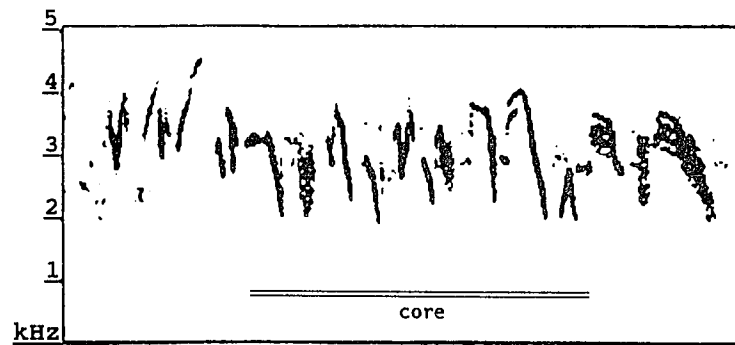


C. Theme P1

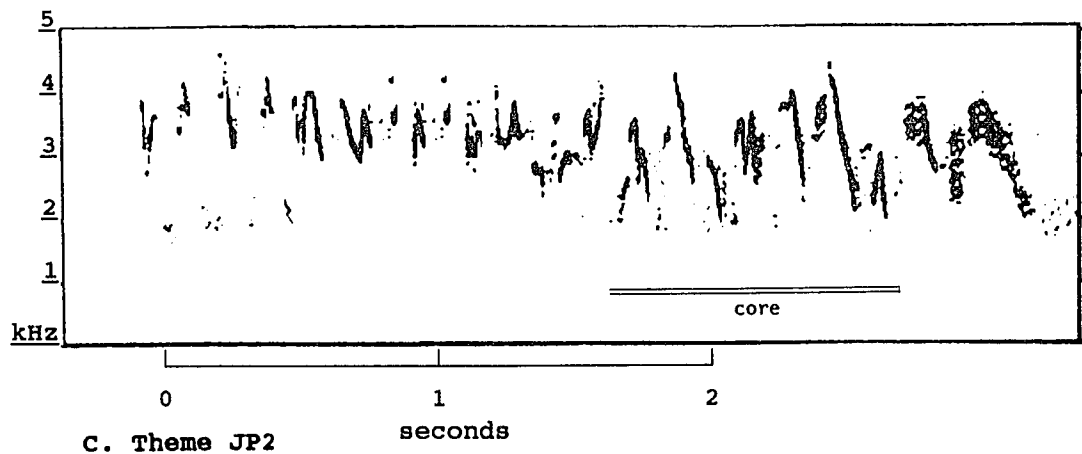
Figure A.9: Sonograms of Dennis theme D1, Harwich theme H1, and Provincetown theme P1.



A. Theme WO1



B. Theme JP1



C. Theme JP2

Figure A.10: Sonograms of Woods Hole theme WO1, and Johns Pond themes JP1 and JP2.

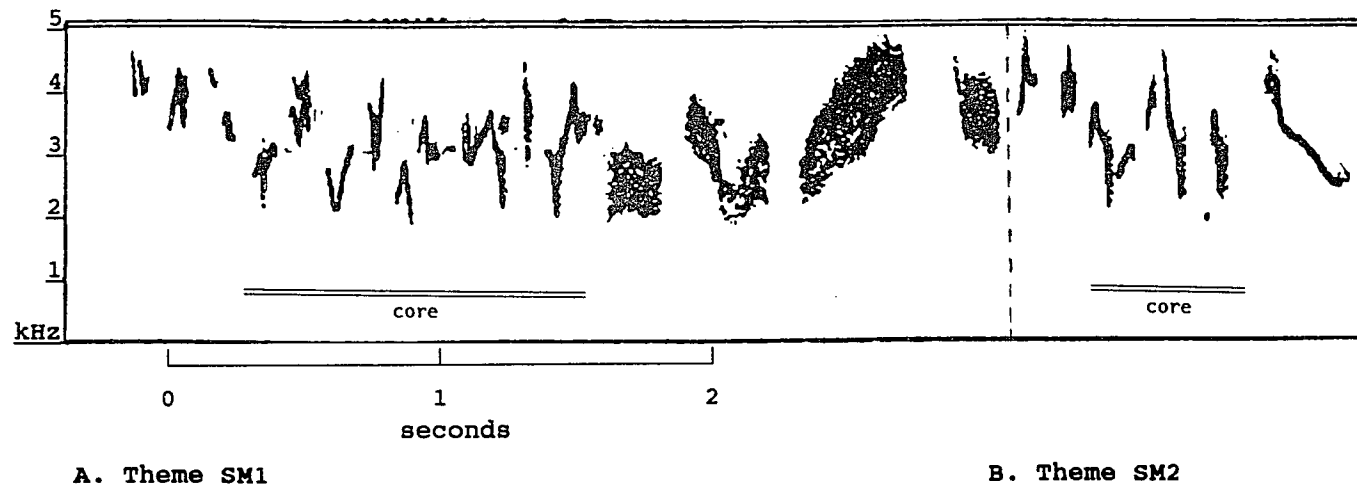
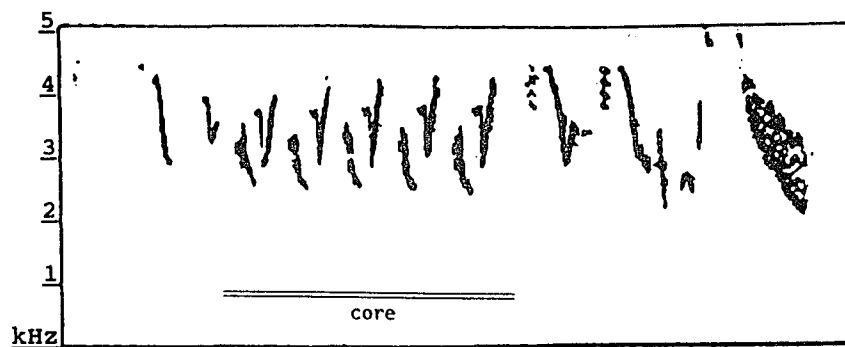
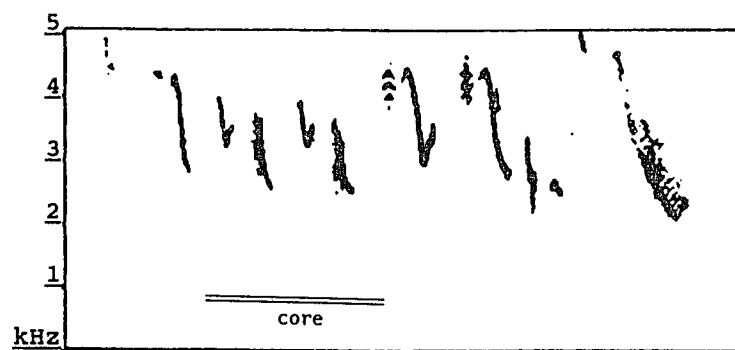


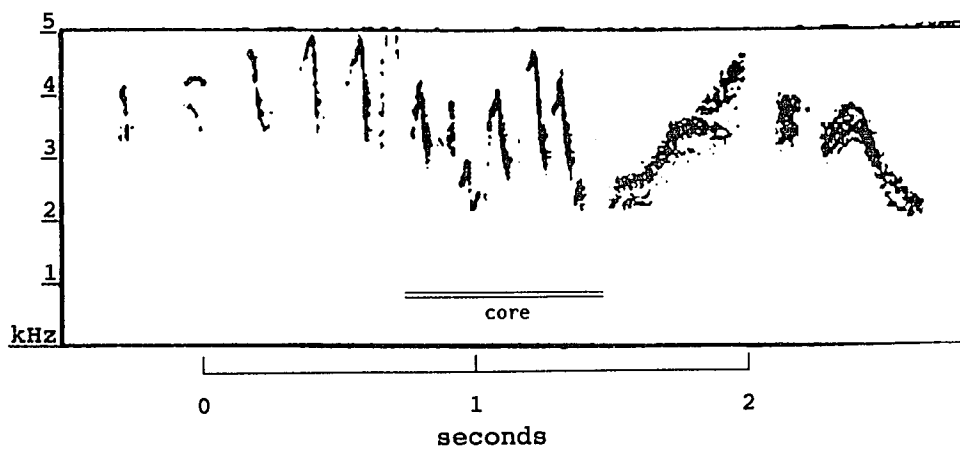
Figure A.11: Sonograms of Salt Marsh themes SM1 and SM2.



A. Theme CL1, variant 1

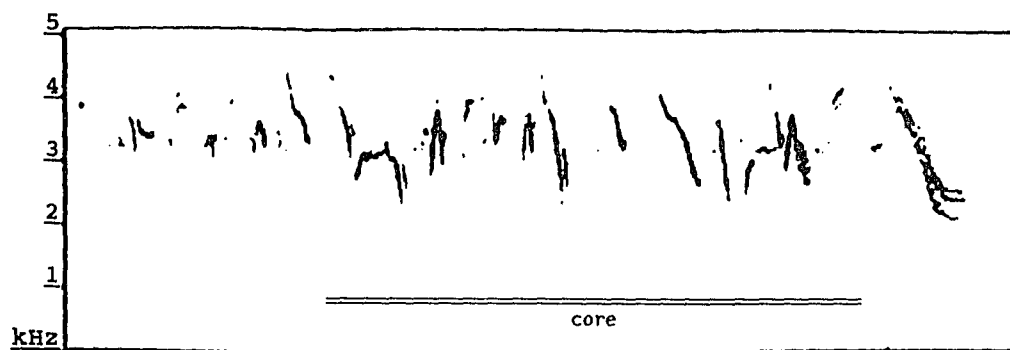


B. Theme CL1, variant 2

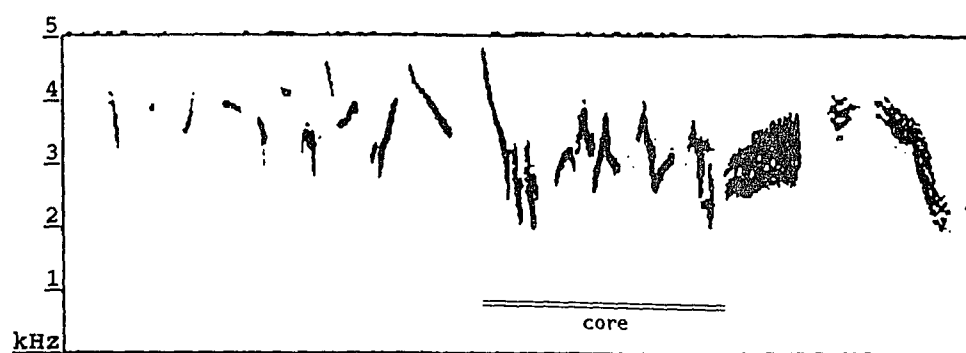


C. Theme HK1

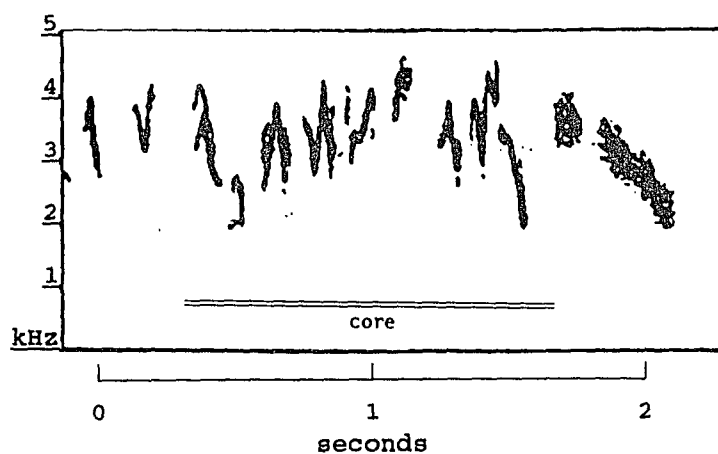
Figure A.12 Sonogram of two variants of Crosby Landing theme CL1, and Herring Brook theme HK1.



