

THE SONG OF THE CHINGOLO, *ZONOTRICHIA CAPENSIS*, IN ARGENTINA: DESCRIPTION AND EVALUATION OF A SYSTEM OF DIALECTS

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Any intelligent statement about the role of dialects in bird song presupposes a knowledge of the functions of song. It has been suggested that song may subserve territorial advertisement, attracting unmated females and repelling other males. Less speculation has attended the possibility that song may stimulate the female to undergo hormonal changes leading towards ovulation or that it may affect other aspects of the integration of breeding behavior.

Using the Chaffinch, *Fringilla coelebs*, as an example, Marler (1956) has indicated that song may convey the following information about the singer: its species, sex, location, individual identity, motivation, and marital status. Attempts at optimally meeting all these communicatory demands may result in some conflict. For example, while species recognition might be served by extremes of stereotypy, individual recognition will be possible only if this species stereotypy breaks down, at least to some extent. In those cases where local song dialects occur, song will carry information about species identity as well as about the identity of a particular population.

Marler (1959, 1960) has emphasized the convenience of looking at song as a communicative channel within a very noisy auditory environment. The number of species sharing a locality will determine the "band width" a channel must have to minimize interspecific confusion. The variation of environmental pressures on the song of a species could favor the adoption of different song types in different localities, in each case maximizing the privacy of the channel.

The existence of song differences between populations of birds of the same species has been known for a long time (Promptoff 1930; Blanchard 1941; Marler 1952; Marler and Tamura 1962; Thielcke 1963; Borror and Gunn 1965; Lemon 1966, 1967; reviews in Borror 1961; Thorpe 1961; Armstrong 1963; Marler 1960; Marler and Hamilton 1966). Despite this abundance of examples, there

has been considerable confusion on the conceptual categorization of the data on hand. As Marler (1960) has indicated, the distinction between geographic variation of song and the existence of song dialects in neighboring populations has seldom been made. Both phenomena have usually been lumped together, with considerable loss of insight into the evolutionary significance of their differences.

Geographic variation in the song of a species refers to differences in song over long distances and between populations which normally do not mix. *Dialects* refer to song differences between neighboring populations, or between populations of potentially interbreeding individuals. It is probably best to restrict the usage of the dialect concept to population differences within the same subspecies and to differences known to be phenotypic or suspected of being so. The possibility that song differences between subspecies have arisen under conditions of geographic isolation cannot be dismissed even though, as will be shown later, it is equally possible that these song variants originated as true dialects and in fact were instrumental in achieving subspeciation.

The probability of gene flow between two distinct populations is small and to find differences in song between these two populations, as presumably there will be in other phenotypic and genotypic characters, is not very surprising. Over long distances many factors in the environment and history of two populations presumably will have left their mark. But when two populations are within earshot of each other, so to speak, with no geographic barriers separating them, and yet each one preserves a dialect of its own, this is surprising. Such an occurrence calls for a special explanation.

This paper presents the incidence of song variation in some Argentine populations of *Zonotrichia capensis*, commonly referred to as the Chingolo in that portion of its range. (This species has also been called Andean

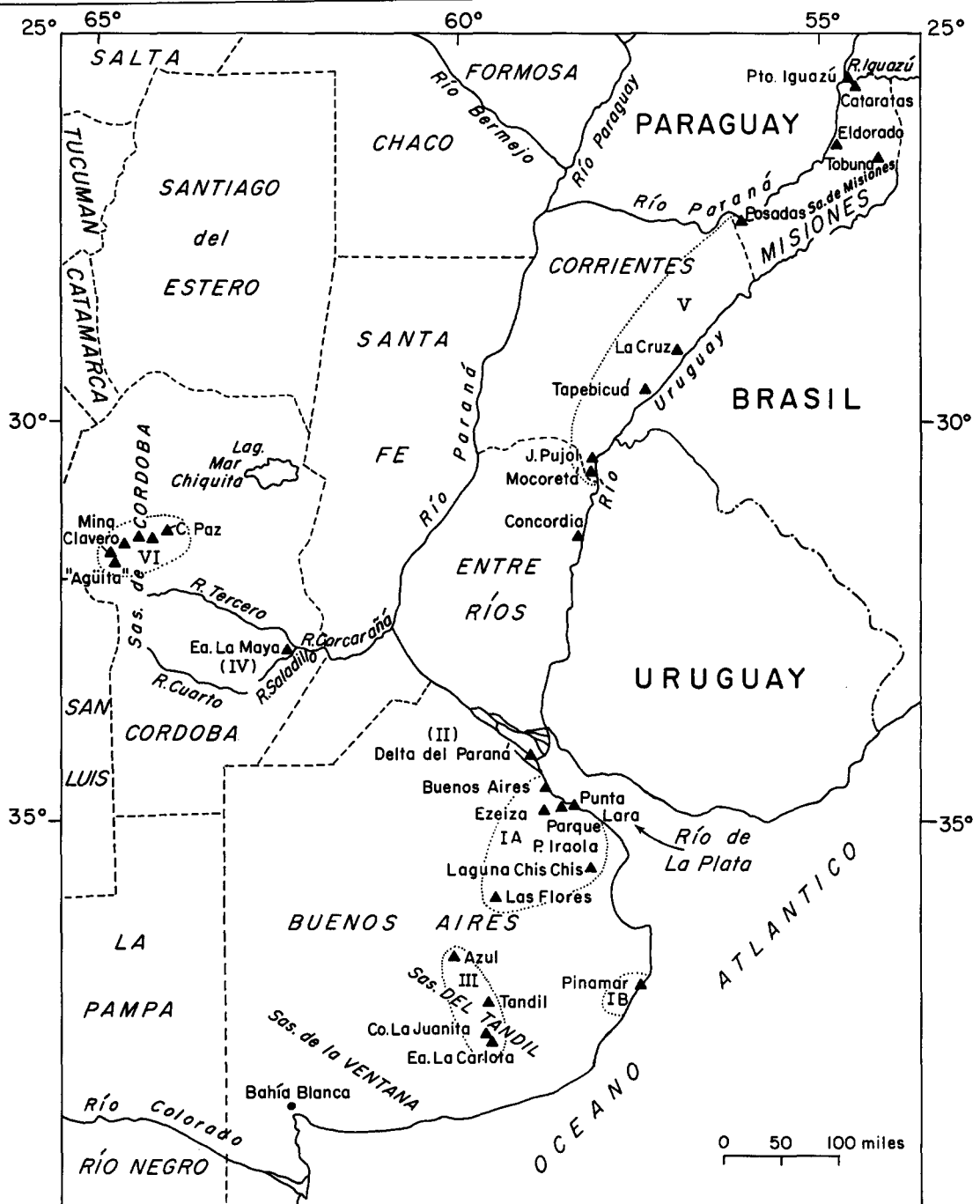


FIGURE 1. Partial map of Argentina. Black triangles indicate localities sampled. Dotted lines enclose study areas, identified by Roman numerals. When a study area comprises only one locality the corresponding numeral is placed next to that locality's name. Only those landmarks relevant to the areas surveyed are included.

Sparrow or Rufous-collared sparrow.) The findings are evaluated so as to determine the evolutionary significance of this phenomenon.

METHODS

This investigation was conducted in Argentina where, due to unexpected circumstances, I was forced

to stay for five months. Study areas were distributed through the provinces of Buenos Aires, Misiones, and Córdoba. Very small samples were also obtained in the provinces of Entre Ríos and Corrientes (fig. 1). A total of 523 individuals are included in this study.

This work was not planned in advance and consequently the standard equipment routinely used in studies of bird song was not available. Since songs

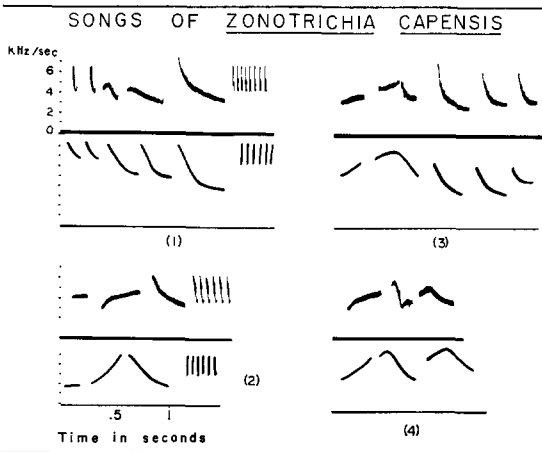


FIGURE 2. Four *Zonotrichia capensis* songs from the following sources: (1) Colombia, bird captured by A. H. Miller and recorded by Peter Marler at Berkeley, California, 2 June 1960; (2) and (4) two different birds recorded by Josué Nuñez, at Boulogne, near Capital Federal, Argentina, October 1967; song (4) is incomplete, lacking a trill; (3) Brazilian Chingolo song, from "Surco" record OL 7012, "Cantos de Aves de América del Sur," by Johan Dalgas Frisch. Each song is represented by a sound-spectrograph (upper) and its corresponding version in field notation system (lower).

could not be recorded on tape, an alternative method was devised that allowed direct transcription of sound in a graphic form. This method retains considerable information about pitch and temporal structure of song even though it is less reliable and objective than tape-recordings and sound-spectrographic analysis. A lengthy experience (Nottebohm 1966, 1967, 1968, and unpublished) with sound-spectrographic analysis of bird song provided a useful background for the transcription of sounds into a visual display. This approach to the collection of data was rendered particularly feasible by the relatively simple structure and tonal quality of the song of the Chingolo. An example is provided (fig. 2) showing sound-spectrographic analysis of four songs and the conversion of the same songs into the notation system used in the field, which was done before sound spectrograms were seen.

