

NORTHERN CARDINAL SONG IN THREE FOREST HABITATS IN EASTERN TEXAS

MARY E. ANDERSON AND RICHARD N. CONNER

Development of song dialects is influenced by (1) the morphological ability of birds to vary their song (Lanyon 1960); (2) the amount of gene flow between populations (Handford and Nottebohm 1976); (3) contrast reinforcement, the conveyance of specific information against a background of many other sounds (Konishi 1970); and (4) social adaptation, a form of modified behavior in which birds copy songs of their conspecific neighbors in response to social interactions (Payne 1981). Although Treisman (1978) theorized that dialects may help to establish and maintain relatively isolated populations, investigators do not agree on a single functional explanation for the existence of song dialects (Hartshorne 1956, Krebs 1977).

Biologists have begun to study the relationships between songs of birds and the efficiency of sound transmission through different acoustic environments (Ficken and Ficken 1962, Morton 1975, Wasserman 1979). Hansen (1979) suggested that young males selectively learn those song elements with acoustic properties that suffer the least amount of distortion during transmission. Acting as very sensitive receivers, young birds would preserve only those sounds which were best adapted for the particular acoustic environment in which they were raised. Gish and Morton's (1981) work on Carolina Wrens (*Thryothorus ludovicianus*) supports Hansen's hypothesis concerning vocal learning in birds. They determined that wren songs transmitted longer distances and retained acoustical properties better when propagated in their native localities than in other habitat conditions. As there is a significant difference in the attenuation rates of the same signal in different environments, the environment itself may be operating as a "filter" between sender and receiver, preventing a bird from copying those sounds which are quickly lost or distorted. Morton et al. (in press), however, recently reported that wrens can reproduce some songs in an undegraded form that they have only heard in degraded form. Morton (1982) advanced a "ranging hypothesis" that suggests that male birds learn the undegraded form of a neighbor's song in order to tell the distance of the singing neighbor. The amount of degradation in the song would help a male determine distances more accurately and know when to challenge if the singer is near and ignore him if far enough away.

Our study examined vocal patterns of three populations of Northern Cardinals (*Cardinalis cardinalis*) in eastern Texas. Our objectives were

to (1) examine differences in the repertoire size and syllable types of the three populations, (2) analyze and compare the morphology of the syllable types, and (3) note trends in acoustic structure and use in different vegetation.

STUDY AREAS

Three relatively homogeneous pine-hardwood stands in the Angelina National Forest were selected as study sites. The three stands were approximately 4.5 km from each other and ranged from mesic to xeric sandy uplands. No major geographical or biotic barriers existed between the sites. They differed primarily in age class of pines and the density of midstory and understory foliage (Ehrhart 1981).

Study area A was a pine sapling stand approximately 18 years old. The small, closely spaced pines characterizing this area averaged 10 m in height. A thick shrub layer occurred between 2 and 4 m. The dominant species of trees in terms of relative abundance were shortleaf pine (*Pinus echinata*), blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), and longleaf pine (*P. palustris*).

Study area B was a pine pole stand approximately 43 years old. The larger pines and hardwoods (31–45 cm diameter at breast height) formed a canopy at 25 m. A very thin shrub layer was measured as high as 3 m. Loblolly pine (*P. taeda*), shortleaf pine, and longleaf pine were the dominant species of trees.

Study area C, a sawtimber stand approximately 59 years old, had an upper tree canopy between 17 and 29 m. Midstory foliage of small diameter hardwoods was present between 7 and 12 m. Due to this extensive overstory cover, the understory was relatively sparse with few shrubs and minimal ground cover. The dominant species of trees were shortleaf pine, post oak, sweetgum (*Liquidambar styraciflua*), and flowering dogwood (*Cornus florida*).

METHODS

A 6-ha grid of ¼-ha plots was marked off to provide reference points when mapping the territories of cardinals. A total of 70 days was spent observing birds between 24 March and 18 July 1979. We visited sites on a rotating basis, usually every 3 days. Territories were determined by noting singing posts of males and those points where fights and chases took place (International Bird Census Committee 1970). Simultaneous bout singing was also used to affirm boundaries between adjacent territories.