A. Theme PP1

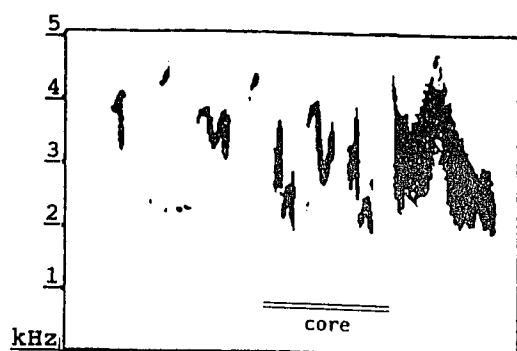


B. Theme SP1

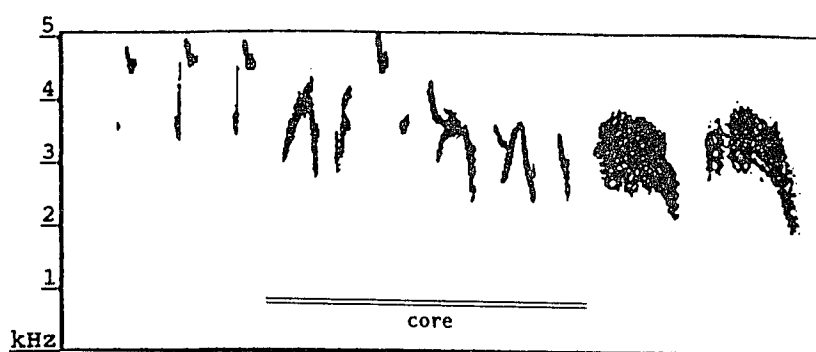


C. Theme SP2

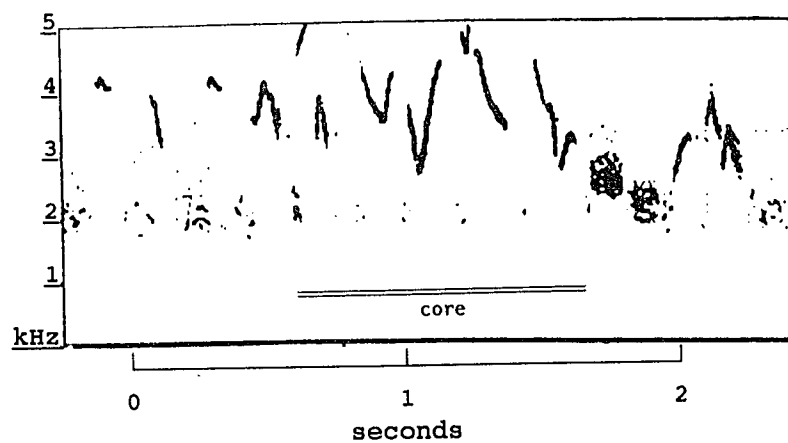
Figure A.13: Sonograms of Pimlico Pond theme PP1, and Spectacle Pond themes SP1 and SP2.



A. Theme SC1

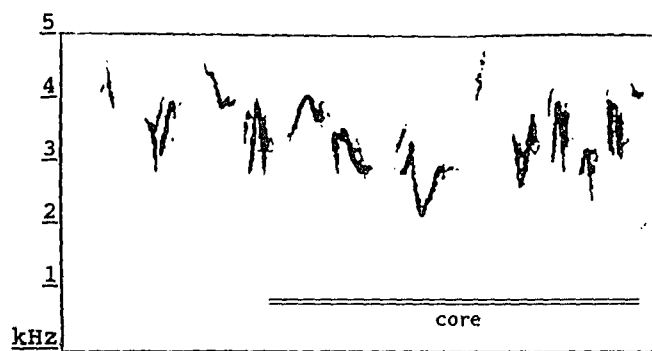


B. Theme SW1

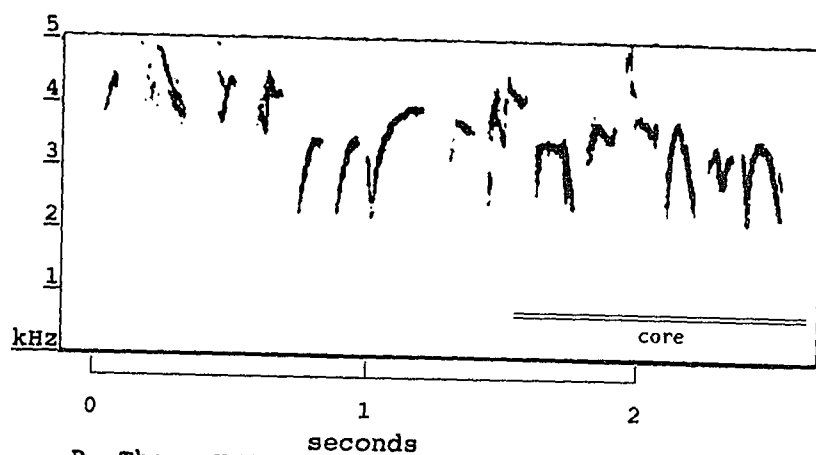


C. Theme KM1

Figure A.14: Sonograms of Sandy Pond Camp theme SC1, Swallow Lane theme SW1, and Kompass Lane theme KM1.

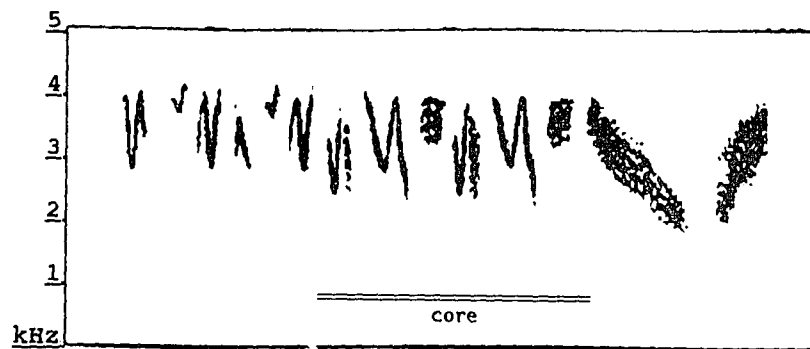


A. Theme PL1

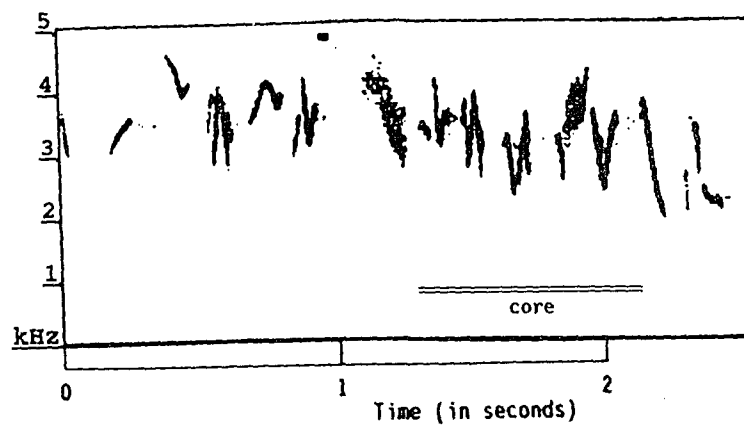


B. Theme YM1

Figure A.15: Sonograms of Phyllis Lane theme PL1, and Yarmouth theme YM1.

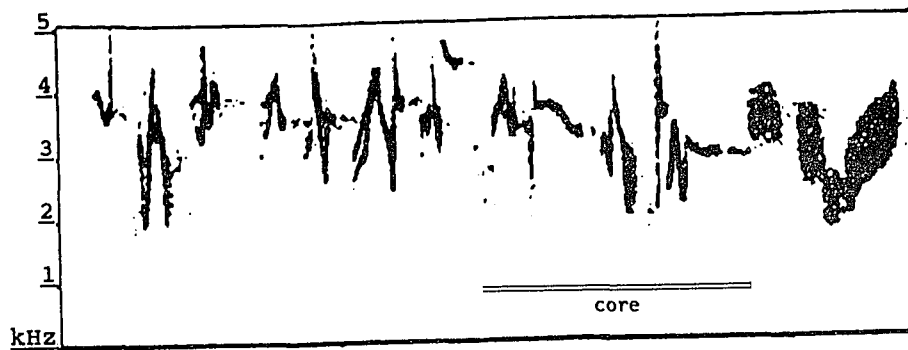


A. Theme ML1

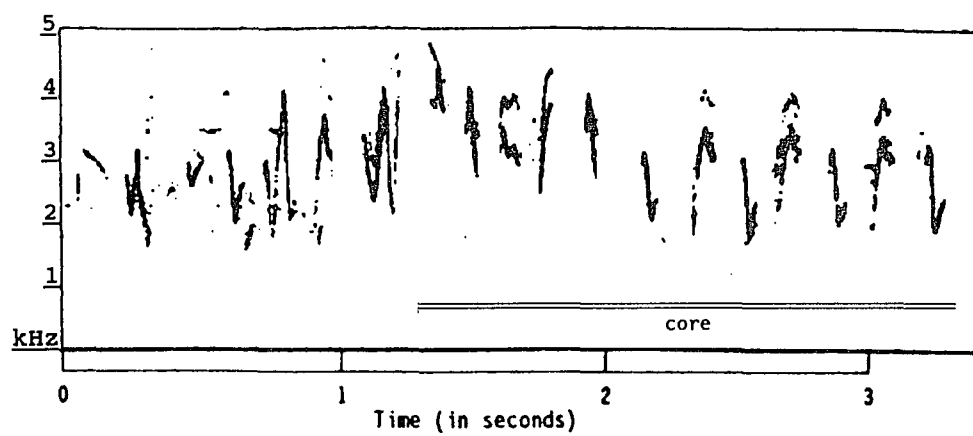


B. Theme ML2

Figure A.16: Sonograms of Marston's Lane themes ML1 and ML2.



A. Theme LP1



B. Theme DR1

Figure A.17: Sonograms of Long Pond theme LP1, and Doane Road theme DR1.

APPENDIX B

TECHNICAL COMPARISONS OF

CAPE COD HOUSE FINCH SONGS WITH

SONGS IN OTHER REGIONS

Several songs recorded on Cape Cod were also recorded from populations located in other areas of the north eastern United States. Following is a technical comparison of Cape Cod song patterns and the patterns of songs from other populations. Discussion of these similarities is found in Chapter 6.

Themes of the Chatham institution included phrasing and syllable pronunciations that appeared to be related to Long Island songs - notably themes recorded by Mundinger (1975) in Peningo (or Mamaroneck), Harrison, and Larchmont, N.Y. The syllables sung on Cape Cod sometimes are strongly modified from the New York songs, but the sequence of presentation is the same as in the NY songs if deletions, [-], and insertions, [+], are disregarded. In the following examples, I followed the rule of priority and used syllable identifications for the Chatham syllables that coincide with Mundinger's (1982) notations.

Figure B.1: Sonogram comparison of Falmouth sub-themes F1B and F1A, Barnstable sub-themes B1A and B1B, and theme PS1 (a culturally related theme sung in the town of Portsmouth, RI).

Versions of theme F1 were sung by birds in Mattapoiset and Marion to the west along the coast. The more distant theme, MT1, from Mattapoiset, showed the closest similarities with the Falmouth theme. Syllables x06 through x08 were sung with close fidelity. The Marian version of this theme, MR1, was aberrant. Syllables x06, x16, x09, and x09, although recognizable, were modified from their Falmouth versions. Four syllables (x06, x16, x07, and x08) were each repeated once in the theme. In addition, individuals that sang theme MR1 (Marian) sometimes sang more and sometimes fewer repetitions of these four syllables. Thus some songs might include four or five repetitions of one syllable while another version sung by that individual might include only one utterance of the same syllable.

