ANALYSIS OF SYMPATRY OF GREAT-TAILED AND BOAT-TAILED GRACKLES

By Robert K. Selander and Donald R. Giller

Although the biological species concept has been adopted by almost all zoologists, opinions as to the systematic status of most allopatric populations continue to rest largely on application of the morphological criterion of relationship. Working with allopatric populations, the systematist rarely has sufficient field data on behavior and ecology; and, for practical reasons, he must base many taxonomic decisions on morphological evidence alone. It follows that where morphological divergence has not kept pace with the evolution of physiological, ecological, or ethological isolating mechanisms, allopatric populations that have reached the species level of differentiation may go unrecognized as such. Only through comparative biological studies, combined, where possible, with investigations in zones of contact, can the true status of these populations be determined (Miller, 1955:3).

Since about 1900, steadily increasing numbers of morphologically similar allopatric populations have been considered conspecific by systematists. In this country, Ridgway and Hellmayr took the lead in "lumping" a large number of nominal avian species into a lesser number of polytypic species. The result, as recently noted by Mayr (1957: 383), has been "a simplification of classification which is not only of practical help to the working taxonomist but also actually aids the understanding of distribution, ecology, and phylogeny." It is to be expected, however, that a number of populations currently listed as subspecies in our classifications are, in fact, species, that is, are reproductively isolated from related populations (Vaurie, 1955). An excellent example is provided by the grackles of the genus *Cassidix*.

In all recent classifications of *Cassidix* (for example, the A.O.U. Check-list, 1957), the form *major*, which inhabits coastal marshes of the southeastern United States, is regarded as a race of *mexicanus*, a grackle ranging from Texas, New Mexico, and Arizona south through México and Central America to northwestern Perú and the Caribbean coast of Colombia. These two grackles are so similar morphologically that museum systematists have generally accepted without question their designation as subspecies by Ridgway in 1901. However, over 30 years ago, Townsend (1927) and Brooks (1928, 1932), both of whom were familiar with the two birds in the field, called attention to differences in vocalizations and claimed that these grackles are more distantly related than their morphological characters might suggest. They were also considered specifically distinct by Harper (1934), "by reason of significant differences in both morphology and behavior, which I expect to discuss in detail in a subsequent paper." The promised discussion failed to appear, however; and, with the description, in 1938, of a Texas race, *prosopidicola*, intermediate in size between, and reportedly intergrading with, *mexicanus* of México and *major* of Louisiana, the problem of the systematic relationship of these grackles seemed finally resolved. But our recent field studies in southeastern Texas and southwestern Louisiana have revealed that *major* and *mexicanus* are sympatric without interbreeding. The supposed races are actually distinct biological species differing markedly in behavior and in ecology.

This report deals with geographical and ecological distribution, morphology, and certain aspects of behavior and breeding biology of the two species in their narrow zone of sympatry. A comprehensive ethological study of these grackles will be presented elsewhere.

MATERIALS AND METHODS

Contact between *C. mexicanus* and *C. major* was first studied on the coastal lowlands of the Gulf of Mexico from June 2 to 10, 1959, in the region between Lake Charles, Louisiana, on the east, and Houston, Texas, on the west. Additional studies of *C. major* were made in this area and elsewhere in southern Louisiana from July 8 to 15, 1959, and from March 30 to April 4, 1960. Our collection of specimens from the zone of sympatry includes 154 study skins of adult, first-year, and juvenal individuals, 101 nestlings preserved in alcohol, and 23 complete or partial sets of eggs, most of which have been deposited in the Museum of Vertebrate Zoology, Berkeley. For comparative purposes, we have had available specimens of all races of *C. mexicanus*, including a large collection of skins and skeletons of *C. mexicanus prosopidicola* from the Austin region, Travis County, south-central Texas, a series of skins of *C. major* from eastern Louisiana, and series of skeletons of *C. major* from Florida and of *C. mexicanus mexicanus* from Veracruz, México.

Recordings of vocalizations were made at a tape speed of 15 inches per second on a Magnemite 610, employing an Electro-Voice 630 microphone mounted on a 24-inch parabolic mirror. Sound spectrographs were made on a Kay Electric Company Sonagraph, using the "high-shape" filter setting.