The direct recording system used in the field is fraught with all the shortcomings inherent in subjective evaluation of sensory input. I am confident, however, that it rendered information representative of the material available in the field. No doubt fast and subtle fluctuations in song structure (e.g., the exact number and shape of notes in a trill) are not as well recorded as the more marked structural details. Amplitude of songs or of components within songs are not recorded. The method used is well suited to the retention of information about many kinds of differences between song themes, even if the representation of these differences is at times somewhat arbitrary.

The material presented here was obtained from

sparrows singing in their natural habitat. Contact with a particular bird was maintained while the bird sang at least five times, and occasionally until it produced as many as 30 or more consecutive songs. Some sparrows, identified by the tree or the restricted area where they sang, were recorded on successive days. An estimate was thus obtained of the stability of their individual themes and richness of their repertoire. None of the birds recorded in this study was collected. The age, sex, and gonadal condition of the individuals recorded remains unknown. It is presumed that they were all males.

The song sample obtained in each of the localities visited was as large as time and terrain allowed. A sample of 20 to 40 individuals was considered to be representative when the area sampled was about one square mile. In no case did a sample include ringed birds. Consequently precautions were adopted so as not to record the same bird twice. Minimal distance between two consecutive recordings was set at 150 ft. When two or more neighbors were singing at the same time and their identity was clear, the distance between birds could be considerably less. Since the sampling approach used was developed gradually as the study got under way, some of the localities initially visited (e.g., September visits to Parque Pereya Iraola and Punta Lara in Buenos Aires province) are represented by samples that fall short of the size later considered desirable.

W. H. Hudson (1920), referring to *Z. capensis* in the neighborhood of Buenos Aires, comments, "The Chingolos pair about the end of September, and at that time their battles are frequent. . . . Two broods are reared in the season, the first in October, the second in February or March." It seems likely, therefore, that all observations included in the present study were made during the breeding season of *Z. capensis*.

THE SONG OF THE CHINGOLO

The limited time spent in Argentina did not permit me to observe the entire annual cycle of the Chingolo. Field observations were started in the first days of September, early spring in the Southern Hemisphere. At that time many Chingolos were already singing in a stable and stereotyped fashion, while others still foraged in flocks of five to ten individuals. Shortly thereafter, and with the broader onset of territorial behavior, flocking disappeared.

"The Chingolo is a very constant singer, his song beginning with the dawn of day in spring and continuing until evening." (Hudson 1920). A Chingolo song lasts one to two seconds; the frequency of its fundamental falls between 2 and 7 kHz/sec. Its structure consists of two basic parts. An introductory part consists of one to four whistled notes (a "note" is herein considered as an uninterrupted sound, as shown by a continuous tracing in a

sound-spectrograph); more than one note type is usually represented here. A trailing part is formed by a series of similar notes. Depending on the length of this note and on the separation between its successive renderings, the end product will sound like a trill (a "trill" is defined as the repetition of the same or a very similar note at very close intervals), or like a series of emphatic whistles, or will fall somewhere between these two extremes. When a clearly discernible trill is lacking, the impression given is that the song is composed only of its first part, the second one having been omitted (e.g., compare figs. 5 and 9).

The song of the Chingolo varies considerably in Argentina. This is particularly noticeable as one visits some of the different habitat types, and life-zones within habitat types in which this almost ubiquitous bird can be found. A broad sample of songs from different parts of the country reveals considerable variability in note-types, trill-types, separation between notes, and number of notes per song. Superimposed on this variability one finds homogeneity in other physical characters of the song as previously described.

SONG DIALECTS AND INDIVIDUAL VARIABILITY

The trailing part of the Chingolo song has characteristics of pitch, rate of delivery, and note structure that may differ noticeably between localities. Within an ecologically homogeneous area, however, these characteristics tend to remain very stable, giving rise to dialects. The introductory part of this same song may differ from individual to individual. Various combinations of notes within this part result in the occurrence of several song themes in a local population. ("Theme" and "motif" are used here interchangeably, referring to a particular series of notes always rendered in the same order and with set pitch relationships.) It is common to find two or more individuals in one population singing the same theme. When this is so, their respective versions of that theme are usually very similar, but never identical (fig. 3). The decision whether to characterize songs as versions of a theme or as different themes can sometimes become an arbitrary one. Fortunately this problem does not crop up very often; usually there is little question as to which theme the bird is singing. Repetitions of a song theme by the same individual are extremely stereotyped (fig. 3).

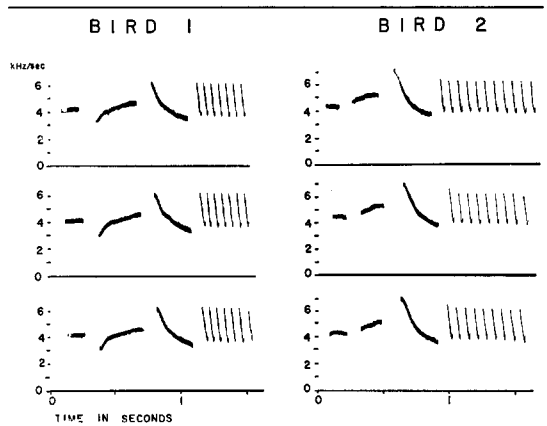


FIGURE 3. Three consecutive songs by two neighboring Chingolos that were singing simultaneously (recorded by J. Núñez at Boulogne, in the outskirts of Buenos Aires city).

SEQUENTIAL PROGRAMMING OF SONG

Most Chingolos probably include only one motif in their song repertoires. Out of 523 individuals sampled, 17 were heard singing two themes each, while two more individuals had a repertoire of three themes each. With longer recording sessions per individual, song repertoires of two or three themes might have been found to be more common.

When a Chingolo includes more than one theme in its song repertoire, themes are not sung randomly. A particular motif is produced a number of times (3-43) before it is replaced by another one, which in turn will be repeated a number of times, and so on. Temporal separation between songs is of the order of 10-20 sec. In this way an individual bird can render in an almost continuous fashion some 30 to 50 songs before it interrupts its singing with some other activity. Four examples of sequential programming follow. Capital letters identify the motifs sung; the continuous lines represent silent periods.

- 1) 2 L, 6 A, 6L 3 min 5 L, 9 A, 5 L, 3 A
- 2) 10 J, 3 A, 2 min 3 J, 7 A, 8 J
- 3) 9 D, 4 J, 12 D, 8 J
- 4) 10 N, 40 L 5 min 12 N, 43 L

The first three examples, corresponding to three different birds, were recorded in Estancia La Maya, southeastern Córdoba. (Area IV, fig. 7). The last example corresponds to Parque Pereyra Iraola, south of Buenos Aires (Area IA, fig. 5).

The number of times a theme is sung in succession varies from bird to bird and is

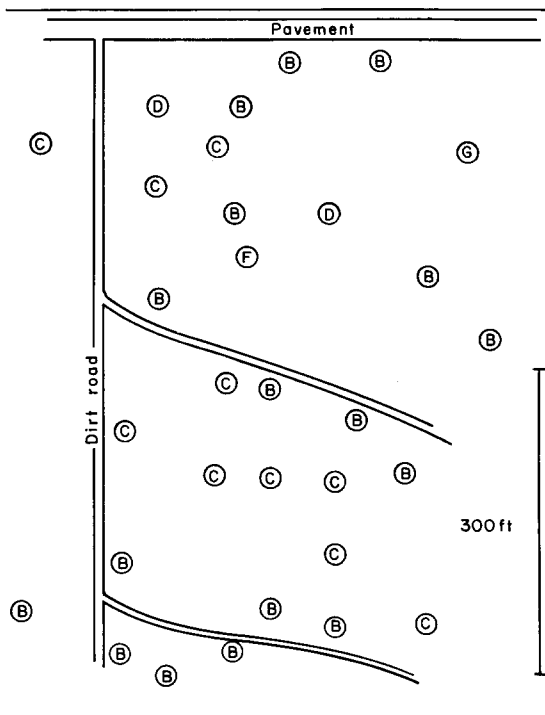


FIGURE 4. Distribution of Chingolos singing in a eucalyptus wood at Ezeiza, province of Buenos Aires, 17 November 1966. Each circle indicates a bird, the letter circled referring to the theme sung by that individual.

probably influenced by the acoustic stimuli an individual receives from its neighbors. When a Chingolo has two song themes, and only one of them is shared by neighbors, the shared theme constitutes the greater percentage of the total number of songs it delivers. The fourth of the above listed examples is

representative of this kind of occurrence (see also fig. 4).

