THE VOCAL BEHAVIOR OF CARDINALS AND PYRRHULOXIAS IN TEXAS

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The song of the Cardinal (*Richmondena cardinalis*) includes several distinctive types per bird, each normally sung in long series or bouts (Lemon 1965). Certain song types are shared by neighboring birds but may differ from those of birds in other localities (Lemon 1966). Other richmondenine finches in North America sing in patterns quite different from the Cardinal, but undocumented reports have suggested similarities between the Cardinal and the Pyrrhuloxia (*Pyrrhuloxia sinuata*), not only in organization of the song components but also in the actual sounds themselves (Gould 1961; Robbins et al. 1966). The latter reference also suggested that the calls of these two species were similar. Gould reported no major competition between the two species where they occur sympatrically in southern Arizona, and since the territories of the two species overlapped, there seemed little need for common patterns. In fact, it seemed more probable that selection would favor differences of song, as has been shown in various other closely related species (see, for example, Dilger 1956; Stein 1963).

The present paper describes in detail the songs and certain calls of the two species from localities in Texas. It considers also experimental evidence on the possible exchange of song between the two species, and other aspects of vocal and other behaviors. Such comparisons should lead ultimately to considerably more understanding of the great variation exhibited in the vocal repertoires of song birds.

MATERIALS AND METHODS

When recording the singing of Cardinals, attempts were made to obtain all the song types within a bird's repertoire; hence, the birds were often stimulated by play-back or by a captive decoy placed within the bird's territory. Recording was done with two Uher 4000 tape recorders, supplemented by a Philips 100 tape recorder. A Kay Electric Sonagraph, model 6061a, analyzed the recordings.

The plots of land were laid out in measurements to the nearest chain (66 feet), facilitating conversion to acres. No elaborate means of sighting was employed.

In censusing the plots, those at the Welder Refuge received at least six visits which lasted at least two hours apiece. The plots at Falcon Park were visited only three times each, the visits lasting from one-half to two hours. The positions of the birds, especially the singing posts, were plotted on a grid and their territories were outlined accordingly. Although the territories are shown in the figures to have abrupt boundaries, these are abstractions that only approximate the real situation.

In both species, the males sing far more than the females, and all references here are to the songs of males.

AREAS OF STUDY

The studies reported herein were made at two localities in Texas, one in the refuge of the Welder Wildlife Foundation seven miles north of Sinton, the other in Falcon State Park adjacent to the Falcon Reservoir dam on the Rio Grande River, approximately 150 miles south of the Welder Refuge. Studies at the first location were conducted between 9 and 31 May 1967, and were concentrated in three areas, A, B and C, the first two being laid out as formal plots (fig. 1). The descriptions of the vegetation in these plots are based on the study of Box and Chamrad (1966).

Plot A, an area of approximately 40 acres (16 hectares), was located in open or semi-open brush land. The area was transected by a road and clearing along a power line, so the actual areas covered by useable vegetation was closer to 35 acres (14 ha). Towards the south the main vegetation was a mesquite-buffalo grass community, but this merged in the north with a chaparral-bristelgrass community. In addition to Cardinals and Pyrrhuloxias, plot A had the following species represented in varying numbers: Bobwhite (*Colinus virginianus*), Roadrunner (*Geococcyx californianus*), Scissor-tailed Flycatcher (*Muscivora forficata*), Mockingbird (*Mimus polyglottos*), White-eyed Vireo (*Vireo griseus*), Painted Bunting (*Passerina cyanea*), Lark Sparrow (*Chondestes grammacus*) and Black-throated Sparrow (*Amphispiza bilineata*).

Plot B was slightly tapered and consisted of about 15 acres (6 ha) lying along the Aransas River. This area, known locally as Hackberry Motte, had a considerable growth

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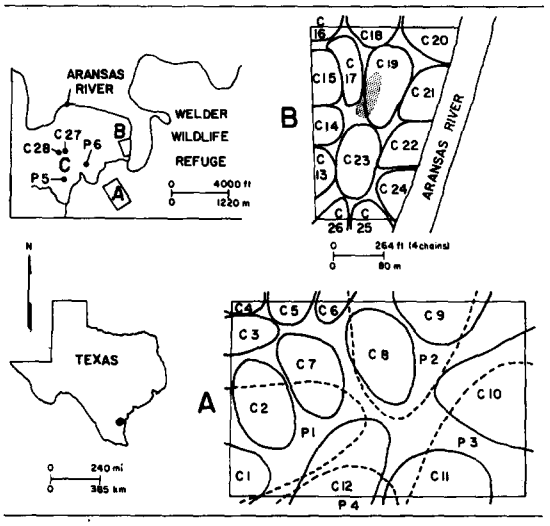

FIGURE 1. The dispositions of territories of Cardinals (C17, solid lines) and Pyrrhuloxias (Pl, dotted lines) in plots A and B at the Welder Refuge, Sinton, Texas, May 1967.

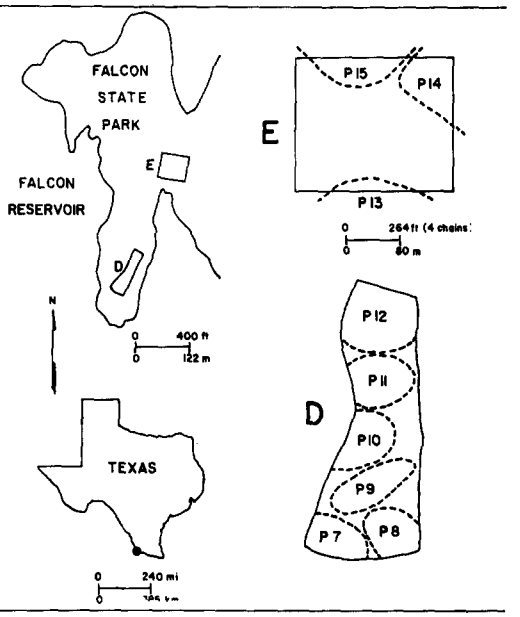

FIGURE 2. The dispositions of territories of Pyrrhuloxias in plots D and E at Falcon State Park, Texas, June 1967.

of hackberry (*Celtis laevigata*) along the ridges running the length of the plot. Thus, the center of the plot with its large trees had an open understory. A small pond (shown as stippling in the figure) was present. Along the river the vegetation was dense, with shrubs and vines interwining with the mature trees. Along the western edge there was a strip of dense chaparral, tapering in width from one-half chain in the south to four chains or more in the north. This vegetation was so dense that it was impossible to penetrate in many places by normal means, and, as a result, visual observation there was especially difficult. In addition to Cardinals, plot B had a pair of Red-shouldered Hawks (*Buteo lineatus*), various species of flycatchers (Trannidae), Carolina Chickadees (*Parus carolinensis*), Carolina Wrens (*Thryothorus ludovicianus*), vireos (*Vireo sp.*), and undoubtedly others.

Area C was adjacent to the refuge headquarters and dormitory. This area was vegetated by a live oak (*Quercus virginiana*)—chaparral community. Therefore, area C had large trees, but the vegetation was much more open than plot B. Most of the avian species from plot A were represented in area C also, with the possible exception of the Roadrunner and the Black-throated Sparrow. Other species also occurring in area C were the Ground Dove (*Columbigallina passerina*), various flycatchers, Black-crested Titmice (*Parus atricristatus*), Bewick's Wren (*Thryomanes bewickii*) and the Brown-headed Cowbird (*Molothrus ater*).