The song repertoires of 16 cardinals were sampled: 5 cardinals each in the sapling and pole stands, and 6 cardinals in the sawtimber stand. By plotting the number of new syllables recorded vs total syllables recorded, we estimated that 90 to 110 songs were required to obtain an approximate measure of syllable repertoire. Fewer than 50 songs were recorded for 2 of the 6 cardinals in the sawtimber area. Data collected on these 2 birds were used only when testing for differences among the three populations. Repertoire sizes of one male from the sapling area ($N = 73$) and one male from the sawtimber area ($N = 77$) may have been underestimated slightly for between-bird comparisons.

Playback tapes were not used to promote singing. All recordings were made with a Uher 4000 Report L recorder at a tape speed of 19 cm/sec. A 40-cm parabolic reflector was used to focus the sound on a Dan Gibson EPM P-650 electronic microphone. Most recordings were made within 8 m of singing males.

All field recordings were reviewed at ¼ tape speed (4.7 cm/sec), and syllable types were identified. We verified syllable patterns with sonagrams made on a Kay Elemetrics model 7029A Sonagraph using the wide band setting with a frequency range of 80–8000 Hz. We

noted the kinds and numbers of syllables used in each song as well as song length and intersong interval. The last two variables were measured to the nearest 0.1 sec using an electronic stopwatch.

In order to describe syllable structure of each population, a random sample of 100 syllables was taken from each cardinal population. Within each population, an equal number of syllables was sampled randomly for each bird: 20 syllables per bird (5 birds) in the sapling and pole stands, and 25 syllables per bird (4 birds) in the sawtimber stand. Sonagrams were made on all 300 syllables using the wide band filter setting. Seven measurements were taken from these sonagrams: frequency range, frequency modulation, frequency with the greatest amplitude, highest frequency, lowest frequency, syllable duration (sec), and the time between syllables (sec). We also noted the number of elements in each syllable. The first three variables parallel those Morton (1975) used to arrive at his song-habitat correlations.

Frequency modulation of syllables was evaluated as an angular measurement of the rate of frequency change. Each syllable was divided into four equal segments, with five vertical lines; this provided five possible points of intersection with the syllable. At each point, the angle of inclination was measured in degrees with respect to the horizontal axis. Each angle was recorded as an acute angle, without regard for the quadrant in which it fell. Measurements were then totaled, and the average final angle was used as the index of frequency modulation, a measurement of the change in frequency over time.

RESULTS

Vegetation.—Foliage-height profiles were constructed to characterize the physiognomy of each study area (Fig. 1). The sapling stand, the youngest of the three areas, had a very thick understory consisting of numerous woody and herbaceous species, and was the only site that lacked an upper tree canopy. Both of the older stands had sparse understories beneath foliage in the upper and midstory vegetation.

Repertoires.—Thirty-two different syllable types were identified in our study: 23 syllables in both the sapling and pole stands, and 20 in the sawtimber stand. Four of the 11 syllables shared among the three areas were simple, one-element sounds (Table 1). Of the 23 syllables recorded in the sapling stand, 15 were sung by four of five cardinals in the area (Table 1). Syllable repertoires of cardinals averaged 16.4 syllables (range = 9–21) in the sapling stand, 13 (8–17) in the pole stand, and 12.5 (8–16) in the sawtimber stand. Differences in repertoire size among the three areas were not significant (Kruskal-Wallis one-way ANOVA, $P > 0.1$).

The average number of syllables in a song was the most variable song parameter in each study area (Table 2). Of the songs recorded, 65% consisted of two syllables; 33% had just one syllable; the remaining 2% consisted of combinations of three syllables.