RESULTS

A complete listing of the localities sampled follows. It includes dates when these localities were visited and an estimate of the area covered. Each sample is accompanied by a brief description of its corresponding topography and type of vegetation cover. When a sample was taken predominantly along one axis, "maximal distance" refers to the separation between the individuals at the extremes. For each locality visited a complete list of all the themes canvassed is given. In some cases it was possible to estimate the number of individuals singing per acre. Presumably, by and large, only male Chingolos sing, as is the case in other *Zonotrichia* species. It seems probable that the incidence of song varied during the different phases of territorial behavior, e.g., before a male was paired, during nest building, during the incubation period, and after the young hatched. To this extent, the number of males singing per unit area at any one time may be a misleading index for estimating the density of a breeding population. However, such figures obtained during the breeding season may serve for comparing roughly the densities in different areas (table 1).

To facilitate the analysis of the information collected, all localities visited are grouped into geographic "areas" and "sub-areas." Within a particular geographic area all themes are identified by a constellation of capital letters. The identification of themes are not interchangeable between areas, but subareas

TABLE 1. Estimated diversity of Chingolo song themes by locality.

Area	Locality	No. birds recorded	Estimated density per acre	No. themes recorded	Most common themes	% representation of the most common themes
IA	1.b Parque P. Iraola	43	5	9	B and D	74
IA	2.b Punta Lara	42	*	7	B and A	85
IA	3.a Ezeiza	23	4	5	B and C	69
IA	3.b Ezeiza	43	5	6	B and C	86
IB	8. Pinamar	38	2-3	10	A and K	64
II	9. Delta	23	very low ^a	11	H and I	48
III	10. Tandil	31	0.5	13	C and A	55
IV	11.b "La Maya"	53	1	8	J and B ^b	47
VA	12. Eldorado	31	1	16	A and I	52
VB	13. Puerto Iguazú	21	low ^a	9	D' and W	52
VC	14. Tobuna	20	1	8	D' and T.2	57
VI	15. Sample I, Sierra Grande	53	1	2	F	96
VI	15. Sample III, Sierra Grande	28	*	3	E	93

^a Density of birds singing per acre was not evaluated for samples 2b and 15 (III); sample 9 was well below one individual singing per acre; sample 13 was probably close to one individual singing per acre.

^b Same as J and B, area I.

within an area share the same system of letters (e.g., 1A and 1B). On occasion, when two themes in the same area were similar enough to raise some doubt as to their separate identities, both are labelled with the same letter plus a prime sign for one of them (e.g., C, C' and D, D', fig. 6; D and D', figs. 9, 10). When the number of themes in an area exceeds that of letters available, the remaining themes are identified by a letter followed by a number (e.g., themes P.1 and P.2, figs. 6, 10). The number in parentheses following each theme indicates how many birds sang that theme in that sample. In those cases where the sample size is larger than 20 individuals, song variability is computed in terms of percentage of birds singing either of the two most common themes in that sample. This information is presented in table 1. Samples smaller than 20 individuals are not included in that table.

AREA 1A. PROVINCE OF BUENOS AIRES (Fig. 5)

Referring to the area around Buenos Aires, Hudson (1920) wrote: "On the treeless desert pampas the Chingolo is rarely seen, but wherever man builds a house and plants a tree there it comes to keep him company, while in cultivated and thickly settled districts it is excessively abundant."

1a. Parque Pereyra Iraola. Near Estación Villa Elisa, 29 September 1966. Observations were conducted in a man-made park with predominance of mature trees; interspersed among the latter were brushy thickets and grassy fields. Maximal distance between extremes of sample, 1.2 miles. Number of individuals recorded, 14. Estimated density, 3 males per acre. Themes recorded: B(7), D(3), H(2), K(2), J(2). Two individuals had two song themes each: one of them sang H and J, and the other one B and K.

1b. Parque Pereyra Iraola. Same location as previous sample 18 November 1966. Number of individuals recorded, 43. Estimated density, five males per acre. Themes recorded: B(18), D(13), L(4), C(2), K(2), A(1), M(1), N(1), G(1), E(1). The most common themes, B and D, are represented in the song of 74 percent of the individuals included in this sample. One Chingolo in this locality sang two themes, N and L.

2a. Punta Lara. 29 September 1966. Riparian woodland, mostly native species of deciduous trees; some marshland with rushes, etc., and higher ground with grass cover. Maximal distance between extremes of sample, 1 mile. Number of individuals recorded, 4. Themes represented: B(2), A(2), R(1). One bird sang two themes, B and A.

2b. Punta Lara. Same locality as previous sample, but covering larger area, 19 November 1966. Maximal distance, 2 miles. Sample size, 42 individuals. Themes recorded: A(9), B(27), K(3), Q(1), R(1), T(1), U(1). One bird was heard singing two themes, B and R. The two most common themes in this locality, B and A, were sung by 86 percent of the individuals.

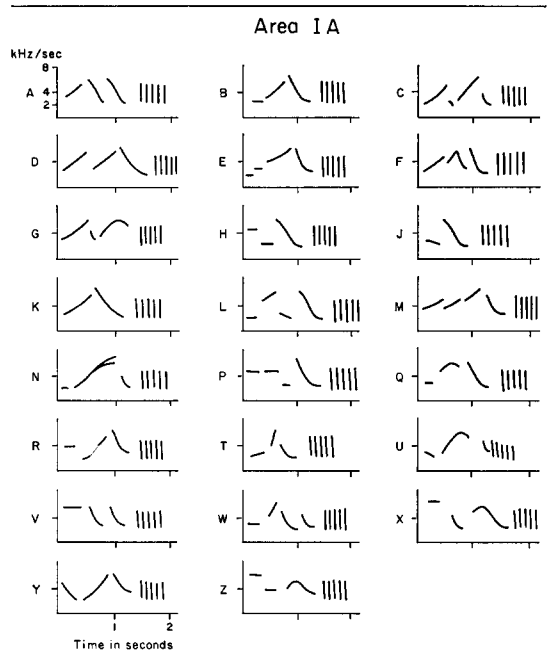


FIGURE 5. Area 1A. Chingolo song themes recorded at Capital Federal, Ezeiza, Punta Lara, Parque P. Iraola, Laguna Chis Chis, and Las Flores, all in Buenos Aires Province, September through November 1966. (The second note of song N acquires a jangling tone as it rises in pitch, which is indicated by a double trace.)

3a. Ezeiza. 3 October 1966. Parkland vegetation, introduced species with predominance of eucalyptus, grassy fields interspersed. Maximal distance, 0.5 miles. Sample size, 23 individuals. Estimated density, 4 males per acre. Themes recorded: B(12), C(4), A(4), D(2), E(1). The two most common themes in this locality were sung by 69.5 percent of the individuals recorded (in this case either C or A can be considered second most common theme).

3b. Ezeiza. Same location as previous sample but covering a larger area, 17 November 1966. Sample size, 43 individuals. Estimated density, 5 males per acre. Themes recorded: B(25), C(12), D(3), E(1), F(1), G(1). B and C, the two most common themes, were sung by 86 percent of the individuals in this sample.

4. Capital Federal. Palermo park next to municipal airport, 29 September 1966. Park vegetation and grass cover. Three neighboring birds sang theme D.

5. Capital Federal. Belgrano, 4 October 1966. Residential quarter, gardens and parks. A Chingolo sang theme D. On the following day a second bird was heard singing theme P in the immediate area of the previous day's recording. This second bird, however, was not heard again on subsequent days. The bird that sang theme D stayed in the neighborhood and its song, apparently consisting of this single theme, was heard until mid-December, when observations were discontinued.