SPECIES OF THE GENUS CASSIDIX

The genus *Cassidix* includes four species: the Boat-tailed Grackle (*C. major*), the Great-tailed Grackle (*C. mexicanus*), the Slender-billed Grackle (*C. palustris*), and the Nicaraguan Grackle (*C. nicaraguensis*). The latter two forms have very small ranges and are poorly known (Hellmayr, 1937). *Cassidix palustris* formerly occurred in marshes in the vicinity of Mexico City, but it has not been reported in recent years and is probably extinct; only a few study skins have been preserved and nothing has been recorded concerning its behavior and ecology, except that it inhabited marshes. *Cassidix nicaraguensis* is a small species which Hellmayr (1937:94) regarded as "very distinct . . . although allied to *C. palustris*." It is apparently limited in distribution to the shores of Lake Managua and Lake Nicaragua, Nicaragua, and, presumably, it is also a marsh-dweller.

GEOGRAPHIC VARIATION

Cassidix mexicanus is a common and widely distributed species in which several subspecies have been distinguished, although a comprehensive study of geographic
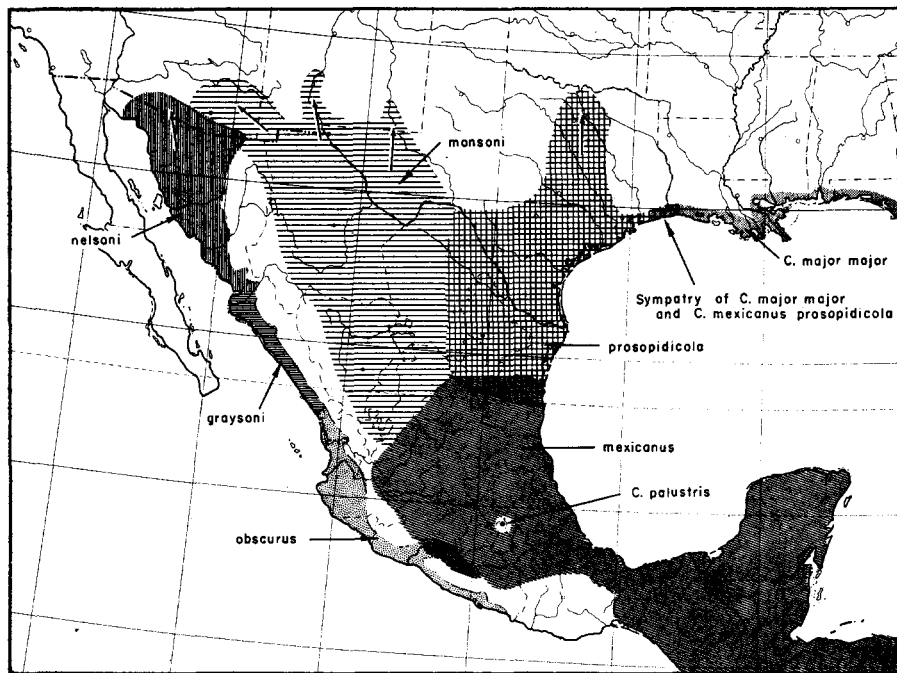
Fig. 1. Distribution of *Cassidix major major*, *C. palustris*, and the subspecies of C. *mexicanus*, based on recent check-lists. Reported intergradation between *C. m. prosopidicola* and *C. m. mexicanus* and between the latter race and *C. m. obscurus* is indicated by overlapping patterns. The race *C. m. monsoni* is similar morphologically and behaviorally to *C. m. mexicanus* and *C. m. prosopidicola*, with which it presumably intergrades.

variation has not been made. The breeding ranges of the races are outlined in figure 1, which is based in large part on the A.O.U. Check-list (1957) and part two of the Mexican Check-list (1957). The subspecies in contact with *C. major* is *C. mexicanus prosopidicola* (Lowery, 1938), with type locality at Brownsville, Cameron County, Texas. For descriptions of other subspecies of *C. mexicanus*, the reader is referred to papers by Ridgway (1902) and Phillips (1950).