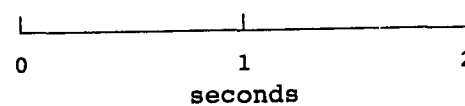
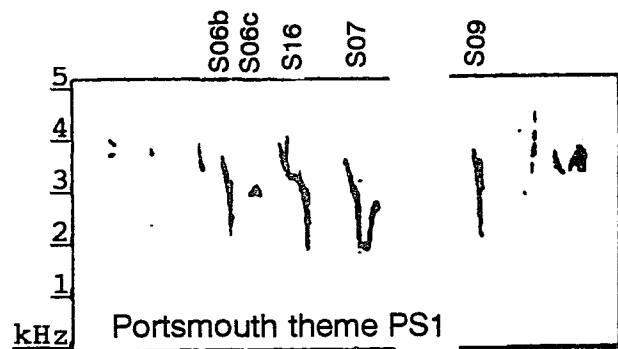
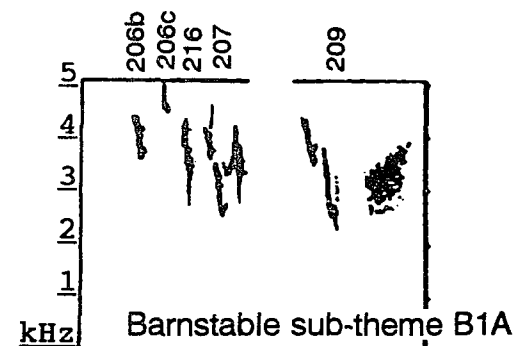
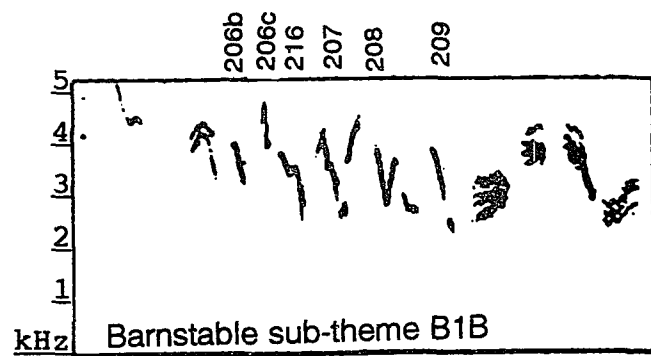
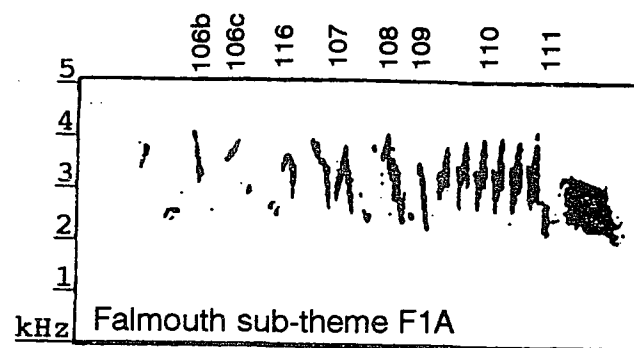
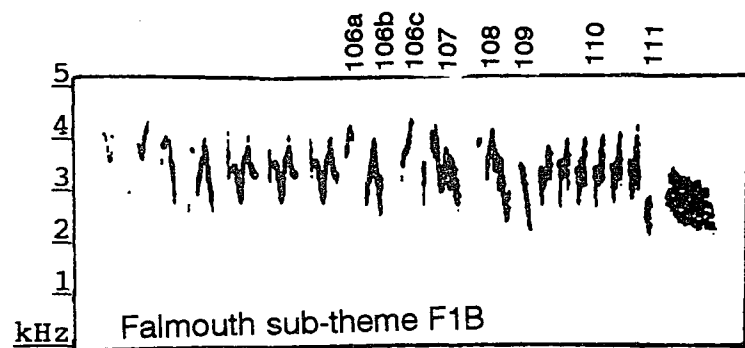


Figure B.2: Sonograms of Falmouth theme F1B (A) and culturally related themes sung in the towns of Mattapoiset, MA (B), and Marian, MA (C).

A variant of theme B2 or F1B was sung in Portsmouth, Rhode Island. Syllables x06, x07, and x09 were sung in all of the themes and their sub-themes (F1A, F1B, B1A, B1B, and PS1). Syllable x08 was sung in sub-themes F1B, F1A, and B1B. In theme F1A, syllable x16 was inserted after syllable x06. Syllable x16 was also sung after syllable x06 in sub themes B1A and B1B, and in theme PS1. Although the trill composed of syllables 110 and 111 was found only in Falmouth songs, a trill of two to five repetitions of syllable 931 (having different derivation from syllable 110) was sung in Barnstable theme B2. Barnstable sub-theme B1B often included a more complex introduction (not pictured). Pronunciation differences and the presence of syllable 221, however, were sufficient to distinguish between theme B1A and B1B.

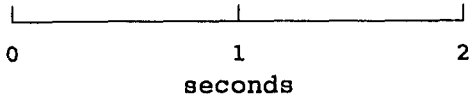
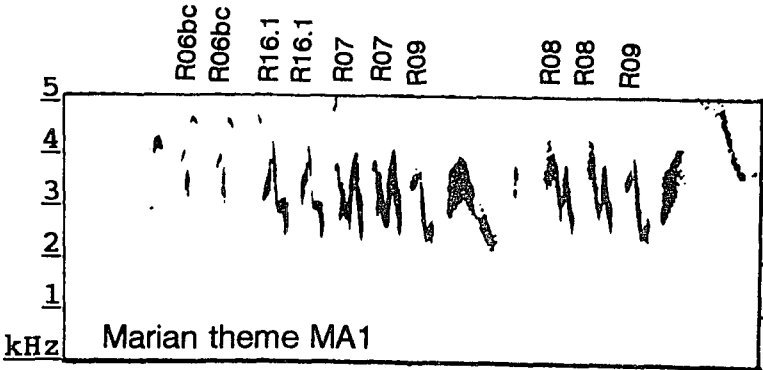
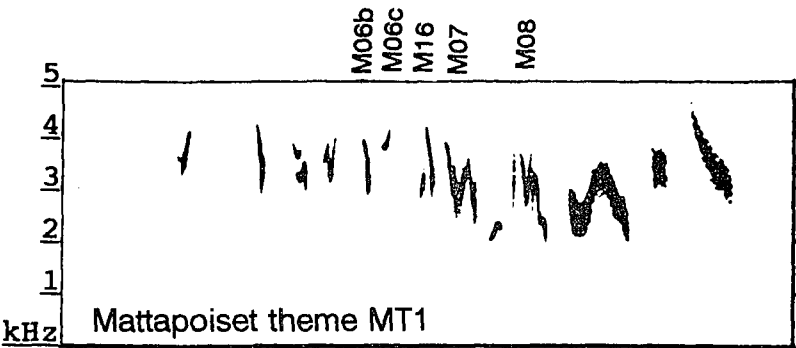
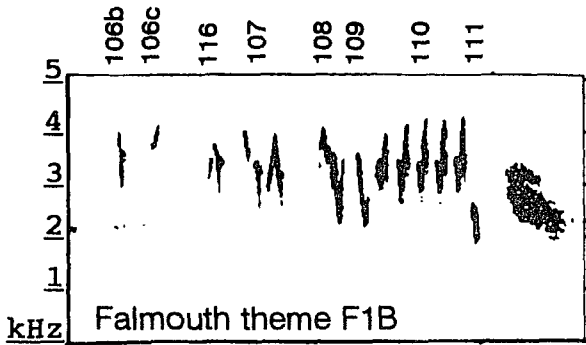


Figure B.3: Two forms of theme A1 sung in Wareham compared with similar themes sung in East Lyme, CT, Newport, RI, and Farmingdale, NY.

Two themes, each with some syllables similar to syllables sung in theme A1 of the Wareham institution, were sung by a population in East Lyme, CT. Similar themes were also sung in Farmingdale, NY and Newport, RI. Syllable x07 was sung in all regions (but not in theme EL2 or sub-theme A1B). The endings of the themes in this figure were also shared. Each population included syllables 915 and 918. The three New England populations also included syllable 916. Syllables x05, x07, and the sequence x10 x11 x12 was sung in both Wareham and East Lyme. Syllables 614 (new) and syllable x27 (sung in theme EL2) were inserted after syllable x07 in Wareham theme A1A (taking the place of syllables x08 and x09. One variant of theme A1 (A1B, Wareham) was more closely derived from theme EL2. In this variant syllables x26 x27 and the sequence x11 x12 x13 (only x11 shown in theme A1B) were sung.

Syllable x09 was sung in Farmingdale, NY, East Lyme ,CT, and Newport, RI. The Newport theme also shared syllable syllable x55 with Farmingdale. Following is a syllable homology comparison for the several themes. The first significant digit is dropped except for the ending syllables.

		core										ending		
Farmingdale	(FD1)			7	8	55						12	915	918
Newport	(NP1)			7	[-]	55	9						915 916 917	918
East Lyme	(EL1)	5	6	7	8	[-]	9		10	11	12	915(916		918)
Wareham	(A1A)	5		7	[-]	[-]	14[-]	27	10	11	12	915 916		918
East Lyme	(EL2)					55		27	10	11	12			
Wareham	(A1B)	5				55 14		27(10)	11(12	915	916			918)

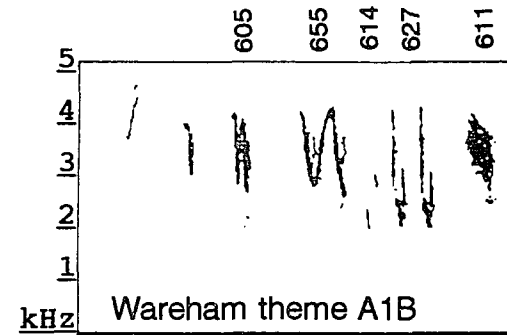
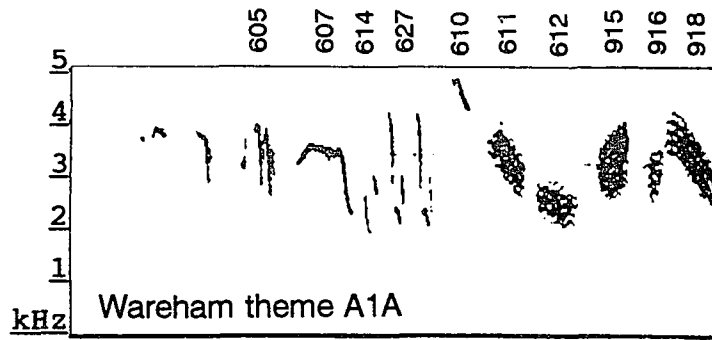
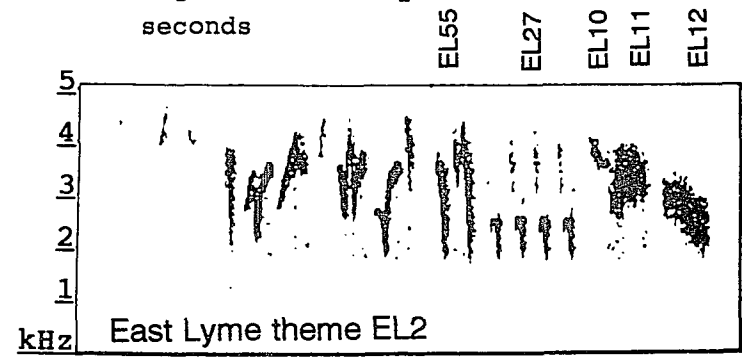
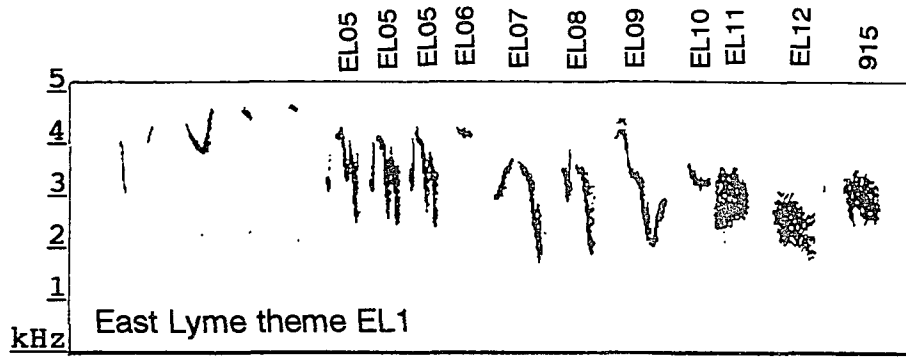
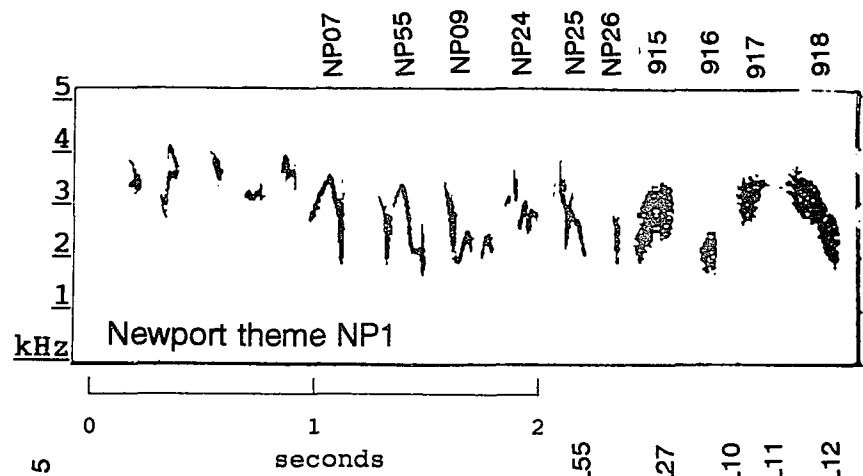
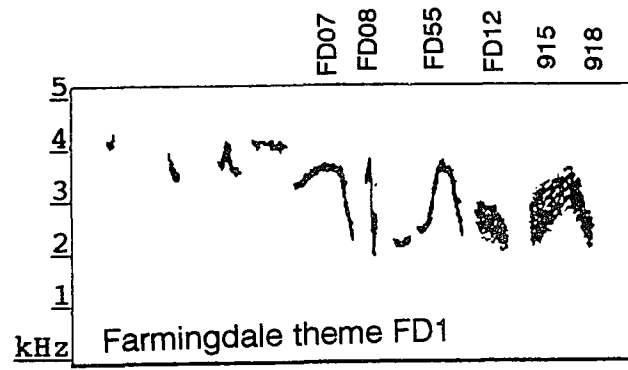