6. Laguna Chis Chis. Edge of an extensive marsh, 7 October 1966. Recordings were done on the grassy embankments of a road traversing this lowland area; a few willows grew at the edge of the marsh. Two

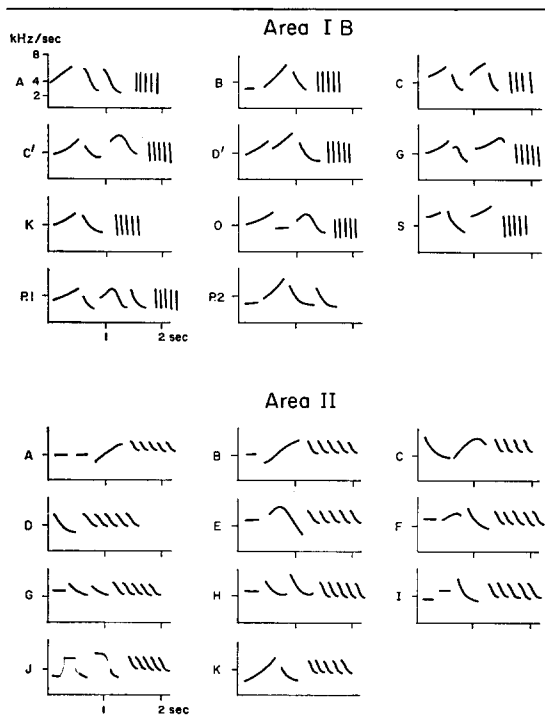


FIGURE 6. Area I B. Chingolo song themes recorded at Pinamar, Province of Buenos Aires, 9–12 October 1966. Area II. Song themes recorded at the Delta of the Paraná River, September and November 1966.

neighboring Chingolos had two themes each: one song V and W, the other one B and Z.

7. *Km. 152, Route No. 3, near Las Flores.* Two birds singing on the side of the road, next to a planted row of eucalyptus trees. One of the birds sang Y and the other one sang theme X.

AREA I B. PROVINCE OF BUENOS AIRES (Fig. 6)

8. *Pinamar.* 9–12 October 1966. Residential development with relatively few houses and vast plantations of pines, eucalyptus, and *Acacia melanoxylum* trees. Abundant grassy cover. Study area was by the sea, never more than one mile inland. As recently as 20 years ago the predominant topography of this coastal strip was shifting sand dunes and dune grasses, with wet meadows and marshes inland. The present wooded condition of the dunes, a first step towards changing the locality into a sea side resort, has considerably changed the habitat. The sample area was approximately 0.6 miles square, within which 39 birds were recorded singing, a density of two to three individuals singing per acre. The following themes were recorded: A(18), K(7), B(5), C'(3), O(2), P.1(2), C(1), S(1), D'(1), G(1), P.2(1). The most common themes were sung by 64 percent of the individuals in this sample. Theme A was also the predominant one in Ostende and Valeria del Mar, two localities 2 and 5 km south of Pinamar respectively and of similar habitat type. Two of the Pinamar Chingolos sang more than one theme: one bird sang B and K, and the other one sang themes A, O, and P.2.

The data collecting method did not allow for detecting systematic differences between the song samples obtained in Pinamar and those from localities further north (Punta Lara, Ezeiza, and Parque Pereyra Iraola), other than differences in the incidence of various themes.

AREA II. PROVINCE OF BUENOS AIRES (Fig. 6)

9. *Delta of the Paraná River, (area enclosed by Paraná de las Palmas, Río de la Plata, Río Lujan, and Río Carapachay).* Observations in this area were conducted during 23, 28, and 31 September, with additional observations on 20 November. Maximal distance between the extremes of the sampled area, ten miles. The topography here is characterized by marshy islands subjected to periodic floods. In the marshy parts are rushes and grasses of various kinds, the woody vegetation is predominantly willows and ceibos (*Erythrina cristagalli*). In this region Chingolos are found mainly along the higher ground which flanks the water courses. It would seem likely that the numbers of Chingolos in the delta has increased as a result of human activities, which usually produce grassy clearings with a scatter of trees and commercial plantations. Despite this expansion of potential habitat, the Chingolo occurs in the Paraná Delta in low densities. The total sample in this area included 23 individuals. The following themes were recorded: H(8), I(3), G(2), A(2), C(2), B(1), D(1), E(1), F(1), J(1), K(1). Considering the spatial and temporal distribution of this sample and the relatively small number of individuals it includes, it probably should be evaluated with some caution. The two most common themes, H and I, are represented in the song of 48 percent of the individuals recorded. Interestingly enough, when comparing the Delta songs with songs heard in nearby Buenos Aires (Capital Federal and environs), the trilled part of the Chingolo song in the delta sounded as though it had a higher pitch and notes of a more whistled tonal quality. The delta area would seem to have a dialect which does not extend into the neighboring pampas.

AREA III. PROVINCE OF BUENOS AIRES (Fig. 7)

10. *Tandil.* 14–16 October 1966. Two samples were taken in this locality; one of 15 individuals was recorded in Estancia "La Carlota"; 16 individuals were recorded in Sierra La Juanita, 7.5 miles NW of "La Carlota." The topography of both localities sampled is similar: rolling highland country, rocky projections, a predominance of grassy cover, the elevation 900–1500 ft. The density of Chingolos in this country south of the city of Tandil was remarkably lower than that of places like Ezeiza and Parque Pereyra Iraola, probably one bird singing every two acres. The following themes were recorded in "La Carlota": C(7), A(4), B(1), D(1), E(1), F(1), G(1). The sample of Sierra La Juanita rendered: C(4), I(3), A(2), H(2), D(1), B(1), J(1), K(1), L(1), M(1). Altogether, 13 themes were included in these two samples. Two themes, C and A, were sung by 55 percent of the individuals recorded. Two Chingolos in these samples sang more than one theme: one of these birds sang D and E, the other one H and B.

The song of the Chingolos around Tandil is characterized by its trill, the notes of which are emphatic

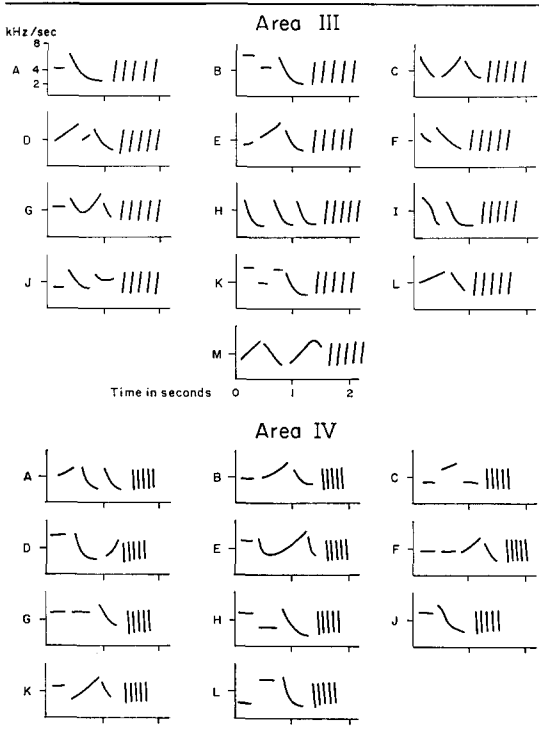


FIGURE 7. Area III. Chingolo song themes recorded in the Sierras of Tandril, Buenos Aires Province, 14–16 October 1966. Area IV. Songs recorded at Estancia “La Maya” Córdoba Province, November and December 1966.

and noticeably more spaced than in Pinamar or in Buenos Aires and environs. This characteristic of the song, which is systematically present in this area and occurs as far north as the city of Azul (no sample presented), suggests that this is a true dialect of broad occurrence in the highlands of the southeastern province of Buenos Aires. This area is ecologically distinct from the lowlands to the east and north.

AREA IV. PROVINCE OF CÓRDOBA (Fig. 7)

11a. Estancia “La Maya.” Ten miles south of Monte Buey, 7–14 September 1966. Area covered, approximately 1 square mile; habitat type, grassland with some planted groves of trees. Nine individuals were recorded; the density of birds singing at that time was not estimated. Themes recorded: A(2), B(2), D(2), C(1), D(1), F(1), G(1). At the time this sample was obtained, the breadth of the present study was yet unclear. Initially my interest was focused on inventorying the maximal number of themes occurring in a locality and the song repertoire of each individual. This resulted in samples which did not represent the proportional incidence of various song themes. One individual in this sample sang themes A and B; two of its neighbors sang, respectively, themes A and B as well.

11b. Estancia “La Maya.” Same locality as previous sample, but covering a larger area, 2.5 square miles, 24 November and 3 December 1966. Total number of individuals recorded, 53; estimated den-

sity, 1 Chingolo singing per acre. Themes recorded: J(14), B(11) A(10), D(10), L(3), E(3), K(2), H(2). The two most common themes, J and B, are represented in the song of 47 per cent of the individuals in this sample. Five Chingolos in this locality sang two themes each: L and A; J, A; L, J; L, D; J, D. Themes J, B, and A are very similar to the corresponding themes (identified with same capitals) of Area I.

No systematic differences were found between the Chingolo songs of southeastern Córdoba and those of eastern Buenos Aires province (Areas IA and IB). This perhaps reveals something about the limitations of the method used. However, it seems likely that if any differences existed between these localities, they must have been subtle ones, clearly not as dramatic as those identifying other dialect areas.