Many more syllables were shared among birds in the sapling stand (16.0) than in either the pole (11.4) or sawtimber (11.5) stands. This higher degree of syllable sharing reflected the intensity of matched countersinging and the higher density of cardinals in the sapling stand. Density of cardinal

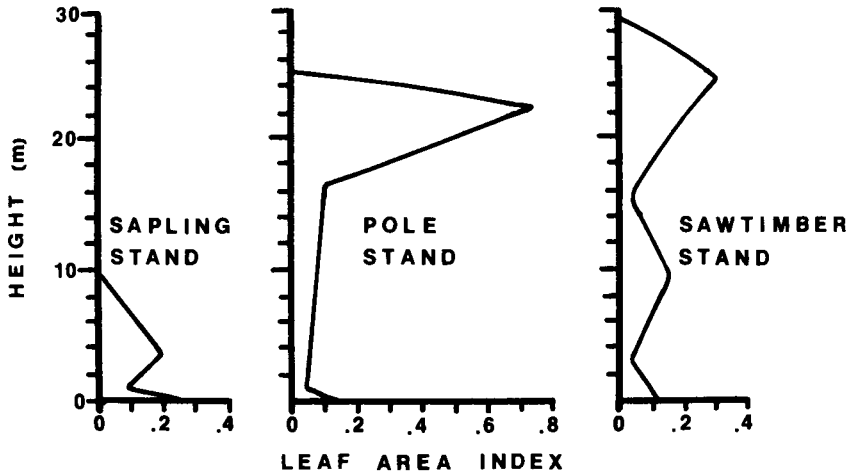


FIG. 1. Vertical foliage profiles of each study area based on foliage density measurements taken at ground level, 1 m, 2 m, 3 m, 7–12 m, 13–20 m, and 20 m (Ehrhart 1981).

pairs was higher in the sapling stand (1.05 pairs/ha) than in the pole (0.94 pairs/ha) or sawtimber (0.88 pairs/ha) stands.

The greatest amount of syllable sharing (percent overlap, Schoener 1970) occurred within each area (Sapling: \bar{x} syllable sharing = 39%, Pole: \bar{x} = 44%, Sawtimber: \bar{x} = 38%) (Table 3); percent overlap was greatest between immediate neighbors. Between areas, substantial syllable sharing was also noted in the repertoires of birds from the pole and sawtimber stands (\bar{x} = 28%). Overlap in syllable usage between cardinals in the sapling and sawtimber stands averaged 24%; between birds in the sapling and pole stands overlap averaged 21%.

Cluster analysis on syllable types (Dixon and Brown 1979) was used to group individual cardinal repertoires (Fig. 2). At the level of three main clusters, syllable usage successfully segregated all but one of the repertoires according to area (cardinal A-5 from the sapling stand). The increase in amalgamation distance obtained by forming two clusters (the sapling cluster and the pole-sawtimber cluster) from the three clusters was 1.8 units (Fig. 2). A 3.4 increase was needed, however, to form the final cluster consisting of all three areas, suggesting again that songs in the pole and sawtimber stands were more similar to each other than they were to songs in the sapling area.

A three-group stepwise discriminant function analysis (DFA) on syllables and song variables (Table 1 and 2) using Rao's *V* to maximize

TABLE 1
THE NUMBER OF CARDINALS IN EACH AREA THAT USED A PARTICULAR SYLLABLE TYPE
AND NUMBER OF SYLLABLES RECORDED

Syllable type	Area							
	Sapling		Pole		Sawtimber		Total	
	No. males	No. recorded	No. males	No. recorded	No. males	No. recorded	No. males	No. recorded
A (3) ^a	4	89	1	2			5	91
B (3)	5	176	1	2			6	178
C (3)	4	65	3	120	1	2	8	187
D (3)	4	157					4	157
E (2)	4	92	4	46			8	138
F (1)	4	86	5	121	3	125	12	332
G (1)	5	189	5	45	2	34	12	268
H (26)	5	101	5	15	2	21	12	137
I (2)	1	10	5	193			6	203
J (3)	4	74					4	74
K (3)	4	74					4	74
L (2)	4	52					4	52
M (2)			3	22	2	123	5	145
N (3)	2	63					2	63
O (2)			1	1	2	67	3	68
P (1)	2	30	4	51	3	134	9	215
Q (2)	5	102	2	53	4	76	11	231
R (1)					4	86	4	86
S (3)			5	82	1	14	6	96
T (1)			2	74	3	174	5	248
U (3)			1	3	3	145	4	148
V (2)	4	114	3	46	3	61	10	221
W (2)	3	35	4	118	3	89	10	242
X (2)			1	10	3	73	4	83
Y (2)	4	23	1	8	3	53	8	84
Z (3)	1	40					1	40
AA (1)	3	97	1	1	1	14	5	112
BB (1)			3	233	2	14	5	247
CC (2)	3	48	1	26	1	35	5	109
DD (2)	3	36					3	36
EE (2)					4	70	4	70
FF (2)	4	127			4	163	8	290