Figure B.4: Themes SM1 and SM2 of the Salt Marsh institution compared with theme PL1 sung in Plymouth, MA.

The Salt Marsh institution themes were sung by a separate institution in Plymouth, MA. The Plymouth theme (PL1) was only one of two themes sung in that institution. The Salt Marsh themes (SM1 and SM2) were both derived from theme PL1, but included different syllables of the postulated original theme (PL1). In theme SM1 two syllables (731 and 732) were substituted for syllable x11 (in theme PL1), and five syllables (733 through 973) replaced syllables x13 and x14 (in theme PL1 and theme SM2). The lexicon of theme SM2 lacked syllables x06 through x10 and 974 (in theme PL1 and theme SM1) and x11 (in theme PL1), but included syllables x13 through x15 (in theme PL1).

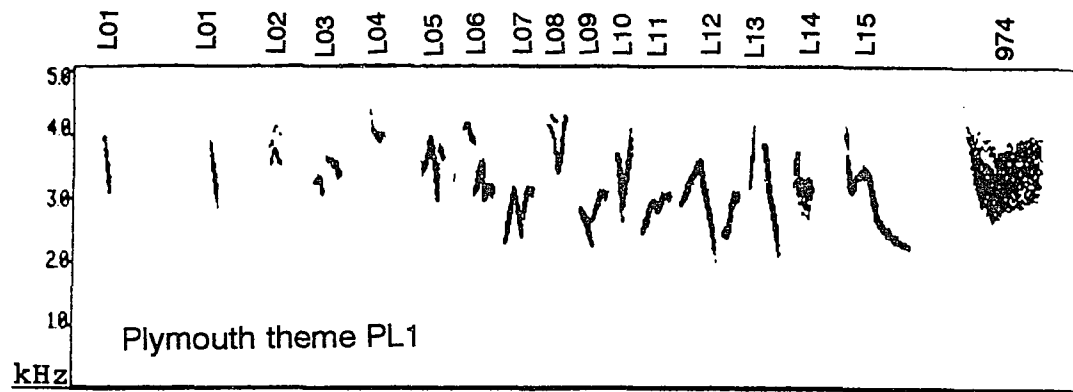
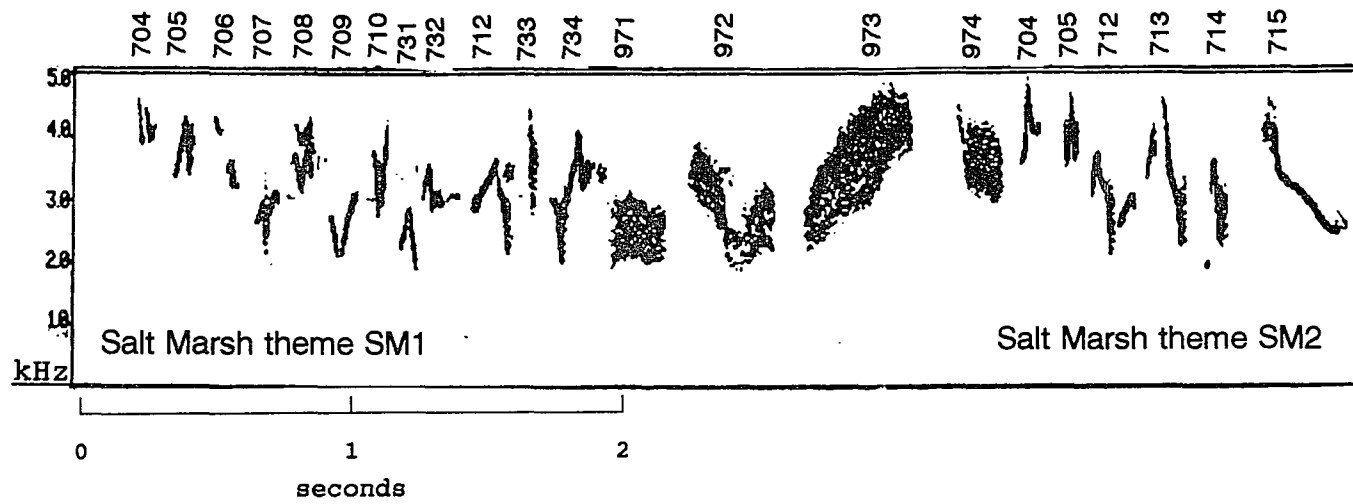


Figure B.5: Theme C1/C2 hybrid sung in Chatham compared with a theme sung in Peningo, NY.

The identifiers of syllables in the Chatham theme were changed to those of their postulated homologs in the Peningo theme. The syllables of Chatham theme C1 appeared to be variants of syllables of Peningo theme P3. Of the postulated homologs, syllables 37, z, and d' and the sequence 36 r s t are the most similar; while the homologies of syllables u, v, and y are less obvious. Several introductory syllables of the Peningo theme were not sung in Chatham and were omitted from this comparison. Following is a syllable homology comparison for the two themes.

Chatham	37	[+][+][+]	36	r	s	t	[+]	u	v	y	z	[-][-][-]	d'		
Peningo	37		36	r	s	t		u	v	y	z	g	h	i	d'

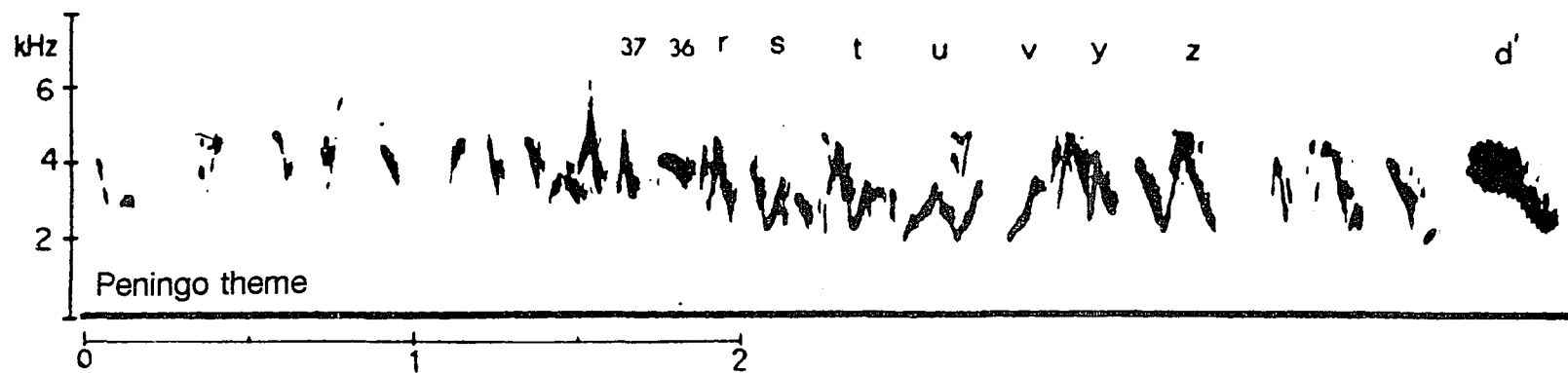
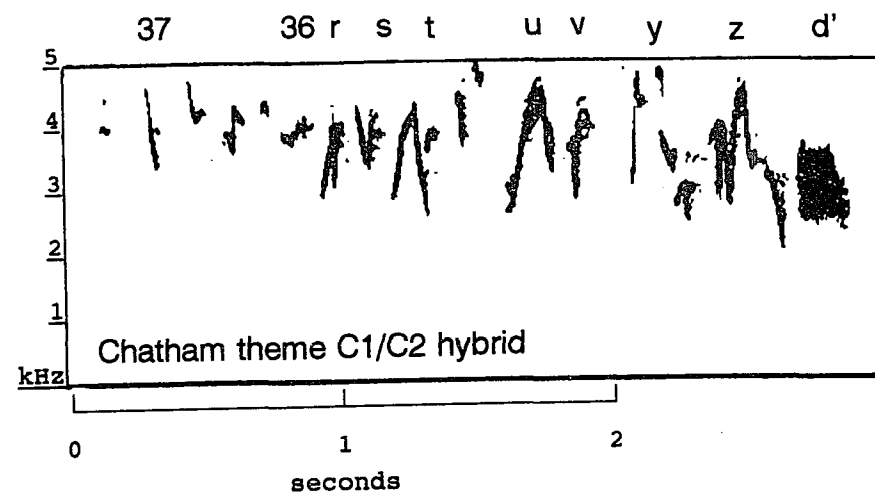


Figure B.6: Theme C2 sung in Chatham compared with a theme sung in Harrison, NY.

The identifiers of syllables in the Chatham theme were changed to those of their postulated homologs in the Harrison theme. Syllables of Chatham theme C2 appeared to be variants of syllables of Harrison theme H3. In this comparison, syllables 33, r, s, x, v, and y are most closely related, while the homologies of syllables 35 and 34 are less obvious. Syllable v of the Harrison theme was shifted in the Chatham sequence (see arrow below) to fall after syllable x. Following is a syllable homology comparison for the two themes.