Cassidix major also varies geographically but, like *C. mexicanus*, has not been studied thoroughly from a systematic standpoint. Two races are currently recognized (A.O.U. Check-list, 1957:538): *C. major major*, a brown-eyed form ranging from southeastern Florida west along the coast of the Gulf of Mexico through Mississippi and Louisiana to extreme southeastern Texas (type locality, New Orleans, New Orleans Parish, Louisiana; Lowery, 1938:4); and *C. major torreyi*, a yellow-eyed race breeding along the South Atlantic coast from Georgia north to southern New Jersey and wintering from Virginia south to Florida (type locality, Chincoteague, Virginia). Iris color seems to be the principal character distinguishing the two populations, but, in addition, *C. major torreyi* is reported (Harper, 1934, and Lowery, 1938:6) to differ in having a longer wing and a more greenish head, back, and breast in the male. We wish to stress the fact that the extent to which the two races of *C. major* overlap in characters through individual variation has not been determined, for Harper (*op. cit.*) gave no indication of ranges of variation in the populations which he studied.

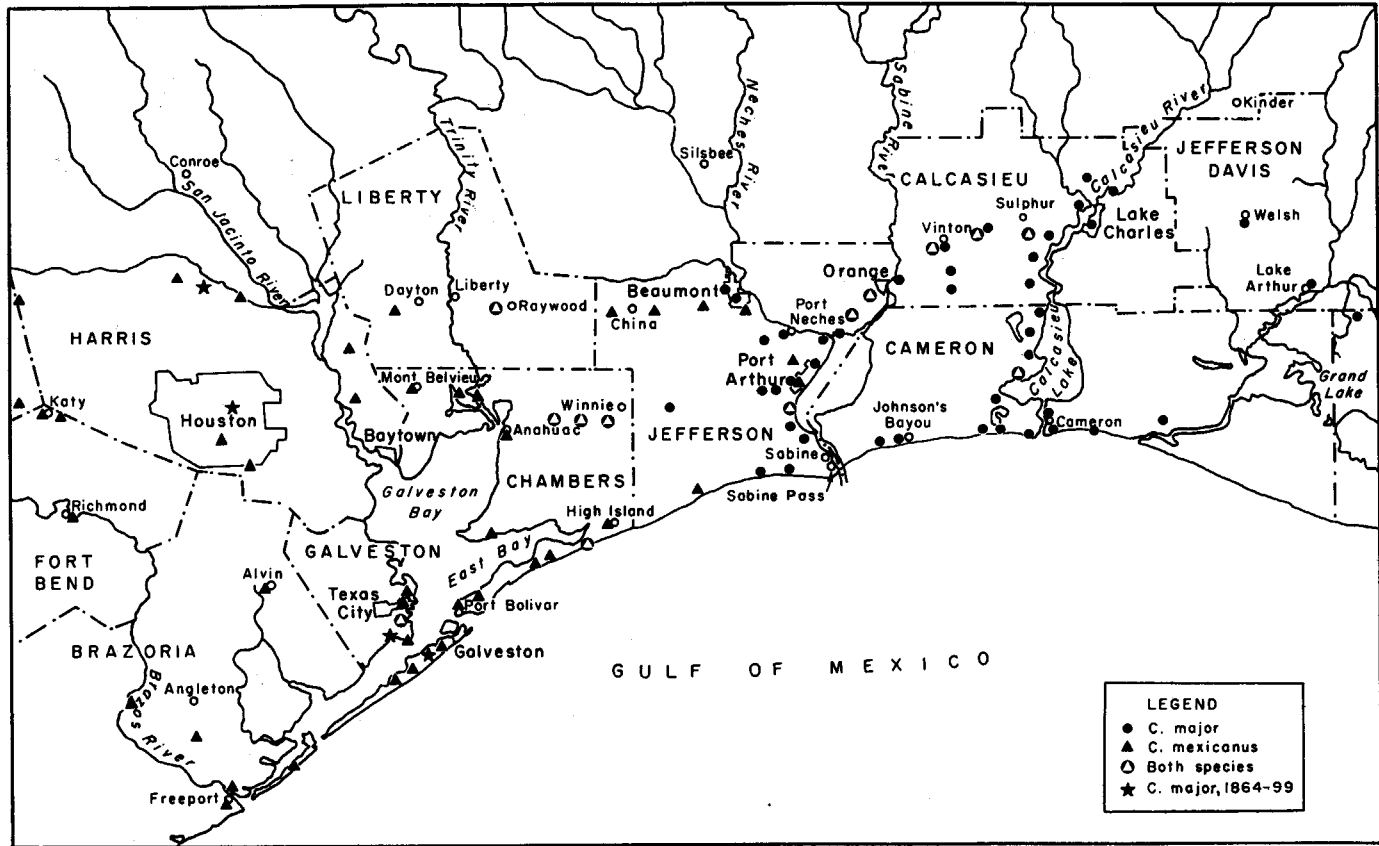A third nominal race, *C. major westoni*, described by Sprunt (1934) from interior