^a Number in parenthesis indicates the number of structural elements in each syllable type.

separation of areas was used to test the integrity of the three dialects identified by cluster analysis (Dixon 1977). Group separation was highly significant ($P < 0.001$); 87.4% of all the songs were correctly classified according to area. Syllables BB, I, and C were the first variables to enter

TABLE 2
STRUCTURE OF CARDINAL SONGS IN THREE FOREST STANDS IN EASTERN TEXAS

	Sapling	Pole	Sawtimber
No. of birds	5	5	6
No. of songs	947	855	809
Song duration (sec)	3.56 ± 0.4 (36) ^b	2.67 ± 0.04 (41)	3.27 ± 0.05 (39)
No. of syllable types per bird ^a	16.4 ± 2.01 (27)	13.0 ± 1.61 (28)	12.5 ± 2.06 (33)
No. of syllables per song	11.28 ± 0.21 (57)	7.88 ± 0.15 (55)	9.49 ± 0.18 (52)
No. of syllable types per song	1.99 ± 0.03 (45)	1.57 ± 0.02 (38)	1.86 ± 0.02 (28)

^a Calculations based on birds with 50 or more recorded songs.

^b Mean ± SE (CV).

the analysis while song length was the fourth. Pearson correlations between the original variables and the first and second discriminant functions revealed that syllables T, B, M, D, BB, FF, and I, as well as song length and the number of syllable transitions per song, were important in separating cardinal song in the three study areas. All of these syllables were used commonly in one or two of the areas (Table 1).

Syllable characteristics.—Northern Cardinal songs ranged from 1000 to 7000 Hz. The mean frequency range for 100 randomly selected syllables in each area was considerably smaller: 3050 Hz in the sapling stand, 2760 Hz in the pole stand, and 2400 Hz in the sawtimber stand (Table 4). For each of these frequency ranges, the mean lower frequency was approximately 1400 Hz (ANOVA, $N = 300$, $P > 0.50$); the frequency with most amplitude was about 2100 Hz for all areas.

Stepwise DFA (using Rao's V to maximize separation of groups) was used to detect differences in the physical nature of cardinal syllables among the study areas. Frequency modulation was the most important variable in the discrimination among syllables in study areas. A one-way ANOVA ($P < 0.01$) and Duncan's New Multiple Range Test ($P < 0.01$) indicated that, with respect to frequency modulation, syllables recorded in the pole and sawtimber stands were similar, but that syllables from the sapling stand were significantly different (Table 4). Cardinals in the pole and sawtimber stands used syllables with relatively "flat" configurations, i.e., less frequency modulation than those used by cardinals in the sapling stand. Although syllable H (a terminal trill note) was used in the first two areas, it was seldom heard and rarely recorded.