Chatham	35	34	33	r	2	[-][-]	s	s	[-][-][-]	x	[+][+]	v	y			
Harrison	35	34	33	r	2	1	r	s	s	u	v	w	x	(v)	y	z

—————>

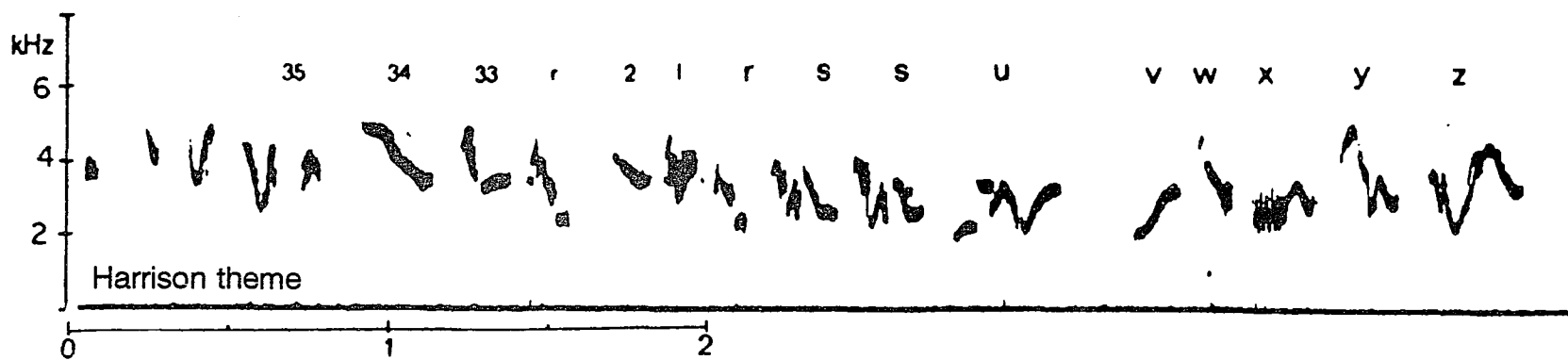
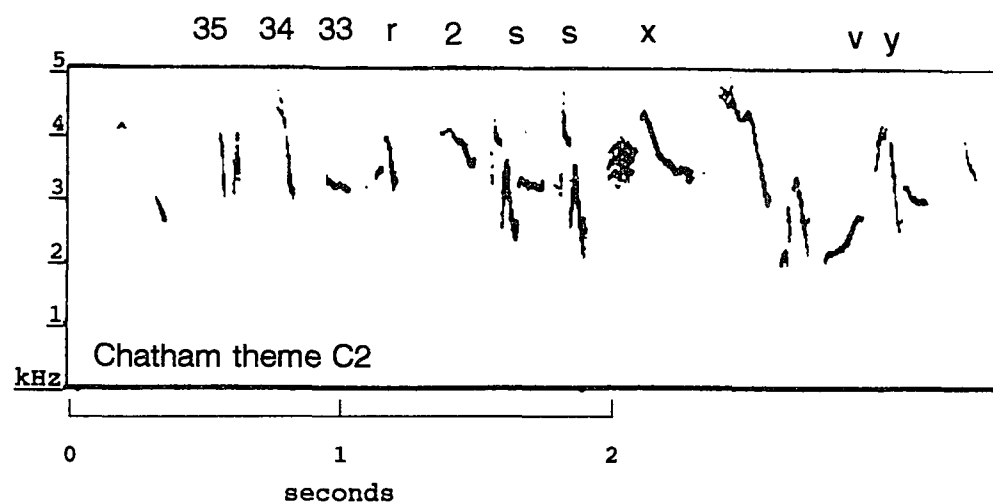
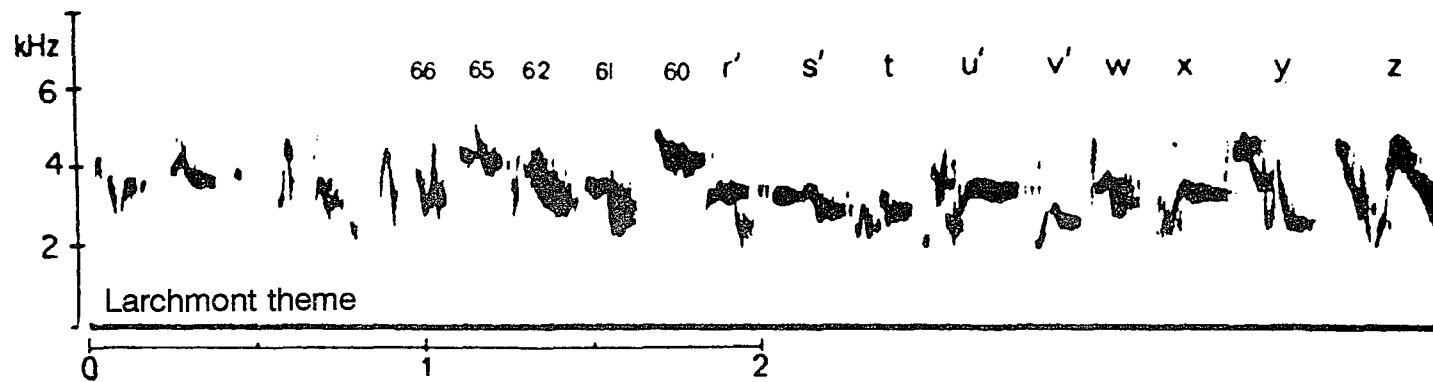
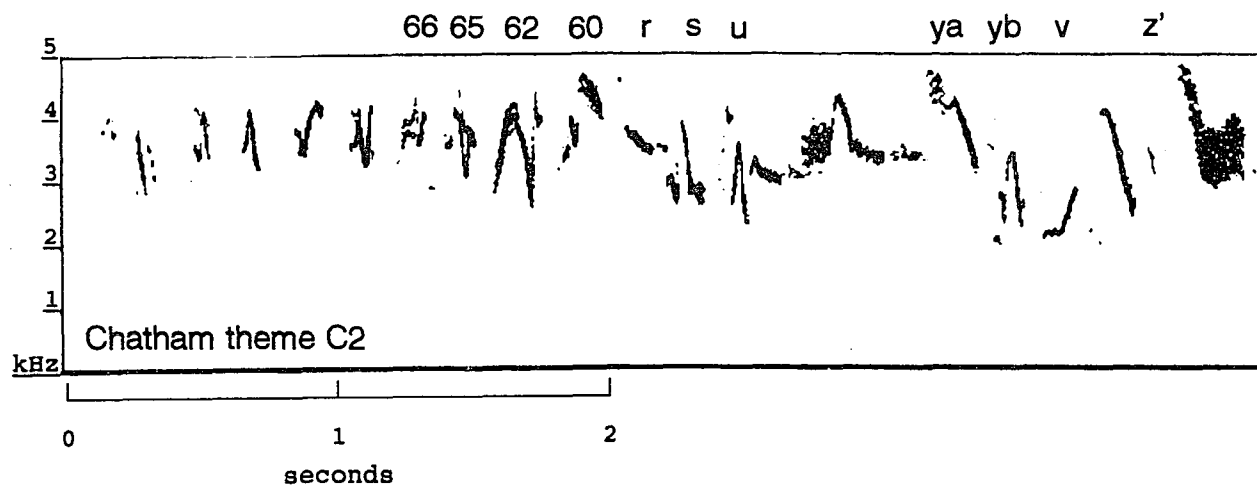


Figure B.7: Theme C2 sung in Chatham compared with a theme sung in Larchmont, NY.

The identifiers of syllables in the Chatham theme were changed to those of their postulated homologs in the Larchmont theme. Syllables of Chatham theme C2 appeared to be variants of syllables of Larchmont Theme L7. The sequence 66 65 62 and syllable u' exhibit the closest homologies in these themes. The sequence r s - u' shows Portions of syllable y of the Larchmont theme appeared to be sung as independent syllables in the Chatham theme. Again, syllable v of the Larchmont theme was shifted in the Chatham sequence, but this time it fell after syllable y of the Chatham theme. Following is a syllable homology comparison for the two themes.

Chatham	66	65	62	[-]	60	r	s	[-]	u	J	K	[-]	[-]	[-]	ya	yb	v	z'
Larchmont	66	65	62	61	60	r'	s'	t	u'	[+]	[+]	v'	w	x	y	(v)	z	

>



APPENDIX C

TECHNICAL COMPARISONS OF

CAPE COD HOUSE FINCH SONGS WITH

SONGS OF OTHER SPECIES

Figure C.1: Theme H1 sung by House Finches in Harwich compared with a theme sung by a Common Yellowthroat.

Sonogram A is a typical rendition of theme H1 sung by House Finches in Harwich. Sonogram B is a song sung by a yellowthroat in the same area. The repeated triplet Y64 Y65 Y66 of the yellowthroat song was also included in the finch theme H1. The House Finch derivation of the triplet 264 265 266 included only the first note of syllable 265, and the syllables were sung at a lower frequency than in the yellowthroat song.

The introduction to the House Finch song (syllables 261-263) was derived from the introduction to Barnstable theme B1A. The ending was also sung by local finches at the end of themes B1B and B2.

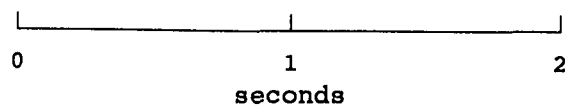
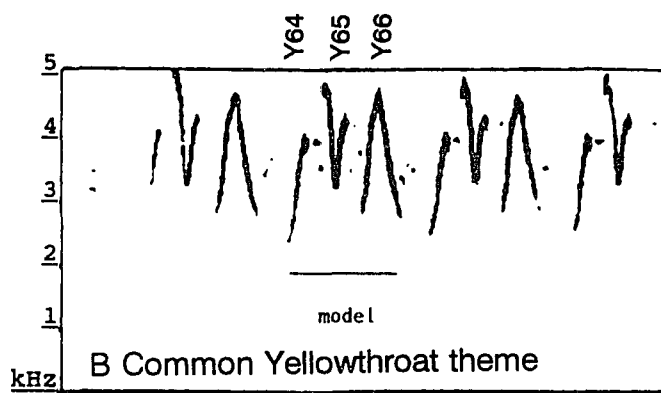
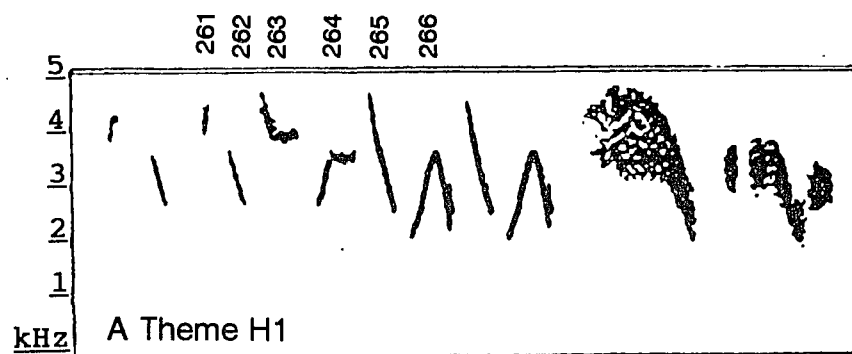


Figure C.2: House Finch theme SP1 sung in Osterville compared with a theme sung by a Common Yellowthroat.

Yellowthroat song seemed to be an acceptable model for House Finches. A variant of theme W4 (sonogram A), sung in Osterville, included complex syllables that seemingly had derived from yellowthroat song (sonogram B). Syllable 254 of the House Finch song is similar to the pattern of syllable 254 of the yellowthroat. The House Finch sequence 254 255 256 is similar to the sequence Y54 Y04 Y05 of the yellowthroat.

The yellowthroat song depicted could not have served as a model for the Osterville dialect because these recordings were made about 100 km apart (the yellowthroat in Provincetown, the finch in Barnstable). Yellowthroats were heard, but not recorded, in Barnstable with songs that sounded similar to the introduction seen in the Osterville dialect.