The studies at Falcon State Park were conducted from 3 to 5 June 1967. The whole area was essentially open brush country. Plot D was elongate (fig. 2), consisting of 12 acres (4.8 ha) and was in an area where the chaparral ranged from 6 to 15 feet, with frequent gaps between shrubs. In or near the plot were Bobwhite, Scaled Quail (*Callipepla squamata*), Roadrunners, Mockingbirds, Curve-billed Thrashers (*Toxostoma curvirostre*), Cactus Wrens (*Campylorhynchus brunneicapillus*), Boat-tailed Grackles (*Cassidix mexicanus*), Blue Grosbeak (*Guiraca caerulea*), and the Black-throated Sparrow.

Plot E, of 12 acres (4.8 ha), was much more open than plot D, having chaparral which usually did not exceed five or six feet in height; also, *Opuntia* and various forms of cactus were more common. This area had fewer birds than did plot D. Ground doves nested there, and Curve-billed Thrashers, Black-throated Sparrows and an unidentified flycatcher occurred also. A Harris's Hawk (*Parabuteo unicinctus*) was seen there twice.

RESULTS

RELATIVE ABUNDANCE OF CARDINALS AND PYRRHULOXIAS

One purpose of the plots was to make possible the determination of the relative abundance of the two species. In plot A, the ratio of Cardinals to Pyrrhuloxias was 12/4 =3/1. The

actual sizes of the territories were difficult to assess since there was usually no clear evidence of sharp boundaries in most areas of the plot. For the Cardinal, though, the smallest territories within plot A were C2 and C7 which had areas of no less than 3 acres (1.2 ha; fig. 1). Territories C3, C4 and C5 may have been smaller since they were located where the vegetation was most dense, but they extended outside the plot and were not measured. The largest Cardinal territories, in the more open areas, were at least 8 to 10 acres (3.2 to 4 ha) in size.

Pyrrhuloxias were probably as common in plot A as anywhere on the Welder Refuge. Four pairs used the plot and others occurred immediately to the north and southeast. None of the pairs was confined to plot A, so the territories were large, most pairs using, apparently for their exclusive purposes, areas in excess of 20 acres (8 ha) and possibly even twice that amount or more. The smallest area used by a pair of Pyrrhuloxias, P1, was an area of at least 8 acres (3.2 ha). This pair confined its activities here because of a nest, and later a fledgling from the nest. Incidentally, there was some confusion associated with this pair. A male Pyrrhuloxia was captured by means of a mist net placed near the nest, and was held for several days. Four days after capture, at the time of the next observation period in this area, another male was seen with the female and fledgling; he was seen also on subsequent occasions. Whether the captured male was the original owner of territory P1, or just a visiting neighbor or unmated male was not determined. The free male showed no reluctance to defend the area against the captured male when the latter was presented in a cage.

Whereas Pyrrhuloxias were absent from the densely vegetated plot B, Cardinals were especially numerous, with at least 13 pairs using the plot, and possibly as many as 15 pairs. Of these, nine were confined to the area while the remainder used additional areas outside the plot. Territories C18 and C26 were somewhat hypothetical, being based on single observations of birds whose identity was in doubt. Another pair to the southwest of plot B may also have used it. The territories along the Aransas River could have extended across it, for the distance was not great; other Cardinals were seen on the far side of the river, however, while those on the near side were in view. So the territories on the near side were likely confined to it. On the opposite side of the plot, a large open field precluded any extension of the territories in that direction. The sizes of the territories were much smaller than those in plot A, and six of the nine confined to the plot were approximately 1 acre (.4 ha; fig. 1). Apparently as a result of this density, trespassing occurred frequently, adding to the difficulty of identification. Females seemed to trespass more freely than did males.

In area C, where the vegetation was more open, Pyrrhuloxias occurred, but less frequently than in plot A. Cardinals were very common, although perhaps somewhat less so than in plot B. Play-back experiments were performed in this area and at least 20 to 30 pairs of Cardinals occurred to two pairs of Pyrrhuloxias, a ratio of at least 10/1. No plot was surveyed in this area, so territories were not accurately measured; however, birds near the dormitory which were seen daily confined their activities to areas estimated to be about 1 acre (0.4 ha).

At Falcon Park, Cardinals were absent, at least within the boundaries of the park, in spite of a claim to the contrary (Texas Parks and Wildlife Department 1967). It is likely that Cardinals occurred along the river below the dam where vegetation was more suitable. The territories of Pyrrhuloxias in plot D were arranged in a roughly linear fashion as a result of the topography of the area, and ranged in size from 1.5 to 2.5 acres (0.6 to 1.0 ha; fig. 2). Three pairs of Pyrrhuloxias used plot E, but they were not confined to it. Their territories probably exceeded the area of the plot, 12 acres (4.8 ha).

THE COMPOSITION OF SONGS

The songs of Cardinals and Pyrrhuloxias were found to be organized in essentially the same manner. The songs consisted of repetitions of sounds or syllables of which each species had several types; each type occurred alone or with another in each utterance of song, the different permutations of syllables being called song types. The syllables, and hence the song types, were numbered without regard to similarity of structure (figs. 3, 4, 5). The time intervals between successive syllables within an utterance were usually less than 0.5 sec, while the intervals between successive utterances were 1 sec or more. Some syllables, especially those of Cardinals, were composed of discrete units or subsyllables, and the intervals between those subsyllables within a syllable were less than, or occasionally equal to, the intervals between successive syllables. A singer gave a series or bout of one song type before changing to another song type.