Factor analysis (Dixon and Brown 1979) revealed a negative relation-

TABLE 3
OVERLAP MATRIX OF CARDINAL SYLLABLE TYPES IN THREE TIMBER STANDS IN EASTERN TEXAS

Bird	Sapling						Pole						Sawtimber			
	Bird 2	Bird 3	Bird 4	Bird 5	Bird 7	Bird 18	Bird 19	Bird 21	Bird 22	Bird 23	Bird 10	Bird 13	Bird 15	Bird 16		
Sapling																
2	—	0.49 ^a	0.39	0.34	0.54	0.40	0.08	0.28	0.26	0.35	0.30	0.21	0.24	0.31		
3	13 ^b	—	0.56	0.19	0.46	0.11	0.02	0.13	0.12	0.16	0.18	0.10	0.17	0.26		
4	14	15	—	0.14	0.46	0.15	0.04	0.14	0.18	0.14	0.20	0.16	0.12	0.23		
5	7	9	6	—	0.35	0.27	0.11	0.18	0.15	0.20	0.19	0.12	0.22	0.36		
7	15	16	15	8	—	0.30	0.20	0.28	0.41	0.47	0.44	0.20	0.33	0.45		
Pole																
18	10	10	8	7	11	—	0.25	0.42	0.24	0.35	0.34	0.31	0.25	0.37		
19	4	3	3	3	5	8	—	0.53	0.69	0.44	0.33	0.09	0.22	0.14		
21	8	8	6	5	10	13	8	—	0.48	0.34	0.47	0.24	0.29	0.28		
22	6	6	5	4	9	9	7	11	—	0.66	0.49	0.13	0.24	0.31		
23	6	8	5	4	9	8	5	10	9	—	0.33	0.08	0.25	0.35		
Sawtimber																
10	9	8	8	4	10	9	4	10	8	7	—	0.28	0.57	0.44		
13	4	4	4	1	5	6	2	4	2	1	7	—	0.20	0.44		
15	6	6	5	4	6	6	4	8	4	4	9	4	—	0.37		
16	7	8	7	2	9	9	3	10	6	7	13	7	7	—		

^a Percent overlap (Schoener 1970) expressed in decimal form appears above the diagonal.

^b Numbers below the diagonal indicate how many syllable types were shared between two individual cardinals.

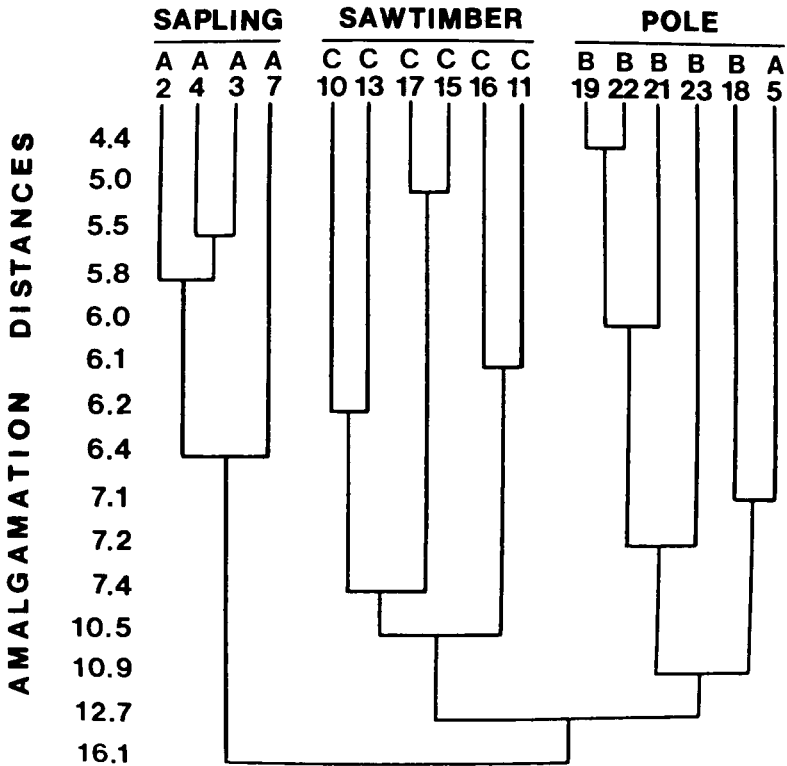


FIG. 2. Dendrogram of three groups formed by cluster analysis based on how many times each syllable type was recorded for each bird. Case labels correspond to the area and territory of each bird; amalgamation distances for each cluster appear to the left of the dendrogram.

ship between frequency modulation and syllable length ($r = -0.62$, $P < 0.01$). As frequency modulation decreased and syllable length increased, syllables became relatively "flat."