SUMMARY AND COMMENTS, AREAS I-IV

The separate identity of a dialect is determined by stereotyped characteristics (pitch, structure of notes, and rate of delivery) of the trilled part of the song. From this survey, three areas emerge as having a distinctive song dialect: the eastern pampas, including southeastern Córdoba and northeastern Buenos Aires province; the delta of the Paraná River; the highlands of Azul and Tandil. The “eastern pampas” area is one of very gradual ecological changes: rainfall decreases from the Atlantic coast west and northwest; similarly, temperature extremes are more pronounced from the coast, inland. However, the relative homogeneity of this area is more striking than the slight and gradual differences over vast sections of it. It is always the pampas, absolutely flat with a rich grassy cover.

The geographic scatter of the localities sampled did not allow accurate demarcation of the boundaries of the dialect areas. It is even possible that in some cases there was a gradual change from one dialect type to a neighboring one. In the Paraná Delta the dialect typical of the area was easier to identify further into the delta habitat. The nature of the song boundary between two dialect areas deserves further study and is of considerable theoretical interest.

In five of the localities surveyed, representative samples were obtained over uniform ground which was explored in a thorough fashion. This was the case in Estancia “La Maya,” Parque P. Iraola, Punta Lara, Ezeiza, and Pinamar. For samples of about 40–50 individuals, the number of themes recorded ranged from six to ten, averaging eight. Despite this apparent multiplicity of song motifs, only a few of these themes were sung by the majority of individuals in a sample (table 1). “B” was the most common theme in Ezeiza, Punta Lara, and Parque P. Iraola. In Pina-

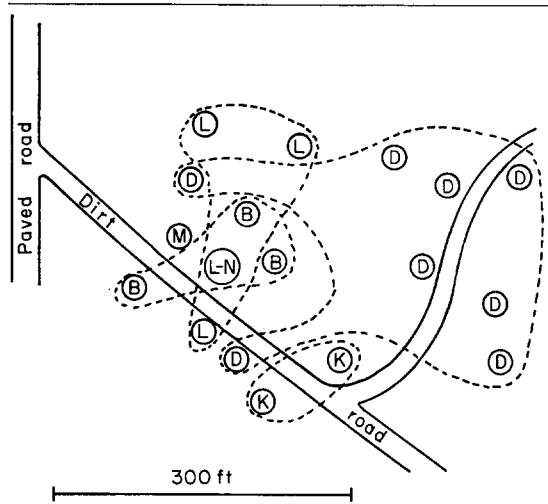


FIGURE 8. Parque Pereyra Iraola, province of Buenos Aires, 18 November 1966. Interpretation same as for figure 4. Dotted lines are drawn around individuals sharing the same theme.

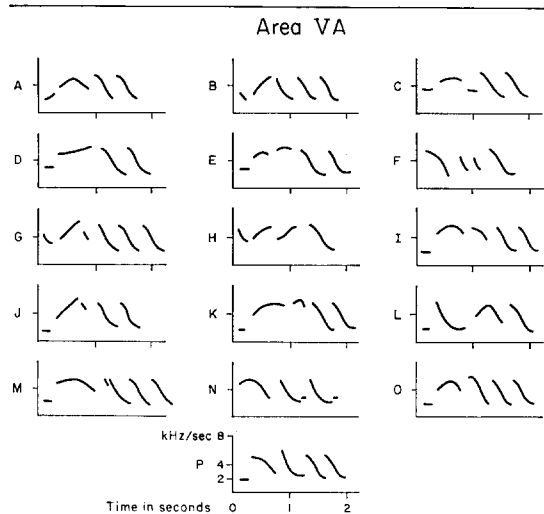


FIGURE 9. Area VA. Chingolo songs recorded at Eldorado, Misiones, 28-30 October 1966.

mar, Ostende, and Valeria del Mar, the most common theme was A. The latter theme was the second most common one in Punta Lara. In Estancia "La Maya" the two most popular motifs were J and B, in that order.

In any particular locality, neighbors within mutual earshot tended to share the same song theme (figs. 3, 4, 8). Within these restricted neighborhoods the homogeneity of Chingolo songs was at times quite marked.

Four of the localities sampled were visited more than once. For only one of these localities, Ezeiza, was a representative sample collected on two consecutive visits. A survey conducted six weeks after the initial sample was obtained produced a comparable coincidence of themes. However, one of the motifs, A, was not recorded during the second visit; two themes, F and G, not recorded during the previous visit were now sung by two individuals. The samples obtained during the two consecutive visits to Ezeiza suggest that there is considerable stability in the song repertoire of a Chingolo population during a particular breeding season.

AREA V. MISIONES PROVINCE (Figs. 9 and 10)

On 26 October 1966 I boarded the train from Buenos Aires to Posadas with the intention of studying the song of *Z. capensis* in a subtropical habitat. When the train made its stops during this trip northwards, any Chingolos singing nearby were recorded. By this sampling method it was found that in eastern Entre Ríos province the "eastern pampas" dialect does not extend north of Concordia. Already in this town the trilled part of the song is unlike that heard around Buenos Aires; the elements of the trill are

separated by longer silent periods. Southern Entre Ríos may have a dialect of which the Concordia songs are representative. Unfortunately, the train traveled through this part of the province at night, and the matter remains unsettled. North of Concordia the typical trill is replaced by one to three emphatically whistled notes with a rather long period separating them. This new version of Chingolo song was recorded from all localities sampled in Argentina's northern Mesopotamia and thus is a rather widespread dialect.

Mesopotamia is that area of northern Argentina delimited by the Paraná and Uruguay Rivers (fig. 1). The following localities in this area were sampled: Mocoretá, J. Pujol, Tapebicúa, La Cruz, and Posadas, all of them train stops. In Misiones province four localities were more intensely surveyed: Eldorado, Puerto Iguazú, Cataratas, and Tobuna. It is possible that within the northern Mesopotamia dialect, subtle, undetected, but systematic song differences existed between areas.

Eldorado, Puerto Iguazú, Cataratas, and Tobuna are towns and villages surrounded by subtropical jungle and plantations. In the Sierra de Misiones, the area around Tobuna is 1500-2100 ft. above sea level. Its ecological characteristics are somewhat different from those found in western Misiones. However, the Chingolo is not a bird of dense forest. Its presence in all these areas has no doubt been favored by man's activities and consequent changes of landscape. It is common around gardens, orchards, and plantations (mate, tung, and citrus trees), as well as around the newly established meadows of the growing cattle industry. The following example gives an impression of the extent of the association between the Chingolo and man's activities in this subtropical area. Around Puerto Iguazú, and over an area of fields and gardens, a three-hour survey yielded 21 individuals singing. On the next day, an early morning walk through the jungle following a road through the Iguazú National Park yielded only two Chingolos singing. The walk lasted four hours. Except for the strip of grass on either side of the road, it traversed undisturbed habitat.

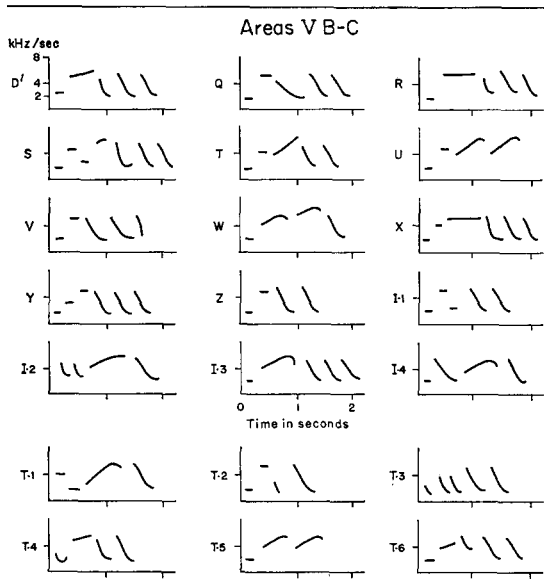


FIGURE 10. Areas VB-C. Chingolo songs recorded at Puerto Iguazú, Cataratas, and Tobuna, Misiones Province, 2-6 November 1966.

12. *Area VA. Eldorado.* 28-30 October 1966. Area covered, 2.5 square miles. Residential neighborhood, predominance of gardens and small fields. Number of individuals in this sample, 31. Estimated density of Chingolos singing, 1 bird per acre. Themes recorded: A(13), I(3), D(2), B(1), C(1), E(1), G(1), H(1), J(1), F(1), K(1), L(1), M(1), N(1), O(1), P(1). The two most common themes, A and I, were sung by 52 per cent of the birds in this sample. It is possible that C and J were only variants of A, and therefore it is uncertain whether they should be classed as independent themes or not.