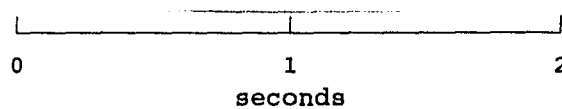
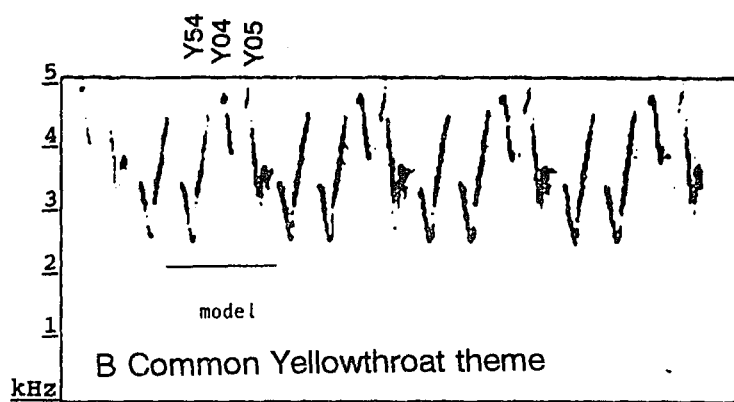
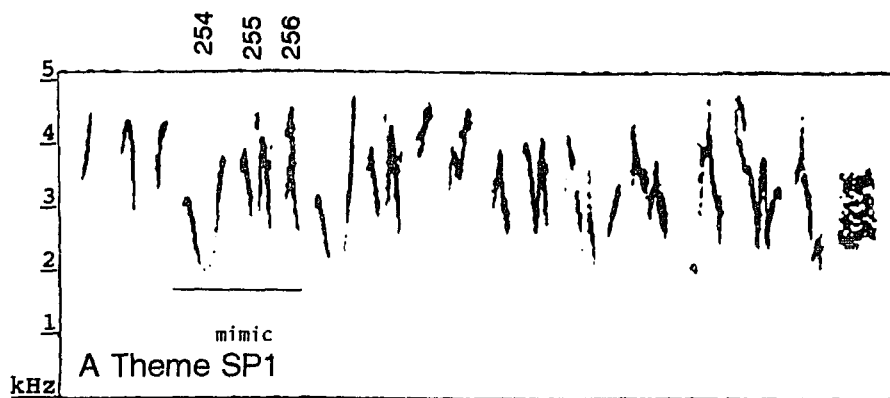


Figure C.3: House Finch theme CL1 sung in Brewster compared with themes sung by an Ovenbird and a Purple Finch.

An unusual trilled syllable (283), in House Finch theme CL1 (sonogram A), was seemingly copied from an Ovenbird syllable (syllable OV3, sonogram B) or Purple Finch (syllable PF3, sonogram C) songs. The House Finch rendition was neither a note-to-note match with, nor sung at the same frequencies as the trilled syllable in the Ovenbird and Purple Finch songs. Unique features of this House Finch pattern were that the repeated syllable was at the beginning of the song, and had the timing and general structure of the Ovenbird pattern. A second feature of this pattern that suggests it was alien-derived is that several finches with this song in their repertoire also sang a strongly modified version of syllable 283 where the third note was dropped (sonogram B, Figure A.).

Three syllables of the ending of the House Finch song (981 982 983) were more similar to the ending syllables of the Purple Finch than they were to ending syllables of other House Finch songs.

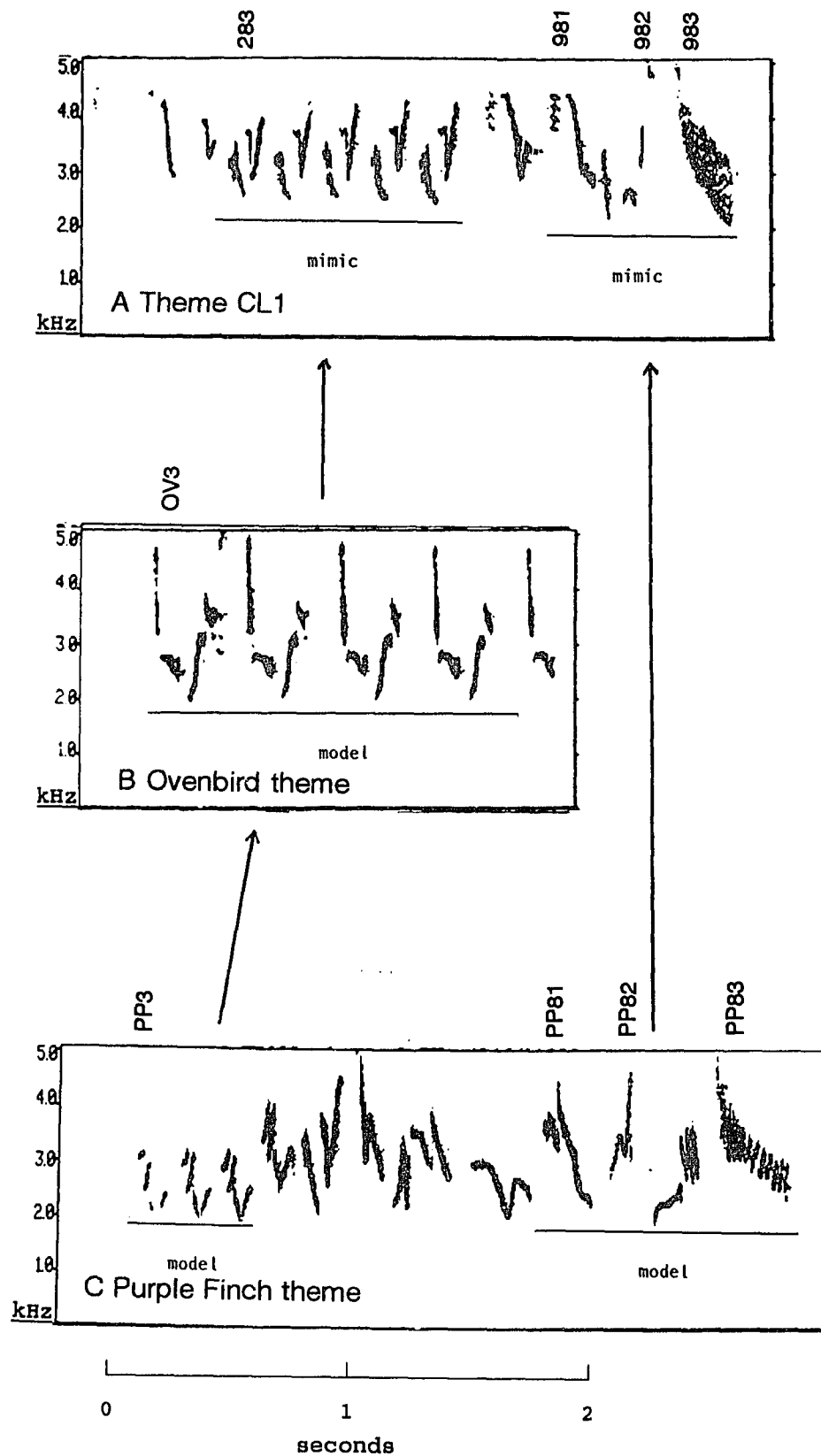


Figure C.4: House Finch theme HK1 sung in Brewster compared with a theme sung by a Goldfinch.

Finches at Herring Brook in Brewster sang introductory trills (sonogram A) which were strongly suggestive of trills in the songs of American Goldfinches (sonogram B). Theme HK1 is a variant of theme B1A, but the syllable pronunciation structures are similar to the goldfinch patterns. This is especially so in the introductory trill (syllable 283, sonogram A), but goldfinch influence also appears in the pronunciations of syllables 287 and 288.

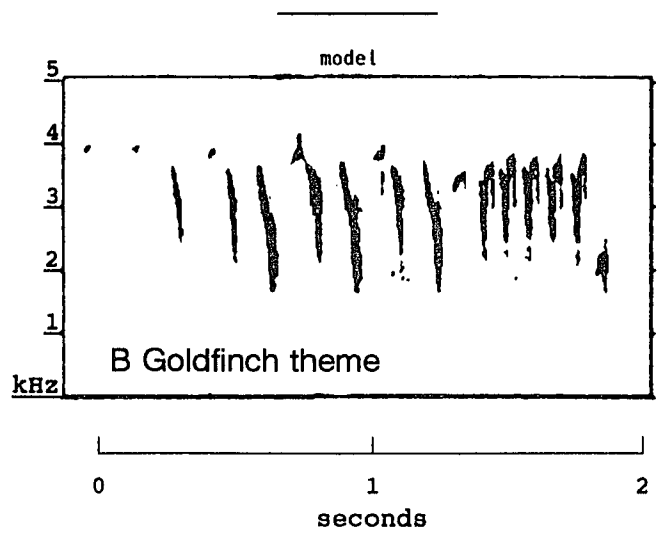
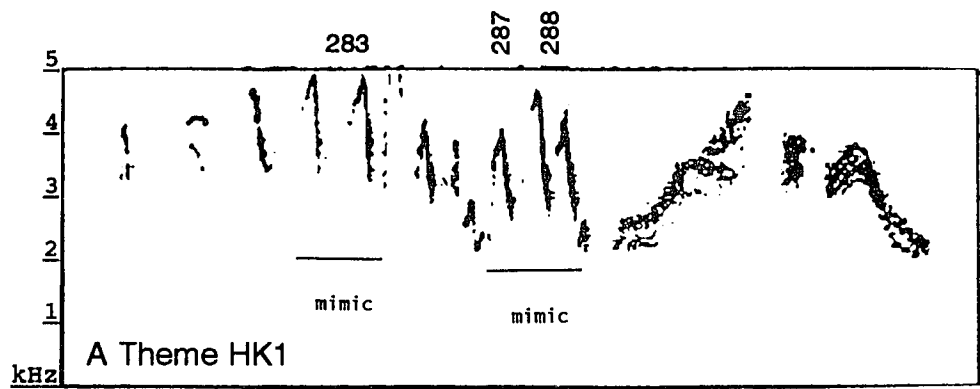


Figure C.5: Variants of House Finch theme YM1 sung in Yarmouth compared with the rattle calls of Downy Woodpeckers and Yellow-shafted Flickers.

Individuals in the Yarmouth dialect of the Barnstable institution sang songs (sonogram A) that appeared to be derived from the rattle call of the Downy Woodpecker (sonogram B). Syllables of this unusual song were modified (sonogram C) and assimilated into the regional dialect (sonogram E). In the intermediate songs (sonogram C), some syllables more closely resembled the rattle call of the Yellow-shafted Flicker (sonogram D).