Four factor analyses were calculated on syllable structure (same variables as in Table 4): one to describe the variance in syllable structure for the three areas combined, and one for each area separately. The composite factor analysis explained 76.1% of the total variation among the three areas with three factors (Table 5). Its first and most important factor, a general frequency factor, explained 34.3% of the observed variation. Three of the four frequency measurements had the highest factor loadings, with highest frequency and frequency range contributing the most. The second factor explained 27.6% of the variation; it defined a reciprocal relationship

TABLE 4
STRUCTURE OF 100 RANDOMLY SELECTED SYLLABLES FROM EACH CARDINAL POPULATION

	Sapling	Pole	Sawtimber
Frequency range (Hz)	3048 (35) ^a	2760 (45)	2408 (38)
Frequency modulation (degree)	51 (28)	44 (31)	43 (29)
Frequency with greatest amplitude (Hz)	2139 (17)	2197 (12)	2078 (16)
Highest frequency (Hz)	4410 (24)	4247 (30)	3827 (27)
Lowest frequency (Hz)	1385 (14)	1387 (14)	1419 (17)
Syllable duration (sec)	0.23 (73)	0.25 (67)	0.28 (60)
Time between syllables (sec)	0.12 (72)	0.15 (71)	0.13 (50)
No. of elements in syllable	2.34 (107)	1.93 (36)	1.68 (43)

^a Mean (CV).

between song length, intersyllable interval, and frequency modulation. This factor, therefore, would describe the general configuration of the syllable. The third factor, explaining 14.2% of the variation, specified the number of elements in a syllable, an indication of the complexity of the syllable.

The results obtained in the factor analyses for the pole and sawtimber stands were virtually identical to those discussed above, the only difference being that the pole stand lacked a third factor (Table 5). The three factors derived for the sapling stand, however, were quite different, primarily because the first factor identified syllable configuration (frequency modulation and syllable length), not frequency, as the most variable characteristic.

DISCUSSION

Although Northern Cardinal dialects have been described previously (Lemon 1965, 1966, 1975), they have never been reported for populations separated by very short distances. In our study, significant differences in syllable usage were detected in the songs of three populations located within 4.5 km of one another. Cluster analysis identified three dialects and indicated a rather strong similarity in the dialects for the pole and sawtimber stands (see amalgamation distances, Fig. 2). This high degree of similarity was also noted in the amount of syllable sharing that occurred between those two areas (Table 3).

Syllable sharing occurred both within and among the three areas. In each area, the repertoires of males from adjacent territories were more similar than those of distant neighbors. This pattern of syllable sharing is quite common among songbirds with geographic dialects (Kroodsma 1975, Payne and Payne 1977, Jenkins 1978) and is thought to result from

TABLE 5
VARIMAX ROTATED FACTOR MATRIX FOR EIGHT SYLLABLE CHARACTERISTICS^a

	Factor											
	All three areas			Sapling			Pole			Sawtimber		
	I	II	III	I	II	III	I	II	III	I	II	III
Frequency range	0.96	-0.11	-0.01	0.08	0.94	0.22	0.90	-0.18	0.96	-0.08	0.17	
Frequency modulation	0.13	-0.84	0.01	-0.93	-0.07	0.12	0.18	-0.98	0.14	-0.82	0.18	
Freq. with most amplitude	0.53	0.21	0.11	0.02	0.19	0.55	0.77	0.01	0.54	0.45	-0.34	
Highest frequency	0.99	-0.01	0.02	0.10	0.92	0.38	0.95	-0.09	0.98	0.07	0.17	
Lowest frequency	0.24	0.43	0.14	0.28	0.01	0.59	0.16	0.44	0.43	0.52	0.02	
Syllable duration	0.29	0.70	0.47	0.78	-0.12	0.36	0.59	0.62	0.28	0.85	0.12	
Time between syllables	-0.04	0.75	-0.17	0.64	0.00	0.30	-0.13	0.59	-0.17	0.61	-0.48	
No. of elements	0.01	-0.01	0.63	0.15	-0.34	0.17	0.58	0.17	0.08	-0.02	0.59	
% variance explained	34.3	27.6	14.2	35.1	25.8	14.1	41.7	28.2	39.1	29.7	13.7	
Cumulative %	34.3	61.9	76.1	35.1	60.9	75.0	41.7	69.9	39.1	68.7	82.4	

^a Factor loadings given for each variable analyzed according to area.

frequent interactions (learning) between neighboring territorial males. Payne (1982) suggested that song matching is a form of deceptive mimicry where young males may copy the songs of previous or established males to enhance their own likelihood of success when setting up a territory. McGregor and Krebs (1984), however, suggested that the use of known songs to exchange information on distances between male birds is perhaps a more advantageous reason for song matching.