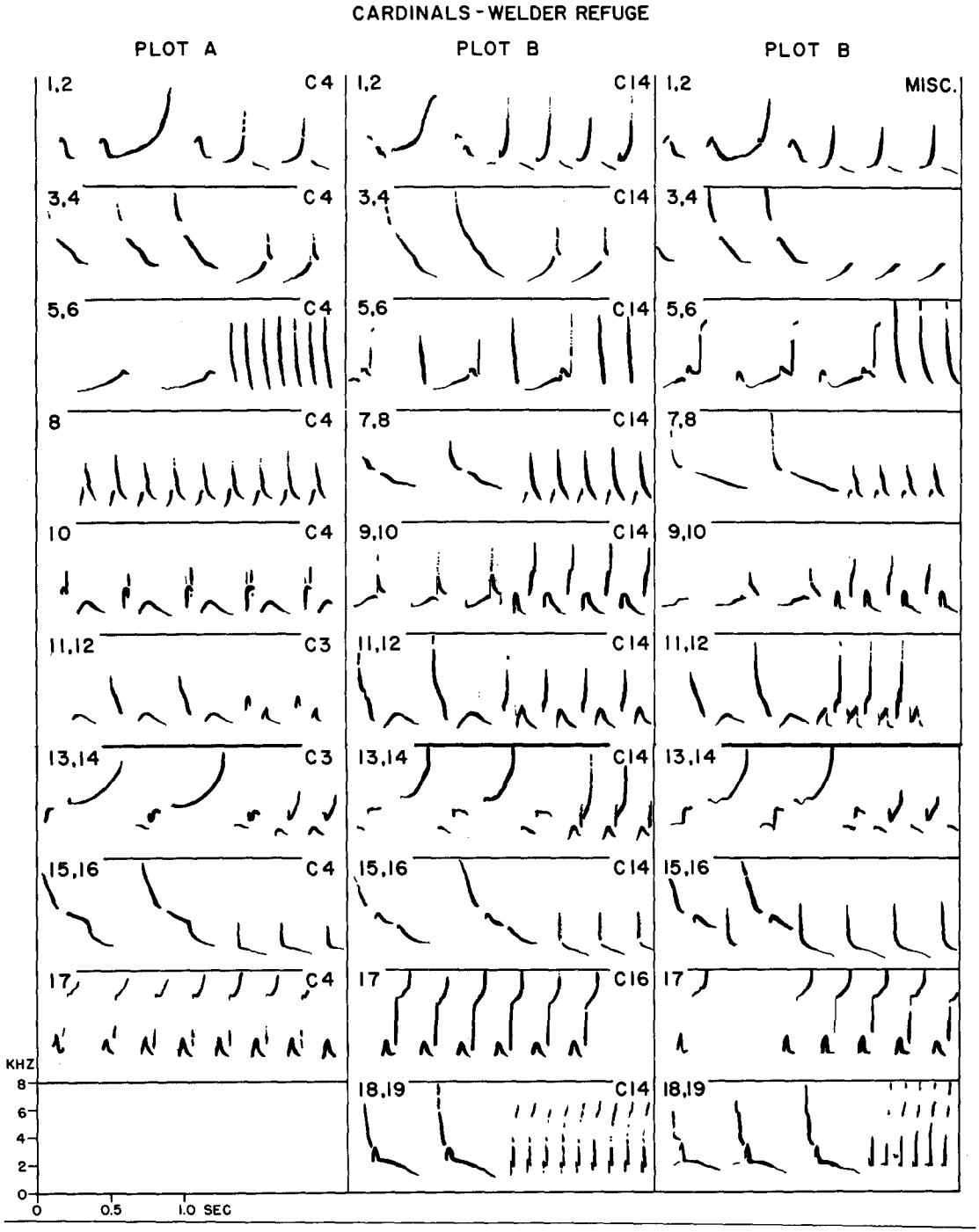

FIGURE 3. Sonagrams of songs of Cardinals from Plots A and B at the Welder Refuge. Note the several patterns per bird and the common patterns between birds. Cardinals are numbered by territory (see fig. 1); syllable types are numbered consecutively (e.g. 15, 16).

The songs of the Cardinals at Sinton were essentially the same in all areas of study, but examples are shown only from plots A and B (fig. 3). The major differences of syllables between plots were peculiar pronunications of syllable 5 in plot B, syllable 10 in all plots, and syllable 15 in plot A. Differences of syllables within a plot, however, were often as great: syllables 4 and 15 of two different unidentified males in plot B (shown under "misc." in fig. 3) were both unusual since they lacked the last portion of each of the syllables.

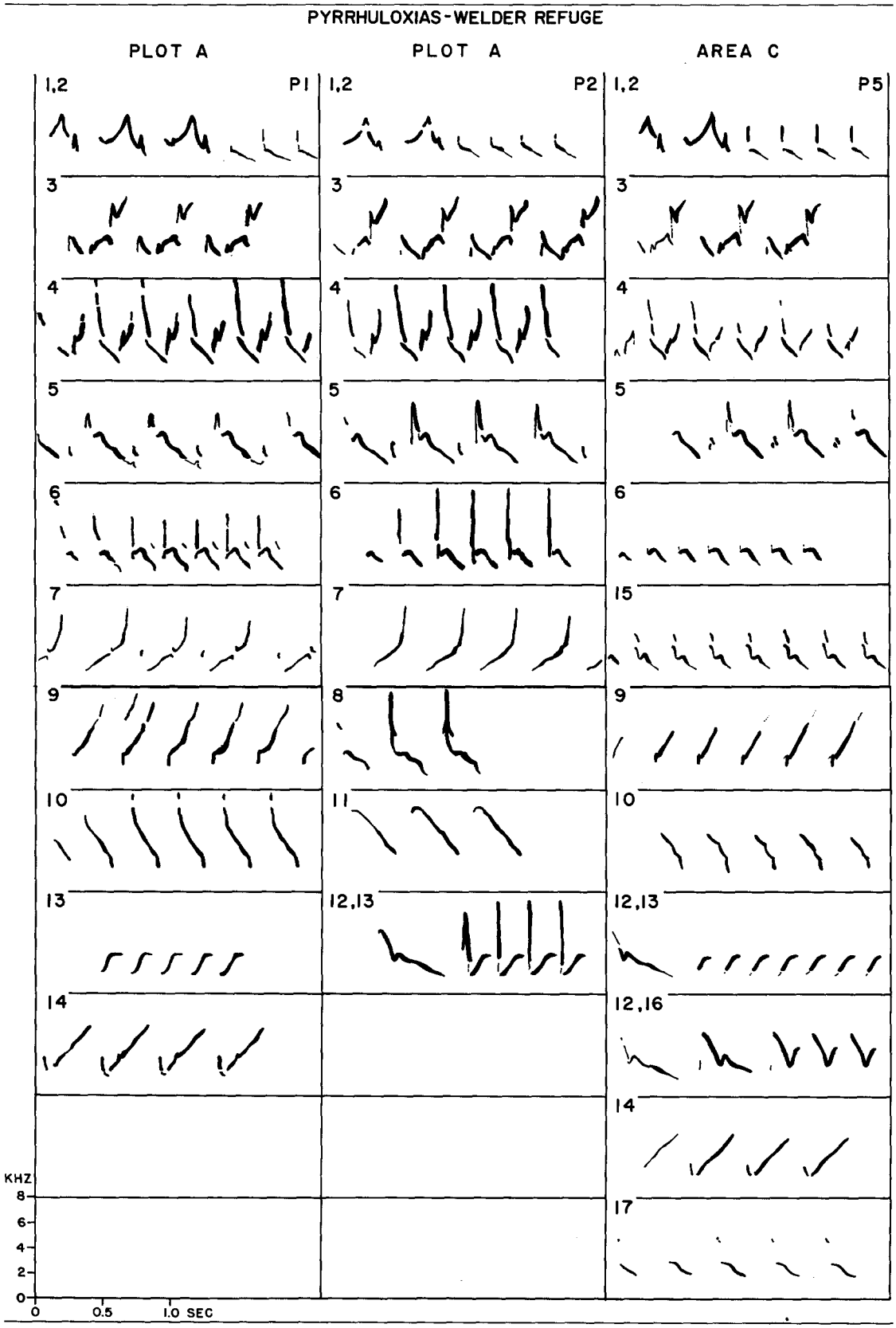

FIGURE 4. Sonagrams of songs of three Pyrrhuloxias in plot A and area C at the Welder Refuge (see fig. 1). Symbols as in fig. 3.