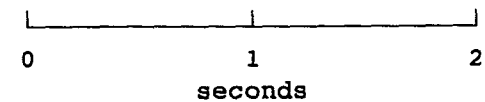
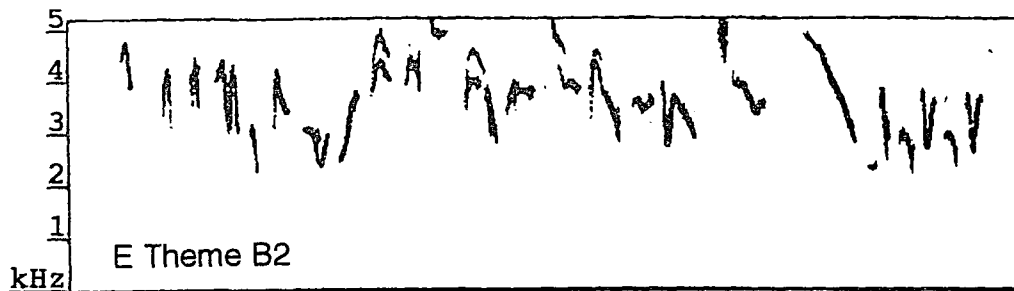
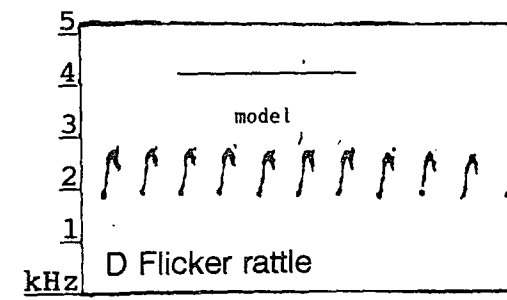
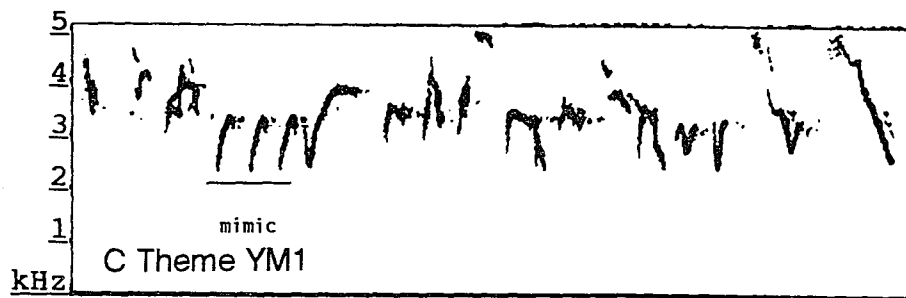
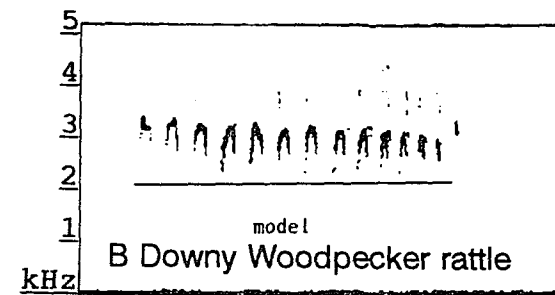
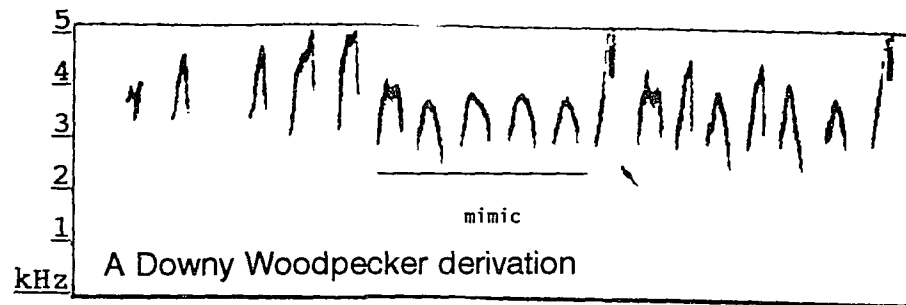
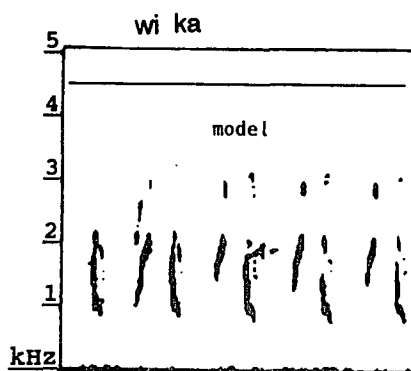
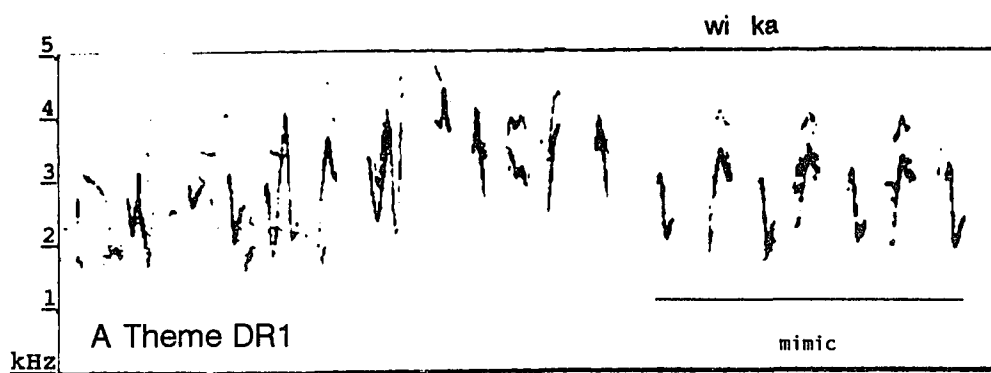


Figure C.6: House Finch theme DR1 sung in Harwich compared with the "wicka wicka" call of the Yellow-shafted Flicker.

The Doane Road population in Harwich ended its song (sonogram A) with a routine (syllables "ka" and "wi") that closely resembled the flicker's "wicka wicka" call (sonogram B). These syllables have the same pronunciation and harmonics as those of the flicker's call notes. The primary difference between the House Finch and flicker renditions is that the House Finch notes are sung at a higher frequency (maximum 3.3 kHz) than those of the flicker (maximum 2.2 kHz).



B Yellow-shafter Flicker "wicka wicka call"

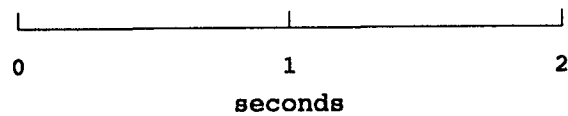


Figure C.7: House Finch theme PL1 sung in Plymouth compared with a song of the Indigo Bunting.

A population of finches in the Plymouth Rock area sang a theme (sonogram A) that included three syllables (PL7, PL8, and PL9) that appeared derived from syllables H, J, and D sung by an Indigo Bunting (sonogram B) recorded two miles away. The sequence PL7 PL8 PL8 PL8 of the finch song reflected the repeat pattern H H J J of the bunting song.

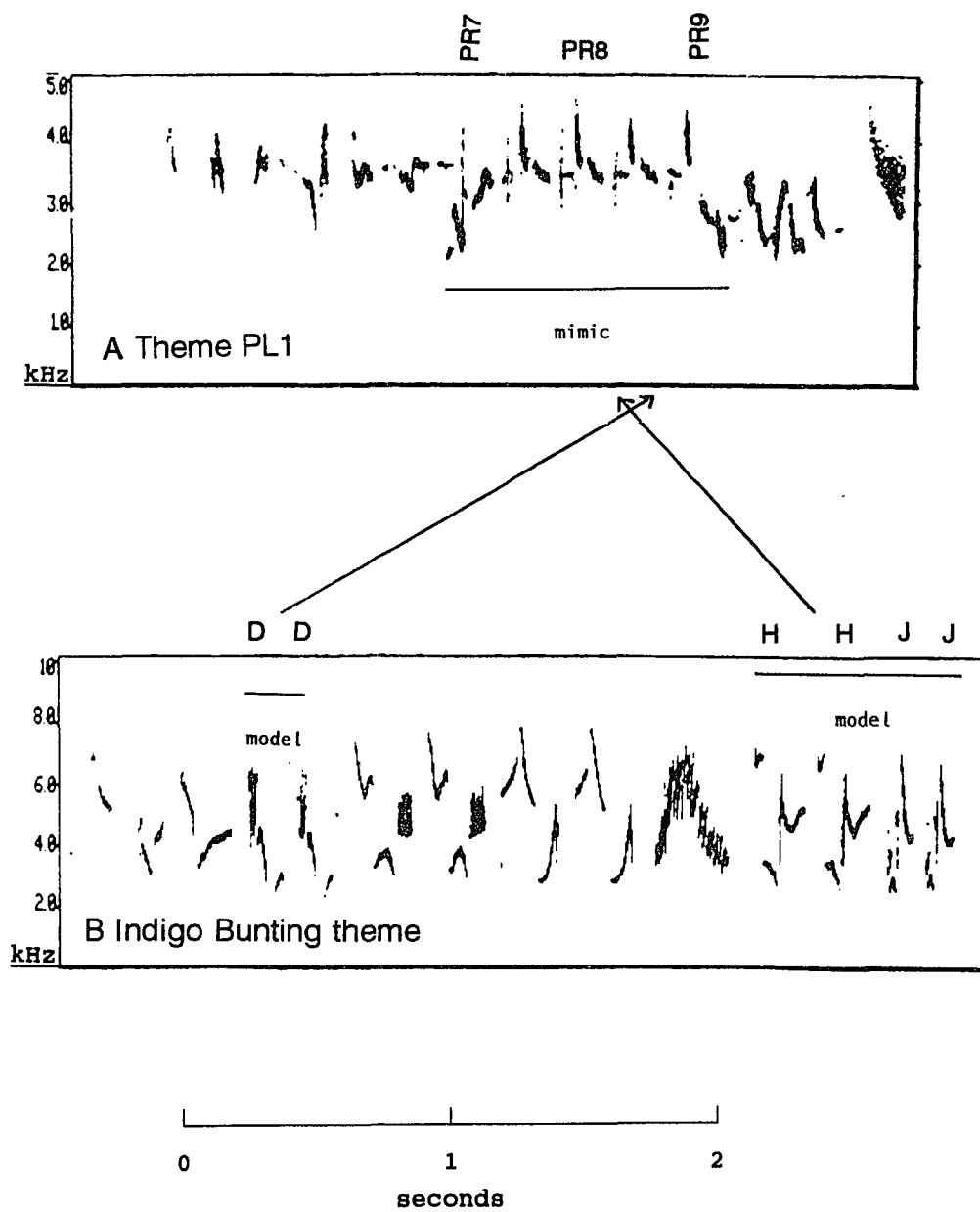


Figure C.8: House Finch theme WO1 sung in Woods Hole compared with a song of the Song Sparrow.

Themes sung by the Woods Hole population (sonogram A) in Falmouth incorporated a trilled syllable 167 and buzzy note 961 which closely resembled a trilled syllable (SS7) and buzzy note (SS9) of a Song Sparrow theme (sonogram B). The frequency change from the trill to the buzzy note, as sung by the House Finch, was similar to the frequency change sung by the Song Sparrow. The absolute frequencies of these notes were approximately 2.5 kHz lower in the finch song.

The Song Sparrow song was recorded only three hundred feet from the finches, thus this pattern could have been the original model for the alien-derived finch song.

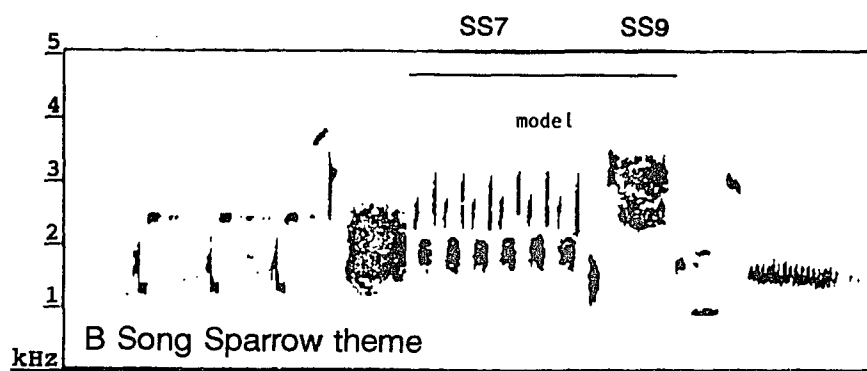
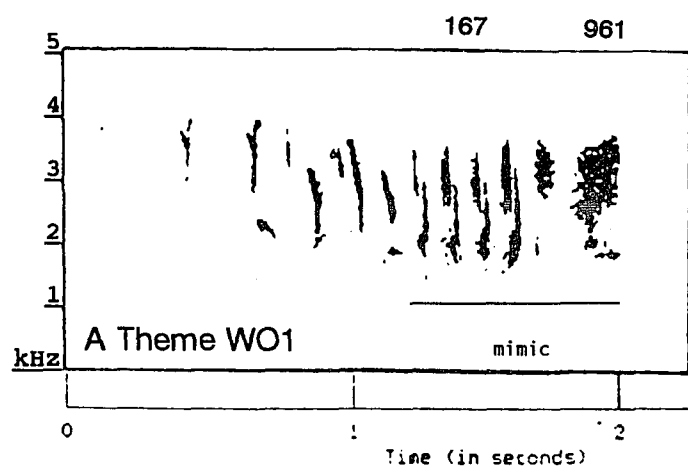


Figure C.9: House Finch theme F1Ba sung in Wareham compared with a trill of the Cardinal.

Most Cape Cod House Finch populations included in their repertoires trills (syllable 110, sonogram A) derived from Cardinal song (sonogram B). In no instance was the finch routine an exact copy of a Cardinal's trill, and the finch trills only included descending syllables (not the ascending syllables also typical of Cardinal song). There were similarities in note pronunciation, inter-syllable intervals, and frequency ranges.