13. *Area VB. Puerto Iguazú.* 2-3 November 1966. Residential area, gardens, orchards, and small fields. Number of individuals recorded, 21. Maximal distance between the extremes of the sample, 2 miles. Themes recorded: D'(7), W(4), Y(2), I.1(2), I.3(2), X(1), Z(1), I.2(1), I.4(1). The two most common themes, D' and W, were represented in the song of 52 per cent of the birds in this sample. A smaller sample comprising five birds was taken at Cataratas, 12.5 miles to the southeast of Puerto Iguazú. The following themes were included in that sample: W, Q, R, V, S, T, U; the last three themes were sung by one individual. Perhaps theme R was only a variant of theme D'.

14. *Area VC. Tobuna.* 6 November 1966. Area sampled, 0.2 square miles, predominantly fields where the forest had been burned down and now cattle grazed. Number of individuals recorded, 20. Estimated density, 1 bird per acre. Themes recorded: D'(9), T.2(3), T.1(2), T.3(2), I.3(2), T.4(1), T.5(1), T.6(1). The two most common themes, D' and T.2, were sung by 57.1 per cent of the individuals in this sample.

SUMMARY AND COMMENTS, AREA V

The sampling in Entre Ríos, Corrientes, and particularly Misiones (fig. 1) produced one common dialect for the northern Mesopo-

tamia. The southern boundary of this dialect area, somewhere in northern Entre Ríos, is highly intriguing since it seems to occur in a region in which there is no obvious ecological discontinuity.

The data collected in Eldorado, Puerto Iguazú, Cataratas, and Tobuna show considerable song variability (table I). Sixteen different themes were included in a sample of 31 individuals at Eldorado; a sample of 26 Chingolos at Puerto Iguazú and Cataratas yielded 15 themes. It would be interesting to know whether the marked song variability in this area is a result of ecological variables unique to the subtropical habitat or is a mere artifact of sampling dispersed individuals over a large area. The more dispersed a population is, the harder to sample it homogeneously so as to include all neighbors. Comparing the results from Misiones with those of Ezeiza, Punta Lara, or Parque Pereyra Iraola, the greater song variability in Misiones is correlated with lower densities of Chingolos singing per acre. A similar correlation of lower densities of Chingolos with greater variability of song is found in Tandil.

Considering jointly the samples of Ezeiza, Punta Lara, and Parque P. Iraola, 15 themes were recorded from a total of 128 individuals distributed along an axis of some 20 miles, and 66 per cent of these 128 birds sang the two predominant themes, B and C. Even though the number of individuals sampled and the area covered are considerably larger, this combined sample yielded less variability than was found in the localities surveyed in Misiones or Tandil. The great variability of song observed in Misiones is not a phenomenon restricted to the subtropical habitat, nor an artifact of sampling a dispersed population, but rather, a variability associated with low densities, wherever these may occur.

However, the correlation between low population densities and high variability of song must be handled cautiously. The density of Chingolo populations was in all cases estimated on the basis of number of birds singing per acre. As mentioned previously, the incidence of song in this species is likely to be controlled by the individual hormonal substrate. Presumably this hormonal substrate changes during the length of the breeding period. So, for example, a visit to southeastern Córdoba (Estancia "La Maya") revealed more individuals singing per acre in early September than two and one-half months later. During the second visit to that area, the variety of themes heard was comparable to that of Ezeiza, Punta Lara, or

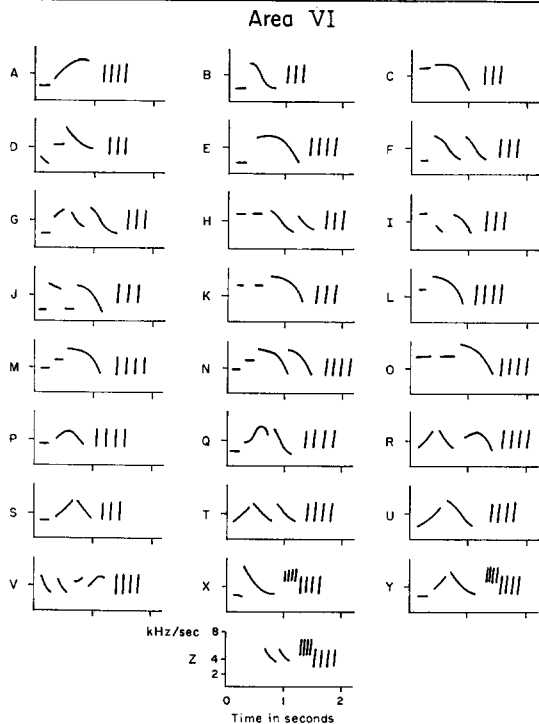


FIGURE 11. Area VI. Chinglo songs recorded at Agüita and Sierra Grande, Córdoba Province, November and December 1966.

Parque P. Iraola, even though the number of individuals singing per acre was smaller. This lower density was accompanied by a more even numerical incidence of the themes represented (table I), an observation that cannot be interpreted at this time. Ideally, to establish a reliable correlation between breeding densities of populations and song variability, both measures should be made for all localities at comparable stages of the breeding cycle. This condition was not met in this study.

AREA VI. SIERRA GRANDE DE CÓRDOBA (Figs. 11, 12, 13)

Two surveys were conducted in this area: one centered in Mina Clavero Valley, six miles south of Mina Clavero; the other one consisted of a SW-NE transect of Sierra Grande, from Mina Clavero to Villa Carlos Paz.

The Sierra Grande ranges from 1500–8400 ft above sea level. Its slopes are abrupt, with quick transitions between life zones. This is clearly manifested in the vegetation, which shifts from a grassy and well-irrigated valley up to drier slopes, leading to the heights of the Pampa de Achala, covered with short grasses and exposed to a rigorous winter. Chingolos, without a break in continuity, inhabit the entire span of these life zones.

15. "Agüita." The survey conducted south of Mina Clavero was centered in "Agüita," a country estate, and comprised a series of samples obtained

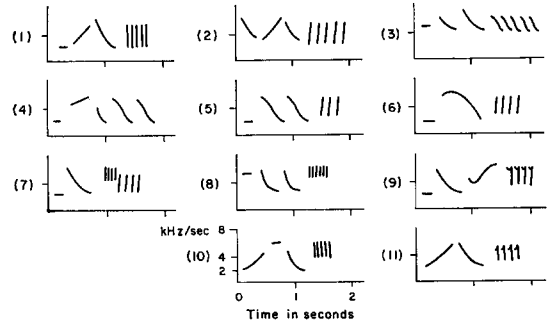


FIGURE 12. Dialects of *Zonotrichia capensis* in various ecological areas. Each of these songs is the most common theme in its corresponding "dialect" or "sub-dialect" in the localities sampled: (1) Eastern pampas; (2) Tandil; (3) Paraná Delta; (4) Misiones; (5) Sample I, Mina Clavero Valley; (6) Sample III, "Agüita," (7) Sample VI, 2100 ft; (8) Sierra Grande, western slope, 4200–5100 ft; (9) Sierra Grande, 6600 ft; (10) Sierra Grande, eastern slope, 4800 ft; (11) Sierra Grande, eastern slope, 3000 ft.

in vertical succession from the bottom of the valley up to a point 2100 ft higher. The altitudinal relationship between these samples can be appreciated in figure 13. Samples I thru VI were obtained over a straight uphill trajectory.

Sample I. 29 November 1966. This sample was taken on the eastern half of the valley, over a north-south distance of a little over two miles. The half-way point in this longitudinal transect corresponds to Las Calles, a small rural village. The terrain covered was mainly devoted to agriculture and grazing and was criss-crossed by irrigation ditches. Fifty-three individuals were recorded singing, of which 51 sang theme F and 2 theme E. The density of Chingolos was one bird singing per acre.

Sample II. 28 November 1966. Area sampled, 0.1 square miles. Located 1.2 miles uphill from the previous sampling transect and some 600–700 ft higher on the mountain side, the terrain was rockier and with a predominant vegetation of native thorn-bearing trees and shrubs. Eighteen Chingolos were recorded in this area, with a density of approximately one individual per acre. Themes noted: E(7), B(2), C(2), F(2), D(1), G(1), H(1), I(1), J(1).

Sample III. 30 November 1966. This sample was taken starting 900 ft uphill from the upper boundary of sample II. Area covered, 0.2 square miles; topography and vegetation very similar to that of previous sample. The 28 birds recorded sang the following themes: E(26), D(1), A(1).

Sample IV. 30 November 1966. Eight birds were recorded over an area of 0.1 square miles, starting 1500 ft uphill from the upper limit of the previous sample, and some 1300 ft above the bottom of the valley. Themes sung: M(2), N(2), O(2), F(1), E(1).

Sample V. 30 November 1966. This sample, including 10 individuals, was obtained 1500 ft uphill from the previous sample, over an area of 20 acres. Themes noted: S(2), P(2), E(2), T(1), U(1), R(1), Q(1).