While studying various song dialects among Darwin's finches, Bowman (1979) found a strong correlation between song bandwidth and the acoustical conditions in the environment of each species. In our study, Northern Cardinals in the sapling stand sang a wider range of frequencies than did those in the sawtimber stand. This supports what Morton (1975) had documented earlier: forest-inhabiting birds use narrower frequency ranges than do birds inhabiting more open areas.

For all three populations, the frequency with most amplitude was about 2100 Hz. Such frequencies are within the range of frequencies (2000–8000 Hz) that distort the least over long-distance transmission (Richards and Wiley 1980); however, extreme attenuation results whenever frequencies less than 2000 Hz are produced just above ground level (Marten et al. 1977). As Northern Cardinals typically sang from high perches, this particular acoustical problem may have been eliminated.

In tropical forest environments, bird sounds typically are pure and tonelike with very little frequency modulation (Morton 1975). Because older forests have closed tree canopies, signals with amplitude modulation and repetitive frequency modulation (trills) transmit poorly due to the echoes and reverberations generated by the forest canopy (Richards and Wiley 1980). This is especially true for long-range communication. It would be disadvantageous for cardinals in either the pole or sawtimber stands to use syllables with significant frequency modulation. In contrast, birds living in relatively open areas can enhance message encodement (using frequency and amplitude modulation) in songs transmitted over long-distance with less risk of distortion (Morton 1975, Richards and Wiley 1980).

The foliage density profiles constructed for each of the three study areas indicated a similarity in the physiognomy of the pole and sawtimber stands (Ehrhart 1981) (Fig. 1). Both had a complete canopy that would cause excessive reverberation in sounds with extensive frequency modulation. In contrast, the sapling stand had dense understory vegetation, no canopy, and several large open areas. Because cardinals in this area typically sang from perches 6–8 m high in the upper branches of the young pine trees, little foliage was present to distort the acoustic signals. In this environment, cardinals used syllables with frequency modulation more

than did cardinals in the pole and sawtimber stands, as predicted from Richards and Wiley (1980).

Nuechterlein (1981) found that auditory signals helped maintain the two color phases of the Western Grebe (*Aechmophorus occidentalis*) even in sympatric populations. He considered this to be a learned behavior operating singly on individuals. The selective advantage of this possible isolating mechanism in pair formation would be recognition of individuals similarly adapted to a particular habitat condition.

SUMMARY

Song repertoires of Northern Cardinal (*Cardinalis cardinalis*) populations in neighboring sapling, pole, and sawtimber stands in eastern Texas were tape recorded during the 1979 breeding season. Cardinals in each area used different syllable types and sang songs of varying duration and complexity. Cluster analysis and discriminant function analysis identified three distinct dialects, one for each of the three study areas. Cardinals in the sapling stand used a wider range of frequencies than did those in the sawtimber stand. Cardinals in the pole stand used a range of frequencies intermediate in size to that of either the sapling or sawtimber stands. For all three populations, the frequency with greatest amplitude was about 2100 Hz, a low frequency that carries better than high frequencies over long distances. In the stand that lacked a closed canopy, cardinals typically used syllables with considerable frequency modulation; however, in the two older stands cardinals seldom used extensive frequency modulation in their songs. Differential singing behavior of this nature probably enhances long-distance communication by minimizing excessive reverberation from canopy foliage. We suggest that some of the differences in syllable structure noted between the three cardinal dialects may be the result of selective pressures exerted by the acoustics of the environment.

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DEPT. BIOLOGY, STEPHEN F. AUSTIN STATE UNIV., NACOGDOCHES, TEXAS 75962 AND WILDLIFE HABITAT AND SILVICULTURE LAB (MAINTAINED IN COOPERATION WITH THE SCHOOL OF FORESTRY, SFASU), SOUTHERN FOREST EXPERIMENT STATION, USDA FOREST SERVICE, NACOGDOCHES, TEXAS 75962. (PRESENT ADDRESS MEA: MATH/SCIENCE DIVISION, BEE COUNTY COLLEGE, BEEVILLE, TEXAS 78102.) ACCEPTED 24 JUNE 1985.