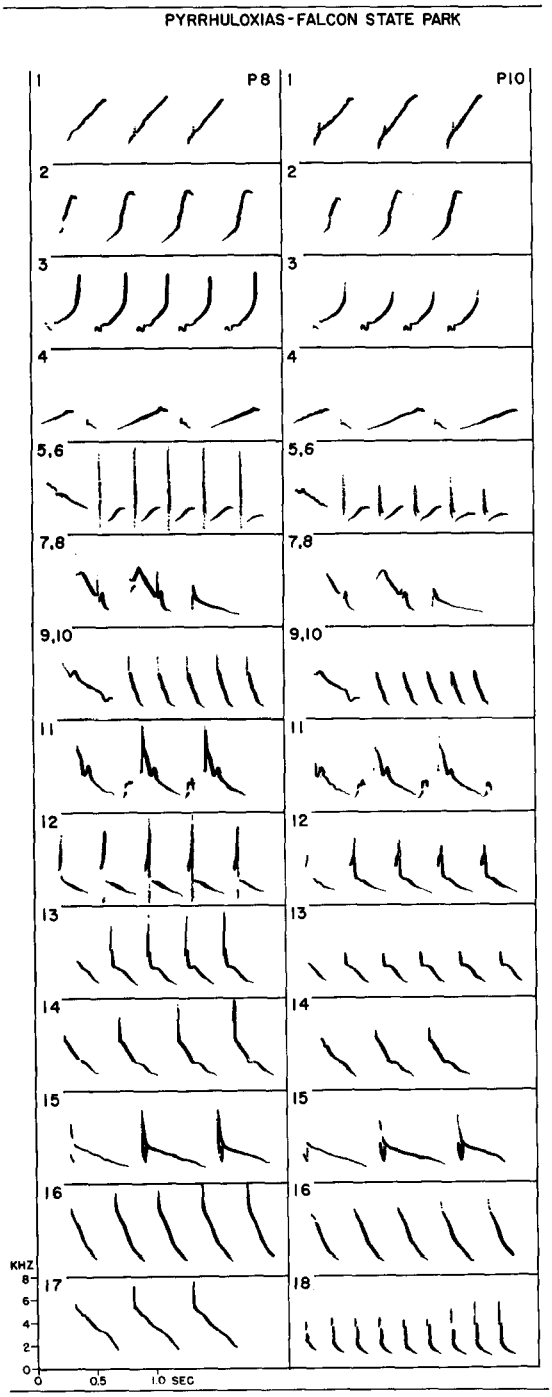

FIGURE 5. Sonagrams of songs of two Pyrrhuloxias in plot D at Falcon State Park (see fig. 2).

The chief differences in the overall repertoires of the birds from the three plots were the apparent absence of syllables 18 and 19 from plot A. Syllable 7, although not shown in figure 3, was present in plot A. The only syllable unique to a plot was 9 in plot B. The permutations of the syllables or the song types, were essentially the same, except where syllables were absent. Song type 8 occurred in plot A, as did the more widespread 7, 8. In plot B, birds alternated syllables 5 and 6 before the final series of syllable 6.

Before considering the songs of Pyrrhuloxias, let us consider some of the difficulties of defining the syllables, using the examples just given. Often there were variations of syllables between birds which were as great as those between recognized syllable types, and were it not for the occurrence of these variants with other particular syllables in the song types, it would have been necessary to class them as different types. For example, recall syllables 4 and 11 in plot B. Also, there were striking similarities of certain syllables within the repertoires of a single bird, such as syllables 10, 12 and 14 (fig. 3). Had these minor variations not occurred separately nor combined with other distinctive syllables, they would have been classed as the same syllable. Syllable 1 presented still another problem, although not a common one, in which only one syllable was complete in each bird, the others lacking the long upward tail or whistle. One might have considered the complete and incomplete parts as distinct syllables, but they do share the same downward slurred part.

The syllables in the songs of the Pyrrhuloxias at the Welder Refuge were different from those of the Cardinals, except one, syllable 2 (fig. 4), which was almost identical with Cardinal syllable 16 (fig. 3), although the latter was longer. As with Cardinals, the syllables and song types were very similar between neighbors within plots, and between plots. The only major difference in pronunciations of syllables within a plot was syllable 7 in plot A. The chief differences between plots were the absences of several syllables, a few of which may have resulted from incomplete sampling, but most of which seem to be valid since the birds within a plot show fewer absences than birds between plots. As with Cardinals, certain syllables were strikingly similar, making classification difficult: note 5, 6, and 8. (The original sonagrams show the similarities better than do the figures.)

At Falcon Park, the syllables used by Pyrrhuloxias were often quite different from those at the Welder Refuge (fig. 5). Some were quite similar, however, such as syllables 6 and 12 (or 13) at Falcon Park and, respectively, 13 and 6 at the Welder Refuge. Note also that the first two listed for each place were associated with somewhat similar syllables in their song types. The samples at Falcon Park

TABLE 1. A summary of the number of syllables and song types of Cardinals and Pyrrhuloxias at Welder Refuge and Falcon Park, Texas.

	Cardinals			Pyrrhuloxias		
	Welder Refuge Plots[a]			Welder Refuge Plots		Falcon Park Plot
	A	B	C	A	C	D
Number of birds sampled[b]	3	6	4	3	3	3
Number of syllables	16	19	18	14	15	18
Maximum number of syllables for one bird	16	18	17	11	14	17
Number of song types	10	11	10	13	13	15
Maximum number of song types for one bird	9	9	10	10	12	14
Totals by locality						
Syllables		19		17		18
Song types		13		16		15

[a] Locations of sample plots are shown in figures 1 and 2.
[b] Includes only those birds from which 5 or more song types were recorded.

were from neighboring birds, and in two sampled well, P8 and P10, the only differences were the presence of one unique syllable each, 17 and 18. Again, some of the syllables within a bird's repertoire showed remarkable similarity, especially 12 and 13, but the sonagrams show several downward slurred syllables which differ in detail only to a minor degree. One other thing to note was the tendency to alter successive syllables within the utterance, illustrated by syllable 6, where the last syllable shown dropped noticeably in frequency.

A feature common to the syllables of both species was the tendency to begin or end many syllables with a percussive sound of broad frequency. These elements are similar to portions of the contact calls which are similar in both species (fig. 7), and one might argue that their presence indicates that song has developed from the contact calls. This may be so, but song normally develops through a stage called subsong in which some of the elements are obviously call notes but many bear little resemblance to them (Lemon and Scott 1966).

Concerning the repertoires as a whole, there were difficulties with the totals of individuals since there was no practical way, aside from repeated recording, of knowing whether one had determined all of a bird's repertoire. The only solution was to record several individuals and to determine the degree of correspondence between the individuals and the group as a whole. It happened that in practice usually there was close agreement between the maximum number of syllables and song types from one bird and those for the group.

Table 1 shows that there were slight differences in totals for Cardinals among the three plots at the Welder Refuge, the actual differences already being noted. Pyrrhuloxias at Sinton had fewer syllables per bird than did either Cardinals there or Pyrrhuloxias at Falcon Park. There were more unique syllables per plot among the Pyrrholuxias at the Welder Refuge, suggesting more individual variation.

The situation with song types was somewhat different. Although the Pyrrhuloxias at Sinton had fewer than did those at Falcon Park, the Cardinals at Sinton had fewer still. This difference in totals from those of the syllables was a consequence of the common use by Cardinals of two kinds of syllables within a song type (in 9 of 10 song types) in contrast with Pyrrhuloxias, whose song types consisted more often of one type of syllable (at Sinton, only 4 of 16 song types had two kinds of syllables; at Falcon Park, only 3 of 15).