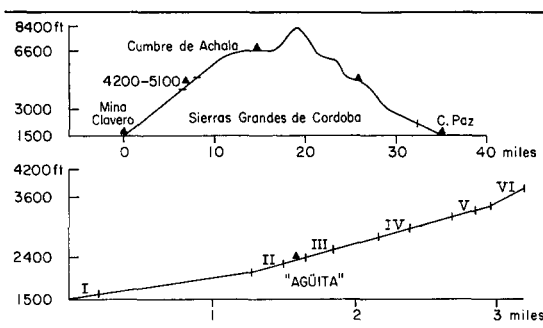


FIGURE 13. Schematized transverse section of the Sierra Grande of Córdoba, between Mina Clavero and Villa Carlos Paz. The highest reaches of the Sierra, up to 8400 ft, fell somewhat south of the actual road followed. Black triangles (\blacktriangle) indicate the approximate height at which different dialects were encountered. The sketch at the bottom presents similar information for the "Agüita" samples. Province of Córdoba, November and December 1966.

Sample VI. 1 December 1966. Twelve birds were recorded over an area of some 20 acres and 2100 ft above the bottom of the valley (sample I); seven of these birds sang a new kind of song with a very peculiar trill consisting of two note types. Three different song themes were sung by these seven individuals: X(4), Y(2), and Z(1), all ending with the same trill pattern (fig. 11). It was not possible to establish whether these birds were in fact an isolated cluster of individuals singing a "dialect" of their own, or whether they represented the lower limit of a population extending uphill. These seven birds were recorded on a ravine and ridge leading up the mountain; at this height trees had virtually disappeared and hardy grasses were the predominant vegetation. Within earshot of these seven birds were five other individuals singing songs of the type heard downhill: B(2), F(1), I(1), V(1), (fig. 11).

These six samples (fig. 13) were recorded over an uphill distance of three miles spanning a difference in altitude of 1500–3600 ft above sea level. At no point did the terrain present abrupt discontinuities; Chingolos could be heard singing everywhere over this distance. From sample I to sample VI there was a graded and continuous change in life zones, dramatized by the relative abundance of different species of trees at different heights and their virtual disappearance above 2000 ft; uphill the trees were gradually replaced by shrubs and grasses. These changes in vegetation were no doubt accompanied by temperature and humidity changes.

16. *Sierra Grande*. On 2 December 1966 I crossed the Sierra Grande by car, following the road from Mina Clavero to Villa Carlos Paz, some 70 miles (fig. 13). Stops were made every 6 to 12 miles and at different altitudes; the songs of any Chingolos heard singing were noted. Three birds were recorded in the outskirts of Mina Clavero, at the beginning of the transect. They sang theme F, the predominant theme at that height six miles south in "Agüita" (sample I). The next two stops were at 4200 and 5100 ft, with a total of eight Chingolos singing a distinct new song type, different from that of Mina Clavero (fig. 12). The trill which characterized this new dialect was higher pitched with notes more

closely spaced. At the Cumbre de Achala, 6600 ft, four Chingolos were recorded. One of these birds sang like the birds of the previous sample; the other three ended their song with a different trill type. One of the latter individuals sang two themes, both ending with this new trill type (fig. 12). On the eastern slope of the sierra, five Chingolos were recorded at 4800 ft; their songs ended with a trill of a type unrecorded so far, indicating the presence of a new dialect area. The last three stops, while approaching Carlos Paz, yielded a fifth dialect for this Sierra Grande transect. Eight birds were recorded, all ending their songs with a similar trill (fig. 12).

SUMMARY AND COMMENTS, AREA VI

The observations in this area showed a twofold variability in the song of Chingolos. Over short distances, moderate and gradual changes in altitude and habitat were accompanied by changes in the relative incidence of different themes. When the widespread occurrence of a theme in one area is accompanied by its virtual exclusion from a neighboring area e.g. "Agüita" samples I and III, (fig. 12), the song differences between two such localities constitute true "sub-dialects." "Agüita's" highly homogeneous samples I and III were separated by a contact zone about one mile wide with considerable variety of themes. It is improbable that different population densities could account for these observed differences in song variability. Uphill from sample III, the Chingolo song once again was quite heterogeneous. It is likely that in the upper reaches of this transect the Chingolos became more sparsely distributed. Whereas in the latter case one could argue that increased song variability accompanied decreasing breeding densities, this argument would not explain the variability of song observed in sample II.

Over greater distances, involving marked altitudinal and ecological changes, the song differences between two populations were more systematic and involved the trill component of song, regardless of the theme sung. This gives rise to true dialects and dialect areas. When two dialect areas meet, an "intermediate" dialect may occasionally arise which combines characteristics of both. This is perhaps the case with "Agüita" sample VI; its trill integrated characteristics of the dialects uphill and downhill (fig. 12; compare song 7 with songs 6 and 8).

The observations made on the Chingolos of Sierra Grande are remarkable in that over a relatively short distance, 38 miles SW-NE, they indicate at least five different song dialects. There seems to be a good correlation between the rather gross and abrupt succes-

sion of life zones and the corresponding occurrence of song dialects. There were no obvious systematic changes of song pitch with altitude. It seems unlikely that the observed incidence of dialects was a direct consequence of the changing composition of the atmosphere.

DISCUSSION

THE RELATION OF SONG DIALECTS TO DESCRIBED SUBSPECIES

The song of the Chingolo consists of two parts, presumably serving different purposes. The first part identifies the individual as well as the theme sung; the second part identifies the dialect or ecologic area to which it corresponds.

The results presented are indicative of the occurrence in *Z. capensis* of a veritable system of dialects, the general effect of which is to identify an area by its song and considerably reduce the heterogeneity of song in any particular locality. The true dialects are those corresponding to areas with well defined ecological characteristics. This study revealed the following "dialect areas": (1) Eastern pampas, (2) Paraná delta, (3) Tandil-Azul Highlands, (4) northern Mesopotamia, (5) a series of dialects in the Sierra Grande of Córdoba. The systematic differences between these song dialects have already been described under the sections corresponding to each of these areas and are schematically presented in figure 12. According to Chapman's (1940) taxonomic revision, areas (1), (2), (3), and (5) correspond to *Z. c. hypoleuca*, while part of area (4), Misiones, corresponds to the distribution of *Z. c. subtorquata*. This indicates that the incidence of dialects in *Z. capensis* is certainly not tied up with the occurrence of sub-species, or at least not with the kind of subspecies recognized until now and which depends on external morphology for identification. The correlation of dialects with ecological areas, however, suggests that from a functional viewpoint dialects could serve to discourage hybridization between populations optimally adapted to local ecological conditions. It is quite likely that part of this adaptation consists of physiological changes not accompanied by changes in external morphology.

It is interesting in this regard to note the following remark by Hudson (1920): "I found . . . the Patagonian Song-Sparrow, *Z. canicapilla* . . . very abundant in Bahía Blanca on the Río Negro. In appearance and habits it was not distinguishable from the Chingolo Song-Sparrow, but differed slightly

in its song, this being without the concluding trill." This remark merits a double comment. According to Chapman's classification, Bahía Blanca (fig. 1) is included in the distribution area of *Z. c. hypoleuca*, the northern limit for the distribution of *Z. c. australis* (*Z. canicapilla*) running through the provinces of Neuquén and Río Negro, further south. It is equally noteworthy that Hudson should decide that since the song of this Chingolo was so different it must be a different species.

THE VARIABILITY OF SONG: AN EVALUATION

Within the areas pertaining to each dialect, a number of different themes are usually encountered. However, at the local level this heterogeneity in the song is reduced in three different ways: (1) The number of themes present in any one locality is considerably less than the total number of themes occurring throughout its corresponding dialect area; two localities within a same dialect area may have no themes in common. (2) In any one locality all themes occurring in it are not equally represented, nor is their numerical incidence a random one; rather it is frequently the case that one or two of a much larger number of themes are represented in the song of two-thirds or more of the individuals in that locality (table 1). (3) At the neighborhood level and during the breeding season, i.e., when males have settled into their territories, there is a high probability that in the immediate neighborhood of any one male there will be one or more males singing its own song theme; the individual differences of these shared themes tend to be slight.

Observations suggest that the local variability of the song of the Chingolo is influenced by two factors: high densities of individuals singing per unit area, and small but consistent ecological differences between two nearby areas of the same dialect. These demographic and ecologic variables seem to be effective in maximizing respectively the homogeneity and identity of the song at any one locality. The geographic variable would seem to be less important in determining the emergence of theme repertoires typical of different localities, as can be corroborated by checking the incidence of various themes in different localities within the eastern pampas dialect area (themes A, B, C, G, and K are shared by birds in areas IA and IB; themes A and B possibly are the same in areas IA, IB, and IV).

If we discard the possibility of the results presented here having arisen through chance,

it is legitimate to inquire how such a system of dialects may affect the species displaying it. What is its function? The answer to such a question would be considerably simpler if we knew for sure the functions subserved by bird-song, a question that must be raised anew for each particular species. The role of song in territorial defense has been shown for some species. Likewise it has been commonly accepted that song attracts unmated females to unmated territorial males. Finally, it is quite possible that song serves to induce hormonal changes in the female resulting in the integration of the reproductive cycle and ovulation.