On two separate occasions while I was recording, a House Finch began to sing a theme with a routine patterned from Cardinal song and within three songs a Cardinal flew to an exposed perch and began singing vigorously with its crest raised¹. This behavior on the part of the Cardinal was similar to the response obtained when a tape recording of Cardinal song is played to a breeding male. Thus, although the House Finch trill (sonogram A) was not similar to the trill recorded from the Cardinal (sonogram B), the House Finch pattern was similar enough to a Cardinal pattern that the Cardinal responded with agonistic behavior.

¹Although the patterns in sonograms A and B do not match, they were included because the theme in sonogram A elicited an agonistic response on the part of a Cardinal. Sonogram A was sung by a House Finch. Sonogram B is the song sung by the Cardinal after hearing the House Finch theme in sonogram A.

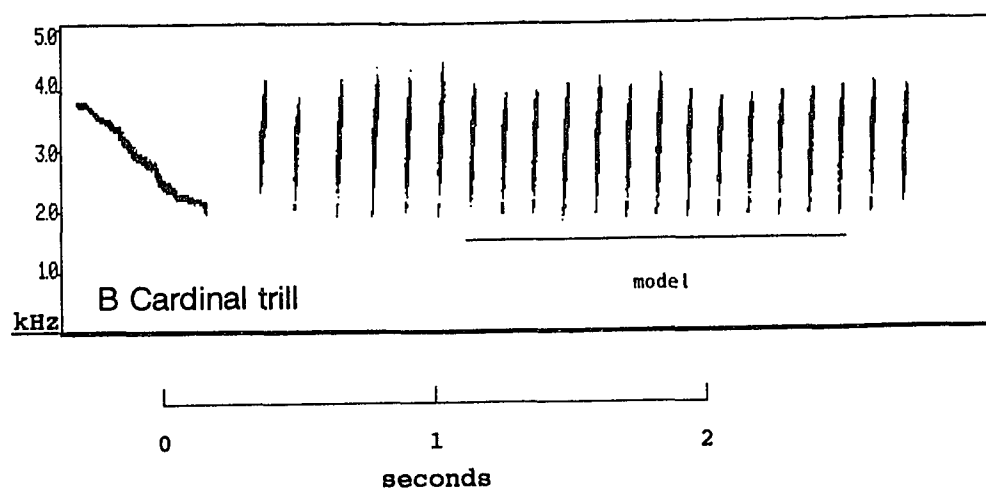
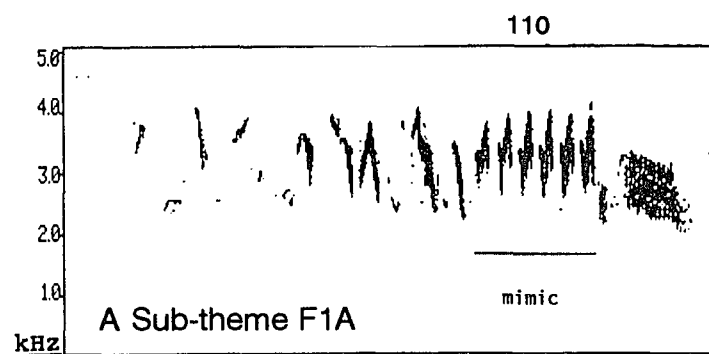
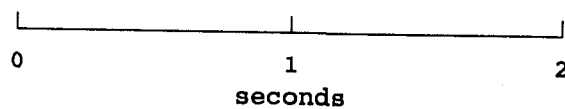
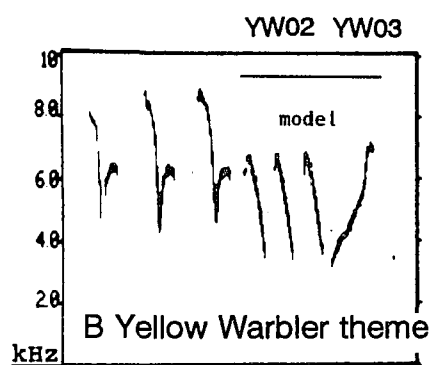
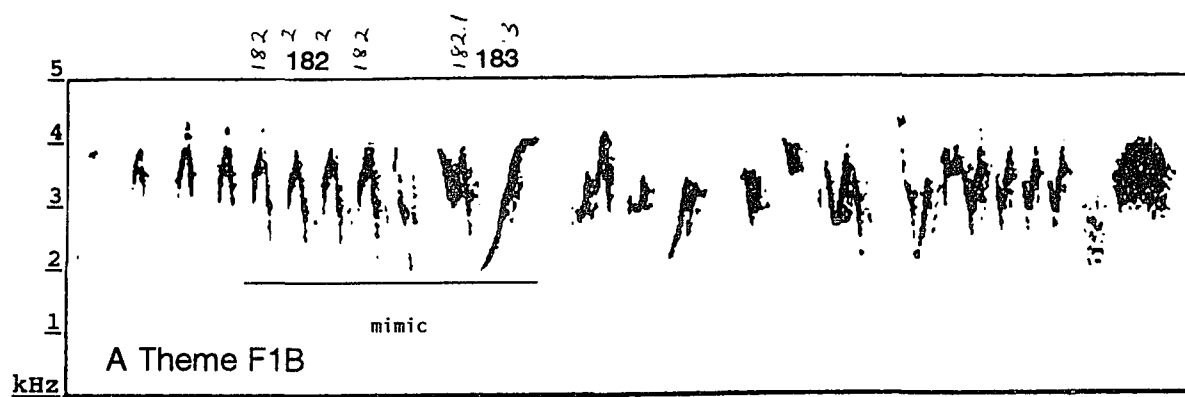


Figure C.10: House Finch theme F1Ba sung in Sandwich compared with a Yellow Warbler song.

The Sandwich dialect (sonogram A) included two syllables (182 and 183) derived from two syllables (YW02 and YW03) sung by a Yellow Warbler recorded in the same neighborhood. Although the Yellow Warbler syllables (sonogram B) were sung at almost twice the frequency of the House Finch copy (7000-3000 kHz vs 4100-2000 kHz), (1) each song contained two trilled syllables followed by syllable YW03/syllable 183 (this was unique among finch songs on Cape Cod), (2) the inter-syllable period of the first trill is longer than the inter-syllable period of the second trill in both songs, (3) the pronunciation of syllable 182 is similar to that of syllable YW02, (4) the pronunciation of the second note of syllable 183.1 was similar to the pronunciation of syllable 181, while (5) the time domain and pronunciation of House Finch syllable 183 were extremely close to those of the warbler syllable YW03. The long, rising slope of syllable 183 was unique among finch songs on Cape Cod.



GLOSSARY:

Definitions of the terms I use in this thesis are presented here.

Alleles (cultural alleles): In this thesis I distinguish between the basic syllable pattern and the pronunciation variant. The variants of syllables are called alleles. The term "allele" was used in a cultural sense by Mundinger (1980) to represent different pronunciation variants of syllables, and has since been adopted as a cultural descriptor. Alleles are used in microgeographic analysis of song distribution, are compared when inferring dispersal routes, and are used to demonstrate cultural relationships. Although I apply allele in a cultural context, this term retains the same connotation as in genetic studies because it refers to variation in expression of a single self-replicating entity (Dawkins 1989). Similarities and differences between alleles are important in analysis of dispersal routes and cultural transmission.

Core Segment: This is a distinct sequence of one to three routines. The pronunciation of syllables in a core segment is rather constant within a population, with one to several alleles of basic syllable patterns being shared by most individuals. Core segment syllable pronunciations usually vary between populations. Although individual males add or subtract syllables or substitute alleles in song repetitions, the sequence in which core segment syllables are presented is constant.

Dialect: Members of a local finch population share the same themes, routines, and syllables. Different local populations may sing variants of the same basic themes. These population variants are called dialects. Males within the same dialect extensively share the same lexicon, syntax, and group of pronunciation alleles. Dialects are important in dispersal analysis, the study of microgeographical affiliations, and cultural transmission. The distribution of dialects is examined extensively in this thesis.

Ending Segment: One to three routines, each composed of two or three syllables, are habitually sung at the end of the song. These ending segment routines are sung over wide geographical areas, different populations singing different alleles of the same syllables. When singing the ending a male may sometimes separate the notes and sometimes join them. Because of this, most ending segment syllables were identified as single notes even when the notes fused into one trace.

Hybrid song: Often a male will sing a song incorporating core routines from two culturally distinct areas joined by a conjunction routine. I used these hybrid songs to determine the boundaries and regions of overlap of these distinct areas at several locations on the cape.

Institution: A set of local populations that share one or more unique themes is identified as a song institution (Munding 1980). Themes sung in one institution may be derivations of themes in another song institution in much the same way that one human language may have components derived from other languages. If themes of different institutions are related, their lexicons, syntax, and syllable pronunciations differ such that the homologies are obscure. The institution is critical for macrogeographical analysis and is an important concept in the thesis.

Introduction Segment: One to several routines sung at the beginning of a song constitute the introduction. There is more variation in the sequencing and pronunciation of introduction segment syllables both within and between individuals than in the rest of the song. Because of this variation, introduction segment syllables were not used for geographic analysis, but were important when analyzing cultural transmission.

Lexicon: This term describes the syllable vocabulary of a song and is used somewhat like linguists use it in the study of human language. The sum of the syllables that make up an individual's or population's songs is its lexicon. The lexicon of a human language is its words.

Note: The note is composed of a single burst of sound which produces one continuous trace on a sonogram. Notes are usually narrow-band, pure tones. House Finch notes are usually frequency modulated, rising or dropping in pitch. I consider a trace that abruptly changes direction to be composed of two or more notes. The term note is not widely used in the thesis, but is basic to the understanding of song structure.

Repertoire: The complete lexicon of one finch or one population is its repertoire. Incompletely sampled repertoires may cause errors such as indicating a lack of relationship between populations. Analysis of virtually complete repertoires is a requirement for many parts of this thesis. Individual males and small populations providing poor samples were eliminated from some procedures requiring analysis of complete repertoires.

Routine: Several syllables, typically two to six, are sung in standardized sequences to produce routines. Routines are usually shared by many males. Occasional individuals may delete from or add to the routine, but the general sequence of syllables within a routine remains constant and this permits the identification of routines and their variants. House Finch songs were often put together in modular fashion using routines as the modules. Routines are extremely important when examining song relationships.

Segment: Segment generally refers to one of the song divisions: introduction, core, or ending. I use the term segment when I do not need to indicate a specific division of the song.

Song: This is one complete vocalization separated in time from other songs by a period of 2.5 to 11 seconds or greater. The song is usually composed of three segments: introduction, core, and ending. Songs typically are 1.5 to 4 seconds in length.

Sub-theme: Several themes were sung in two or more distinct variants. I distinguished these forms as sub-themes. One sub-theme usually included fewer syllables than the other. The alleles of the syllables in the two sub-themes were characteristically related, but not identical.

Syllable: A syllable is a regularly vocalized distinctive pattern composed of one to six notes, usually one to three. For a given syllable pattern, pronunciation (its microstructure) may change between populations, but the basic form or pattern tends to remain constant within a population. The syllable is a key parameter of macrogeographic analysis and is constantly referred to.

Syntax: The order in which song routines are arranged is its syntax. The song syntax consists of a series of syllables usually sung in a proscribed sequence.

Theme: Songs sung with standardized sequences of core routines are called **themes**. Different themes may share one or two common routines. Introductions do not define themes for two reasons. First, introductory routines exhibit the most variation. Second, a given introductory routine may be sung with all themes a bird sings. The finches tend to reserve one to three ending routines (often composed of alleles of the same syllables) to sing with one specific core sequence, and another, nonexclusive group of ending routines to sing with a different core sequence. Thus I use theme to describe a particular sequence of core routines. Males sing two to five themes each. The sequence of routines in the themes sung within a population is an important indicator of song relationships.

Trill: Sequences of 2 or more repetitions of one or more syllables compose a **trill**. The syllables within a trill may change slightly in pronunciation and/or frequency from the beginning to end of the trill. Trills are important in determining cultural relationships.

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