OTHER VARIABLES OF SONG

The number of syllables per utterance often varied considerably, even in repeated utterances of the same song type; in general, though, the shorter syllables were repeated more frequently (fig. 6). This conclusion was based on samples from tape recordings only; the durations of syllables were determined from a single sonagram, whereas the numbers of syllables were determined from the total utterances of the particular song types from the particular bird. There were no significant differences by t tests in the coefficients of the regressions of figure 6 when comparisons were made within each species; but there were significant differences when comparisons were made between species, the comparisons being: C14-P1 ($P < 0.01$), C14-P8 ($P < 0.01$), C28-P2 ($P < 0.025$), C28-P10 ($P < 0.005$). From the figure it is obvious that the main differences resulted from the use by Cardinals of very short syllables. In fact, if we ignore these short syllables and compare that portion of the regression of a Cardinal such as C14, which lies within the

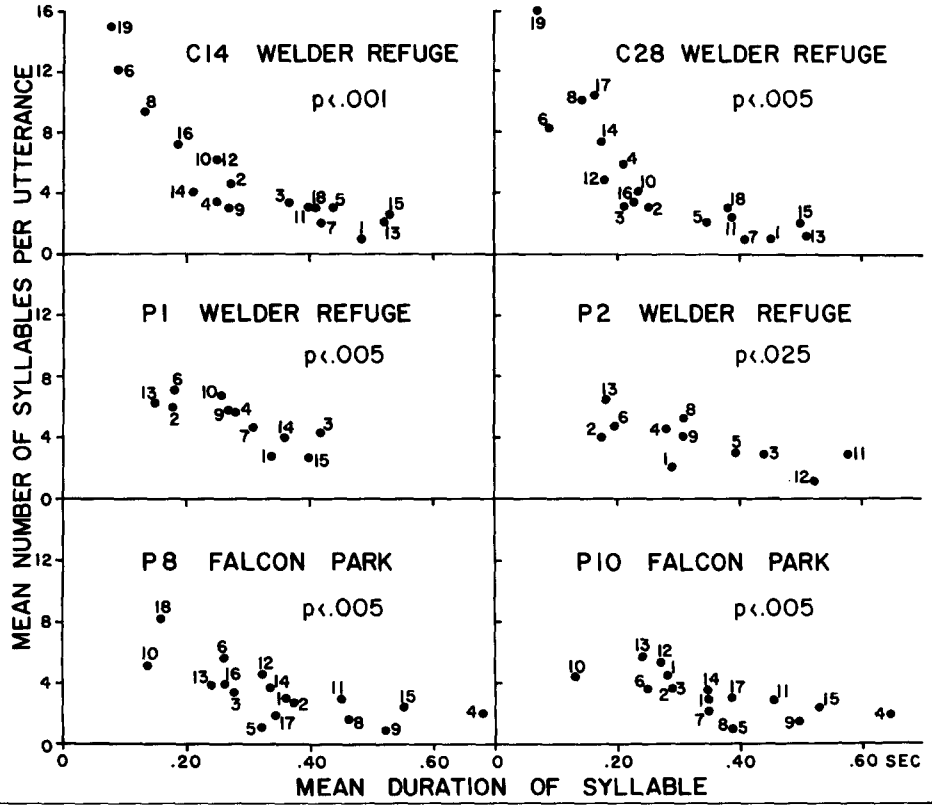

FIGURE 6. The relation between the duration of syllables and the mean number of repetitions of the syllables per utterance of song. The numbers on graph refer to the kinds of syllable; as such they are equivalent only between individuals of the same species in the same locality.

limits of the duration of the syllables of a Pyrrhuloxia, such as P1, there is no significant difference ($P > 0.40$). Also, an analysis of covariance of syllables of similar durations of C14, P1 and P8 shows no significant differences ($F = 0.124$, degrees of freedom 2 and 38; adjusted means: P1 = 0.3317, P8 = 0.3327, C14 = 0.3470). It appears, therefore, that if any Pyrrhuloxias were to sing short syllables, the regressions of the two species would be identical.

Wherever two kinds of syllable occurred together in the same utterance or song type, the first was almost always longer than the second. Hence, the second type of syllable was usually repeated more often than the first, the difference being most prominent where the two types differed considerably, such as in Cardinal songs 5, 6 and 18, 19. The only exception was in song type 7, 8 of the Pyrrhuloxias at Falcon Park, where the two syllables were equal in duration, or 7 was somewhat shorter. One might expect also that where two syllables occurred together the number of each might be less than had they occurred alone. This may be true to a certain extent, but it cannot be too important, otherwise the regression coefficients of the Pyrrhuloxias, which had more song types consisting of one type of syllable, would have been considerably higher than the Cardinals'.

When singing, individuals of both species repeated utterances of the same song type for a variable period of time. Gould (1961) suggested that these series, or bouts, differed in the two species, the Pyrrhuloxia tending to have shorter ones. Samples of the durations of bouts were obtained from three Cardinals at Sinton, and from two Pyrrhuloxias at each of the two localities. The bouts, measured to the nearest minute, were determined by the interval from the first utterance of a particular song type to the first utterance of the next song type. Only samples from birds which had sung continuously for some time, giving a minimum of eight bouts, were considered. The data (table 2) indicate that the durations of the bouts varied considerably, possibly from several influences. For example, the durations may have depended on the song types themselves, but since the samples were small, an analysis of this matter could not be made.

TABLE 2. The durations of bouts of song by individual male Cardinals (C) and Pyrrhuloxias (P) in Texas.

Bird	Locality	Durations of bouts in minutes (mean)
C4	Welder Refuge	1, 4, 5, 6, 10, 13, 15, 16 (8.8)
C14	Welder Refuge	6, 12, 13, 14, 15, 15, 17, 23 (14.4)
C28	Welder Refuge	2, 4, 4, 4, 8, 10, 13, 17, 18, 18, 28, 32, 40 (15.2)
P1	Welder Refuge	3, 3, 4, 4, 4, 9, 10, 12 (6.1)
P2	Welder Refuge	3, 3, 6, 7, 8, 9, 10, 11 (7.1)
P8	Falcon Park	1, 2, 2, 3, 3, 3, 5, 5, 5, 6, 6, 11 (4.3)
P10	Falcon Park	1, 1, 2, 2, 3, 3, 3, 4, 5, 5, 5, 7 (3.4)

Rank tests of significance (two-tailed)
Within groups: C4 × C14, C4 × C28, C14 × C28, P1 × P2, P8 × P10.
Between groups: C14 × P1**, C28 × P1, C14 × P10**, C28 × P10**, P1 × P10, P2 × P10*.
(*, $P < 0.05$; **, $P < 0.01$; others not significantly different).

Also, there were times when singing did not occur, so that some bouts included long periods of silence. There is evidence from Cardinals (Lemon, unpublished) that the durations of the bouts may vary relative to the intensity of the interactions between individuals. The Pyrrhuloxias at Sinton were recorded while under stimulation in the form of a caged decoy within the territory of P1 and tape recordings played in the territory of P2. Hence, these two birds may have had shorter bouts than those recorded under more natural circumstances. At Falcon Park, however, the bouts were shorter still and no artificial stimulation was used. Here the small territories and the smaller distances between the individuals may have resulted in more stimulated singing, and, therefore, the shorter bouts than at Sinton. Because of these possible variations, there is some doubt whether any statistical tests of significance should be made. However, nonparametric rank tests (Ferguson 1966) were performed. For convenience of testing, the birds were grouped by species and locality (table 2). In tests between groups, only certain comparisons were made. Of the two Cardinals tested, C14 and C28, only the first had significantly longer bouts than did P1; but both Cardinals had significantly longer bouts than P10 at Falcon Park. Similarly P2 had significantly longer bouts than P10. It appears, then, that the Pyrrhuloxias often do use shorter bouts than Cardinals, but not always. It is possible that the duration of bouts is inversely related to the size of the repertoire.