The first two functions, male repulsion and female attraction, would seem to favor the individual identification of each male by means of its song, a song otherwise clearly labelled as species specific. It is harder to predict what the ideal song traits would have to be for it to succeed in its third postulated function, that of inducing hormonal changes in the female, particularly since these ideal song traits may vary from species to species. This function, at any rate, has so far only been certainly demonstrated in the budgerigar, *Melopsittacus undulatus* (Brockway 1962), and more tentatively so for the Ring Dove, *Streptopelia risoria* (Nottebohm, unpublished), and the canary, *Serinus canarius* (Mulligan, Nottebohm, and Neal, unpublished).

In the case of the Chingolo, it is conceivable that after the pair bond has been established, the female's hormonal reactions are to a large extent conditioned by the song of its mate. If this is so, the presence within audible range of a number of Chingolos singing in a manner very similar to that of its own mate should multiply the effect of the latter's song. This presumably could result in a more effective integration of the pair's reproductive behavior and an earlier ovulation, all leading to greater reproductive success. This kind of effect, in fact, has been suggested for some of the more colonial species of birds (Lott et al. 1967).

If we accept the plausibility of this kind of interpretation, it is easy to see how those individuals singing more than one theme would be able by this means to attach the positive valence of their song to a greater section of the auditory environment, i.e., to more themes sung by other neighboring males, when the latter is not homogeneous. The fact that only 19 out of 523 birds were observed singing more than one theme does not allow us to draw a realistic estimate of the incidence

of this phenomenon. Most of the individuals included in this study were not observed over a long enough period of time to exclude the possibility that they included more than one theme in their repertoires. This very restriction does not allow us to tell whether the incidence of individuals singing more than one theme varies from area to area and according to local auditory environment. It would be very interesting to know if the individuals singing the less common themes have a lower reproductive success than those males singing the more "popular" themes.

THE EVOLUTIONARY SIGNIFICANCE OF DIALECTS

The meaningfulness of dialects in Chingolo song becomes considerable if we make a few assumptions (Marler and Tamura, 1962; Konishi, 1965). The first of these assumptions is that birds hatched in an area will develop an auditory commitment to the song of that area: males will sing that song when they mature, and females will be selectively attracted to it when they reach breeding condition. Evidence on hand for a closely related species, *Zonotrichia leucophrys*, favors such an assumption in the case of males (Marler and Tamura 1964) and females (Konishi 1965). The second assumption is that birds hatched in a locality will tend to breed in that same general area. Evidence from ringing experiments to support this assumption is still lacking. That males are permanently attached to their natal areas, however, is indirectly suggested by the presence of a critical period for song learning in *Z. leucophrys*. Males acquire their "song template," which corresponds to the local dialect, during their first 100 days of life, while they are still strongly attached to their hatching place (Marler and Tamura 1964). This by itself would seem to commit them to their hatching area, since dialects in this species are stable and homogeneous markers of populations in different localities (Marler and Tamura 1962). If males did not develop a site commitment at the time they acquired their song template, song "dialects" would be found randomly mixed in the song of individuals over vast areas, which is not the case.

Zonotrichia capensis is a widely distributed species ranging from the state of Chiapas in México to the very tip of South America (Chapman 1940). Of northern origin, it has invaded an amazing variety of habitat types, from tropical lowlands at sea level to the high Andes, up to 15,000 ft. This obviously could not have been done within a panmictic

population. The breeding biology and the very physiology of survival must be different in different habitats. Life zones change quickly with altitude, coastal proximity, susceptibility to flooding, and soil types. Yet as we move through this variety of habitats, with the exclusion of few, everywhere we meet the ubiquitous *Z. capensis*. Although it has subspeciated, morphologically delineated subspecies are described for areas as large as nations (Chapman 1940). Within the area allotted to each of the subspecies described there are many habitat types too varied to make the selection of "Jack of all trades" genotypes advantageous.

Natural selection is most effective when it can act over stable populations occupying areas of well defined ecological characteristics. Under these circumstances the optimal genotype for each ecological area can emerge and be maintained. Any system favoring a restriction on the size of the gene pool and the latter's long term identification with an ecological area must have received strong selective encouragement. This must have been particularly true for an invading species taking over environmental possibilities which were not fully exploited.

A system of song dialects such as observed in the Chingolo may have emerged to limit gene pools and allow for fast and stable adaptation to newly colonized habitats. That song dialects are not accompanied by gross morphological changes (even assuming that the latter evidence was thorough and convincing, which it is not) should not concern us. The criterion for the establishment of subspecies is highly arbitrary and classically has been restricted to measurable aspects of external morphology. Some of these, however, will change only when under strong selection. Plumage, which is often associated with many behavioral characteristics indispensable for intra-specific communication, is likely to respond only to a selection strong enough to overcome what might well be a strong behavioral conservatism. For a species such as *Zonotrichia capensis*, which except for its head markings is rather inconspicuously colored, moving from one habitat to another probably meant meeting new physiological stresses more than anything else. It would seem likely that physiological subspeciation will be found closely associated with dialect formation.

Let us assume that in *Z. capensis*, as has been described for *Z. leucophrys*, males and females develop a commitment to the song of the area where they are born, and that

birds hatched in an area will breed within that same general area. How does such a system allow for a stable and restricted gene pool? How are the boundaries of such a gene pool set? Most environments change gradually into a succession of habitat types or life zones with all possible intermediate habitats represented as well. There are no discrete boundaries between habitats as there are between states. These boundaries have to be created unless we want to have an indefinite gene pool with varying rates of gene flow. Song dialects can do precisely this. They can treat a gradually changing environment as a series of discrete steps. Each step delimits a gene pool, a population, a restricted habitat type or life zone. The flow of genes occurs freely within the dialect or sub-dialect area, but is restricted at its boundaries. The population in a geographic area is no longer a potential panmictic continuum, but rather a mosaic of gene pools with emphasis on the boundaries between them. Huxley (1940) called such a system one of "stepped clines." In the case of the Chingolo, even over a few hundred meters of mountainside, selection may be acting to encourage non-interbreeding of the extremes of two populations via deme recognition through dialects.

Gene flow of course is also limited when individuals do not move away from their birthplace for breeding. In still other species this problem is altogether circumvented by their restriction to well defined habitat types and environmental conditions. When a species that shows a broad distribution over a range of ecological variables has neither of these alternative breeding or distribution mechanisms for limiting gene flow, we may well look for isolating mechanisms such as song dialects. Indeed, song dialects might in some cases lead to sympatric sub-division of gene pools.

One may argue that dialects as described in the Chingolo need have no evolutionary significance, that they are merely a result of the restricted exchange of individuals between geographically discrete populations. Such a view would be tenable only when physical discontinuities prevent populations from coming into contact. Such an interpretation becomes untenable for species spread uninterruptedly over broad ecologic continua.

Many problems have been presented during the length of this discussion, many questions opened. Tests for some of the hypotheses offered here will have to wait until the biology of the Chingolo is better known. Information is available on neither the dy-

namics of its populations nor their genetic constitution. Not even their alleged non-migratory status (Chapman 1940) has been satisfactorily established. It will also be indispensable to know the circumstantial and physiological correlates of the presumed song learning in this species, and the effects of song on the female's behavior. Even at this stage one is tempted to forecast that dialects will be proven pivotal in the invasion by some avian species of broad geographic continua which include a variety of habitat types.

SUMMARY

Study of the song of the Chingolo sparrow, *Zonotrichia capensis*, was carried out in Argentina between September and December 1966. A total of 523 individuals were included in this survey. The song of the Chingolo is made up of two parts: the first determines the identity of the theme sung, and the second identifies the dialect area to which it belongs. It was possible to establish the existence of several dialect areas: 1) Eastern pampas, 2) Paraná delta, 3) Tandil-Azul highlands, 4) Northern Mesopotamia, and 5) a series of dialects in the Sierra Grande of Córdoba. Each of these dialect areas seems to correspond to an ecological area or life zone.

As a rule, several themes are present in a population of chingolos. This by itself would result in considerable song heterogeneity. However, the homogeneity of Chingolo song in any particular locality is increased by the numerical preponderance of one or two themes. This phenomenon is in some cases so marked as to lead to the emergence of true "sub-dialects." At the neighborhood level it is common to find several individuals sharing the same theme.

It is hypothesized that a system of dialects such as the one described here may serve to maintain the identity of the gene pools of populations adapted to local habitat conditions. This function of dialects may be particularly widespread among species that are distributed in a continuum over vast geographic areas. It is suggested that dialects of this nature may be instrumental in the emergence of stepped clines. Other aspects of the system of dialects described may maximize the influence of song on the breeding biology of female chingolos.

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