Yet another variable influencing the duration of bouts, although not mentioned above, was the tendency by certain birds to associate certain song types in short alternating bouts. Those so associated were song types 17 and 18, 19 in an unidentified Cardinal in plot B; song types 9 and 10 in P1 and song types 12, 13 and 12, 16 by P5 at Sinton; and 1 and 13 by P8 at Falcon Park. Since the associated song types were not independent, or at least were far less independent than others, they were considered as one in table 2. The results were not affected greatly since only P1 was involved, but had they been presented otherwise, P1 would have had a score closer to P8 and P10.

The rate of singing was variable, but reached maxima of 8 to 9 utterances per minute in both species.

Finally, attempts were made to determine whether Pyrrhuloxias often match their song types when singing together, as do Cardinals. The attempts to demonstrate this matching by having the Pyrrhuloxias sing in response to a series of tape recordings were not successful. With the first male, P5, the bouts of the tape recorder proved too short, some of them being only 30 seconds in duration, and the bird sang much longer bouts. In the second attempt, the bouts of the recorder were too long for the bird tested, P6, even though those of the tape recorder lasted only 90 sec. The differences between the two males were not explicable, but might have been related to the positions of playing within the territories.

During natural singing between males, Pyrrhuloxias at the Welder Refuge matched their patterns on 8 of 13 occasions (62%), whereas at Falcon Park the number of matchings, based on tape recordings, was 17/35 (49%). Oddly enough, the latter totals were recorded also for the Cardinals at the Welder Refuge. Determining the statistical significance of such figures is not feasible, but when one considers the number of patterns each bird possesses, then the chances of two adjacent birds selecting the same pattern at the same time must be considerably smaller than the amount observed. It is reasonable to conclude, then, that Pyrrhuloxias are similar to Cardinals in that they do often match their common patterns when singing together.

TABLE 3. The response of male Cardinal C27 at the Welder Refuge to tape recordings of Cardinal and Pyrrhuloxia songs.

Order of Presentation	Species of song played	No. of utterances of song
1	P	0
2	C	6
3	C	23
4	C	18
5	P	0
6	C	12
7	P	19
8	P	3
9	C	16
10	P	0
11	C	14
12	P	0

Mann-Whitney U-test (one-tailed): $U = 5$, $P < 0.021$.

TABLE 4. A summary of the number of utterances sung by 15 male Cardinals in Area C of the Welder Refuge in response to recordings of Cardinal and Pyrrhuloxia songs.

Bird	Species of first song played	Number of utterances in response to songs of:	
		Cardinal	Pyrrhuloxia
1	C	15	2
2	P	2	11
3	C	26	6
4	C	31	0
5	P	11	0
6	P	11	20
7	P	0	1
8	C	42	0
9	C	7	0
10	C	16	0
11	P	21	5
12	C	18	22
13	P	24	0

Wilcoxen matched-pairs signed-ranks test (one-tailed): Cardinal × Pyrrhuloxia, $T = 10.5$, $P < 0.01$. 1st play × 2nd play, $T = 35$, $P > 0.05$.

RESPONSES OF CARDINALS TO PLAYBACK OF RECORDED SONGS OF BOTH SPECIES

Although the component syllables of song in the two species were generally different, it remained to be confirmed that no communication by song normally occurs between the two, or, in more practical terms, that they normally respond far more to songs of their own species. Hence, some play-back of recorded songs was done at the Welder Refuge. Since Pyrrhuloxias were relatively uncommon there, only Cardinals were tested.

In experiments reported elsewhere (Lemon 1967), two indexes of response were used, including (1) the tendency to approach a loudspeaker playing recordings within a bird's territory, and (2) the number of songs uttered during the playing and immediately after. In some preliminary experiments in the vicinity of plot B, few Cardinals approached the speaker, and it was extremely difficult to see them owing to the density of the vegetation. Therefore it was decided to use only the number of utterances as the index of response.

Two experiments were performed, both in area C. In the first, one male, C27, was exposed to tape recordings from an adjacent territory. To minimize possible differences in response to the different song types, six song types of each species were used. Those of the Cardinal were 3, 4; 7, 8; 9, 10; 11, 12; 13, 14; 18, 19; those of the Pyrrhuloxia were 1, 2; 3; 6; 9; 10; 13. To minimize the influence of song from other birds, or from spontaneous song by C27 himself, no playing was done unless preceded by at least three minutes of silence. Similarly, to minimize any after effects from previous playings, at least 10 minutes had to elapse between playings. Each of the 12 song types was played for three minutes, and the score was obtained by counting the number of utterances during the three minutes of play and the three minutes after play. The order of playing was random. Playing was begun at 12:26 and ended at 16:14, CST. Playing in the afternoon may have seemed unusual but it did avoid much interference from singing males, and yet the response was considerable (table 3).

The differences in response were statistically significant and suggested that Cardinals normally reply far more to songs of their own species than to those of Pyrrhuloxias, if to the latter at all. Male C27 sang on all exposures to Cardinals recordings, but on only two of the six exposures to Pyrrhuloxia songs. One of these two responses to Pyrrhuloxia song was considerable and one might wonder if the song type played was that which shared the similar syllable. This was not so, for the song type in question was 9, whereas the song type with the similar syllable was 1, 2 and this was the eighth presentation.

In the other experiment, many males were used, but they were exposed only to single recordings of a song type of each species, this being done on two successive days at approximately the same time for each bird. The experiments ran from 07:00 to 11:30, CST. The recordings were the same as those used in the previous experiment. Again, to avoid interference from other birds a period of silence by the prospective male was required before playing, the interval in this instance being reduced to two minutes in order to avoid ex-

TABLE 5. Heights of singing perches of Cardinals and Pyrrhuloxias in open country near Plot A, Welder Refuge.

Cardinal		Pyrrhuloxia	
Height[a]	Prominence[b]	Height	Prominence
1	+	3	—
1	—	3	—
1	—	3	+
1	—	4	—
2	—	5	+
5	+	5	+
7	+	6	+
10	+	6	+
12	+	6	—
12	+	7	+
20	+	9	+
25	+	10	+
($\bar{x} = 8.1$)		12	+
		20	+
	8+	($\bar{x} = 7.1$)	10+
	4—		4—

(Rank test of heights, $P > 0.10$ [two-tailed]) (χ^2 test of prominences, $P > 0.05$).

[a] Heights measured to the nearest foot.

[b] Perch considered prominent if within ¼ of top of shrub or site.

tension of the play-back period. No record was kept of the identity of the individual song types because of problems with the recording devices. When the results are considered in matched pairs the differences in relative response were quite significant (table 4), with nine males replying with more song to Cardinal recordings and only four with more to Pyrrhuloxia recordings. The order of play showed no significant difference.

The results of the two experiments were not entirely unequivocal, a fact hardly surprising in view of the frequent interference from other singing birds. Yet they were consistent and did support the contention that Cardinals respond more to the songs of their own species. The fact that birds may sing when recordings of the other species are played does not of necessity mean that they are responding to the recording, for they may be singing spontaneously or may be responding to a near neighbor. Interference from neighbors might have been reduced had the experiments been conducted in plot A where the population was less dense.

OTHER POSSIBLE INTERACTIONS

Aside from song, there were other possible sources of behavioral interaction. As figure 1 indicates, the territories of the two species overlapped in various areas at the Welder Refuge. Observations made in these areas, although greatly limited, showed no agonistic interactions between the two species. On three occasions, members of both species were seen feeding together peacefully on or near the ground. On another occasion a male of either species sang from the same bush, separated from the other bird by only six feet or less; again no intolerance was noted. At yet another time, a male Cardinal gave a courtship display to a female Cardinal while both sat on a power line within five feet of a male Pyrrhuloxia. The latter flew off before the male Cardinal finished his display.

Both species used the same kind of sites for singing. In an area adjacent to plot A where both species occurred, observations were made of heights of singing and their relative prominence. A perch was considered prominent if the bird sang within one-quarter of the top of the object, usually a shrub. No significant differences of choice were noted in either of these two characteristics (table 5). In other areas, the birds sang from higher perches since these were available. Still there were no obvious differences.

The absence of any apparent intolerance between the two species indicates that the birds can distinguish without difficulty not only between the distinctive males but also between the quite similar females. Probably visual means are enough under most conditions, but there must be times when visual clues are of little value. At such times the call notes undoubtedly prove effective. Although the contact calls or *chips* were structurally similar, that of the Pyrrhuloxia was of lower pitch to the human ear, and sonagrams support this contention (fig. 7). The figure illustrates recordings made from two birds held in captivity and it so happens that the recordings were accompanied by much noise resulting from the movement of the birds. As a result, more accurate spectrographic analysis was not possible. The Pyrrhuloxias also used prominently a call which appeared to be modified chips given in long series (fig. 7). The effect was a loud *rattle*, similar in sound to certain calls of other open country birds such as the cowbird and meadowlarks (*Sturnella*). These rattles were heard in what appeared to be normal contact situations, and also in situations of some excitement as when a person was near a nest. The Cardinal has a *chitter* call which is given in situations of high intensity, such as in territorial conflict or when an aerial predator flies over (referred to as a rattle in Lemon and Scott 1966). A similar call sounding like a rattle given at higher pitch and faster rate of emission was heard from a Pyrrhuloxia when a vulture

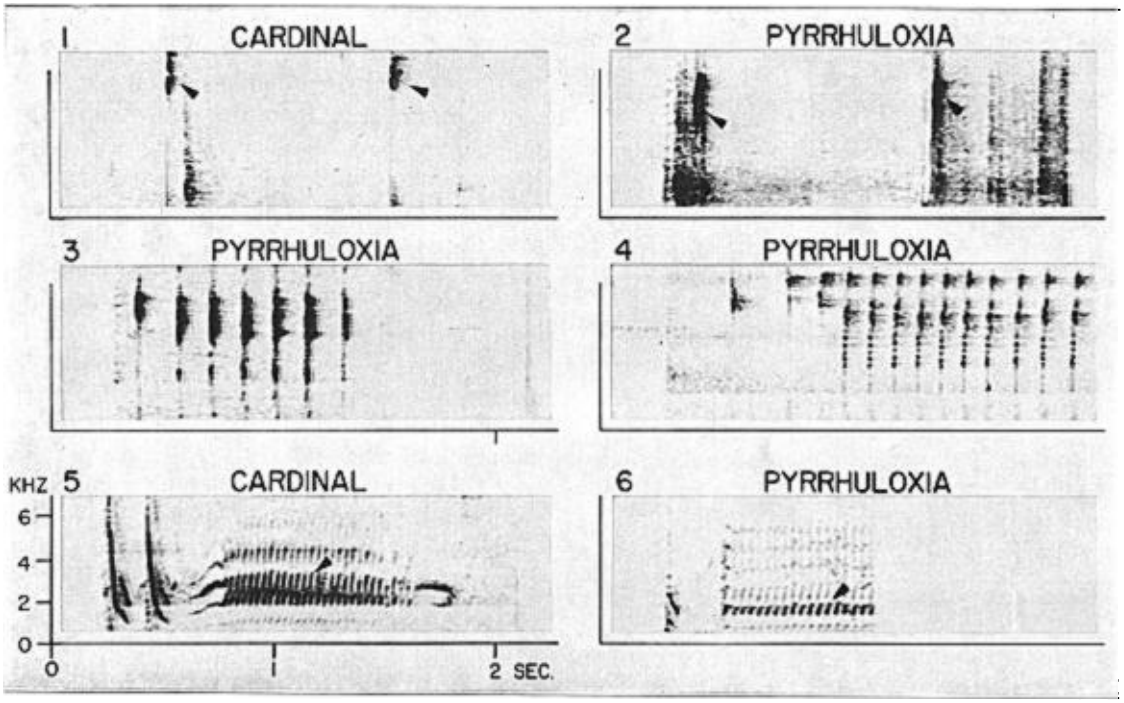

FIGURE 7. Sonagrams of certain calls of Cardinals and Pyrrhuloxias. 1 and 2. Contact *chips* showing the somewhat higher frequency of the Cardinal's. 3 and 4. *Rattles* recorded from two Pyrrhuloxias. 5 and 6. The terminal buzz noted at the ends of some utterances of song.

passed over at high altitude; however, the call was not recorded on tape. It is probable that the chip and chitter are of value in interspecific communications when the two species flock, often together, in winter.

Both species also had an unusual buzzing or whirring sound uttered exclusively at the ends of songs (fig. 7), also described previously from the Cardinal (Lemon and Scott 1966). The sound is not loud, and it may therefore be questioned whether it has any communicative value, either within or between species. It does occur early in the subsong of young Cardinals.

DISCUSSION

The Cardinal and the Pyrrhuloxia are presently placed in separate genera, although some ornithologists consider them congeneric (Mayr and Amadon 1951; Bock 1964). The evidence presented here tends to confirm the proximity of the relationship for there is similarity in the organization of the songs and in the tonal quality and simple structure of the component syllables, in one instance the syllables being nearly identical in form. Also, both species share the odd buzz at the ends of songs and have structurally similar calls.

Of the two species, the Cardinal is much more widely distributed, occurring from southern Canada in eastern North America to southern México, whereas the Pyrrhuloxia is confined to México and adjacent areas of the United States. Although their ranges overlap, there are differences in habitat preference which are probably most prominent where their numbers are least. Hence, the Pyrrhuloxia preferred the more open areas of scrub near the northern edge of its range at the Welder Refuge and did not occur at all in areas of dense vegetation where the Cardinal was numerous. Conversely, the Cardinals avoided completely the scrub areas at Falcon Park, although they did occur in some numbers in open areas at Sinton where they were common. Where the two species were sympatric their territories overlapped and there was no evidence of mutual aggression, a situation similar to that reported from southern Arizona (Gould 1961). No doubt they do share certain features of the environment, such as singing perches and nesting sites, and perhaps some food, although differences in beaks indicate considerable divergence (Bock 1964). However, these items are probably not in short supply and at the Welder Refuge the numbers of the Pyrrhuloxias are so small that interactions are not apt to be frequent.

In the light of their non-exclusive territorial habits, it is not surprising that the songs of the

two species usually differ in detail and that the birds usually respond more to songs of their own species. In contrast, wrens of the genus *Thryothorus* which sometimes have mutually exclusive territories share some elements of song (Grant 1966). One might argue that differences of song between Cardinals and Pyrrhuloxias have developed primarily as isolating mechanisms, that is, as means of preventing crossbreeding. Indeed, such is probably the case since song is included in the courtship displays, at least in those of the Cardinal (Lemon 1968), and normal territorial singing undoubtedly attracts unmated females. In making this argument we are assuming that crossbreeding could occur through the failure of identifying clues other than song; whether this frequently occurs is not known, but recall the similar appearance of the females and similar calls. Yet, the needs for efficient intraspecific communication in the maintenance of territorial integrity are probably sufficient in themselves to select distinctive song patterns, so that the ultimate repertoire may result from selection from several directions.

The Pyrrhuloxia, like the Cardinal (Lemon 1966), exhibits differences of song patterns in widely separated localities, although, also like the Cardinal, some of its patterns occur widely as shown by the similar patterns at the Welder Refuge and Falcon Park. Birds of both species living on the three plots at the Welder Refuge were obviously too close for much differentiation of song, being no more than one mile apart, and any differences between the plots were really of the same order of magnitude as those between individuals.

Why do both species need several distinctive song types which are common to neighbors? The answer apparently lies in the practice of coordinating the singing of two or more birds such that the patterns sung at the same time match. There is evidence from Cardinals (Lemon, in press) that the amount of matching and changing of patterns increases when individuals are more highly stimulated such as when defending their territories against intruders. We find also that Cardinals respond more to recorded songs of their own dialect than to noticeably different patterns from different dialects (Lemon 1967).

Not at all clear is the significance of the number of song types in the two species and why these should differ. In other words it is not clear why there is so much uncertainty or information in the repertoires of each species and why Pyrrhuloxias should require more uncertainty than Cardinals. Uncertainty as to which song pattern will be next in a sequence should be of value in coordinating the singing of two birds. If so there might be more need for greater uncertainty at higher densities of population where there are more communicants than at lower populations. The densities of Cardinals in Ontario are considerably less than those on the Welder Refuge, for their territories range in size from 3 to 10 acres or larger (Lemon 1965, 1967). The repertoires in Texas, however, are only slightly larger, if at all, for most Cardinals in Ontario have repertoires ranging in size from 8 to 10 commonly used song types, or occasionally more. A slight difference also occurred in the repertoires of Falcon Park and the Welder Refuge, again in favor of the locality of higher density, Falcon Park. More samples must be taken before any conclusion is reached concerning such comparisons.

Another matter concerns the different amounts of redundancy in the songs of the two species; that is, why do Cardinals' song types usually consist of two kinds of syllable while those of Pyrrhuloxias' usually consist of one? One might expect more redundancy where the sound environment is of such a complexity as to interfere with the positive identification of simple patterns. Yet one wonders why the two species in the same area are not more similar in this respect. The answer may be that the Pyrrhuloxias perference for more open land normally keeps it in a simpler sound environment. Also, it is possible that the larger repertoire of songs of the Pyrrhuloxia in some way compensates for their apparent simplicity.

The remarkable similarities of song among the individuals of one locality, and yet the differences between localities are primarily the result of learning, at least in Cardinals (Lemon and Scott 1966; Dittus and Lemon, unpublished). Thus these species are like others which show dialects, such as the Chaffinch (Thorpe 1958) and the White-crowned Sparrow (Marler and Tamura 1962, 1964).

A probable advantage in determining the ultimate repertoire of song by learning rather than by inheritance is that learning permits the immediate satisfaction of communicative needs without recourse to tedious selection through several generations. Therefore, a bird could achieve a vocal niche relatively quickly in a complex environment of sound, a problem of special concern where closely related species may occur sympatrically. This implies

that learning normally occurs during the association of the young with their parents, although in captivity Cardinals can be taught to learn from tape recordings unassociated with the sight of a parent or foster parent (Dittus and Lemon, unpublished). In other words, it seems probable that Cardinals and Pyrrhuloxias do not normally learn each others' patterns because they earlier associate certain sounds with their parents.

Learning in many species is confined to the early months of life. In Cardinals learning may continue until the yearling male acquires a territory 8 to 10 months after leaving the nest. This extended period permits young to disperse from one dialect area to another and yet to learn many of the idiosyncracies of the second area. Also, the young will carry into new areas influences from earlier experiences which will lead both to similarities and differences between localities. The Chaffinch is similar to the Cardinal in that it continues to learn throughout much of its first year. The White-crowned Sparrow, however, ceases to learn after three months of age, suggesting that the young normally return to their natal areas to use their songs in proper context.

It is important to remember, though, that the situation in Cardinals and Pyrrhuloxias and other such species with dialects is by no means the rule, for relatively few species exhibit local dialects. The complexity of the relationship between organization of song and its ontogeny may best be appreciated from the studies of Marler (1967) and his students. In three emberizine species there appears a complete range from common patterns to individual patterns, from learning to inheritance. So far, attempts to relate these differences to ecological variables have been unsuccessful. These remarkable differences among close relatives do permit, however, two conclusions. First, the distinction between learning and inheritance in these species must be the result of minor differences in the central nervous system and associated sense organs; and secondly, different species may employ their communicative powers in rather different ways. Our appreciation of some of these ways is only just beginning.

SUMMARY

This paper reports on a comparative study of songs and certain calls of the Cardinal (*Richmondena cardinalis*) and Pyrrhuloxia (*Pyrrhuloxia sinuata*) in Texas. At the Welder Wildlife Refuge near Sinton, Cardinals far outnumbered Pyrrhuloxias. Territories of the former ranged in size from 1 to 10 acres, while those of the latter ranged from 8 to 20 acres or more. At Falcon Park by the Rio Grande River, Cardinals were absent but Pyrrhuloxias were common, having territories in one area equal to 1.5 to 2.5 acres.

The songs of both species were organized in essentially the same manner. Each possessed a series of sounds or syllables organized into definite permutations called song types. All but one of the syllables were different in the two species, the similar pair being somewhat different in duration. At the Welder Refuge, Cardinals usually had 9 to 10 song types per bird and Pyrrhuloxias had 10 to 12 song types. At Falcon Park, Pyrrhuloxias had up to 14 song types per bird. Most of the patterns of Pyrrhuloxia song were different in the two areas.

The number of syllables per utterance was inversely related to the duration of the syllables in both species. Cardinals often used shorter syllables than did Pyrrhuloxias. The bouts of song in both species were highly variable, but often those of the Pyrrhuloxia were significantly shorter than the Cardinal's. Both species often matched the song types of their conspecific fellows when singing together.

Experimental evidence indicates that Cardinals respond most to recordings of their own song types rather than to those of Pyrrhuloxias.

There are similarities in the contact calls of both species, although the Cardinal's is given at a higher pitch. The Pyrrhuloxia also uses a highly distinctive rattle which is a modified contact call. Both species have a peculiar buzz at the ends of some utterances of song.

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