Fig. 2. Distribution of *Cassidix mexicanus* and *C. major* in southeastern Texas and southwestern Louisiana in late spring and summer.

Florida (type locality, St. John's River marshes, Indian County), was found by Lowery (1938:6) to be indistinguishable from *C. major major*, except, perhaps, by average greater wing length. However, until recently (1958) Sprunt (1954:443–445) continued to recognize *westoni*; but, unaccountably, he referred birds from the South Atlantic coast to *C. major major*. The name *westoni* was applied by Sprunt (1954) to brown-eyed populations of interior Florida, which he contrasted with yellow-eyed coastal birds, referring to the latter as *C. major major*. Yet elsewhere on the same page, there is the contradictory statement that *C. major major* occurs in Florida only in the extreme western part west of the Apalachicola River. Further confusion results from Sprunt's failure to indicate the seasonal status of the yellow-eyed birds in Florida and also from his concluding statement (p. 443) that *westoni* "is the bird of the inland lakes and marshes, but the situation is still not quite clear, and overlaps in range occur, as well as the penetration of *westoni* farther up the Atlantic coast than was originally thought."

From these comments by Sprunt, we are unable to form a clear picture of geographic variation in Florida, especially as regards eye color. But inasmuch as D. J. Nicholson (personal communication) reported that yellow-eyed birds do not occur in Florida in the breeding season, we presume that yellow-eyed birds reported in Florida are wintering individuals of *C. m. torreyi*. Pending a comprehensive study of the situation, we follow the A.O.U. Check-list in considering *C. major westoni* a synonym of *C. major major*.

GEOGRAPHIC DISTRIBUTION IN THE ZONE OF SYMPATRY

Records of the two species in southeastern Texas and southwestern Louisiana in late spring and summer are shown in figure 2. The easternmost definite breeding record for *C. mexicanus* is near Sulphur, Calcasieu Parish, Louisiana (see fig. 3 and beyond). *Cassidix major* has been found breeding as far west as central Chambers County, Texas, but it may nest sparingly even farther west, as a first-year male of this species was seen near Texas City in July, 1959, and we have recently received reports of breeding on Galveston Island. Between Sulphur, Louisiana, and Galveston County, there is, at the present time, a zone of sympatry approximately 100 miles in width. A detailed map showing records of occurrence in the eastern part of this zone in the breeding season is presented in figure 3.

As the distribution maps (figs. 2 and 3) indicate, the zone of sympatry is restricted to the Gulf coastal plain, a fact which is understandable considering the habitat preferences of the two grackles and the distribution of vegetation types in this region (fig. 4). The coastal plain proper is bounded on the north by pine-oak and longleaf pine forests (Tharp, 1952:fig. 3), vegetation types which are not inhabited by either species of *Cassidix*. In the zone of sympatry, *C. mexicanus*, extending eastward on the coastal prairie of Texas, meets *C. major*, the distribution of which is largely confined to coastal marshes, and the two grackles occur together in an area of transition between these two major vegetation types.

Seasonal status.—*Cassidix mexicanus* is a permanent resident throughout most of its range, but there appears to be a southward withdrawal in winter of some birds from northern Texas, Arizona, and New Mexico (Mexican Check-list, 1957:280). Also, this species occurs occasionally in winter along the Gulf coast east of its breeding range as far as Avery Island, Iberia Parish, Louisiana, where five female specimens (L.S.U. 999, 2279, 2280, 3762, and 3763) were obtained by E. A. McIlhenny between November 24 and March 5, 1938 to 1940.

Cassidix major torreyi moves south in winter from the northern part of its breeding range, wintering from the Virginia coast south to Florida (A.O.U. Check-list, 1957:538). A winter exodus of *C. major major* from the coast of Mississippi, presumably into
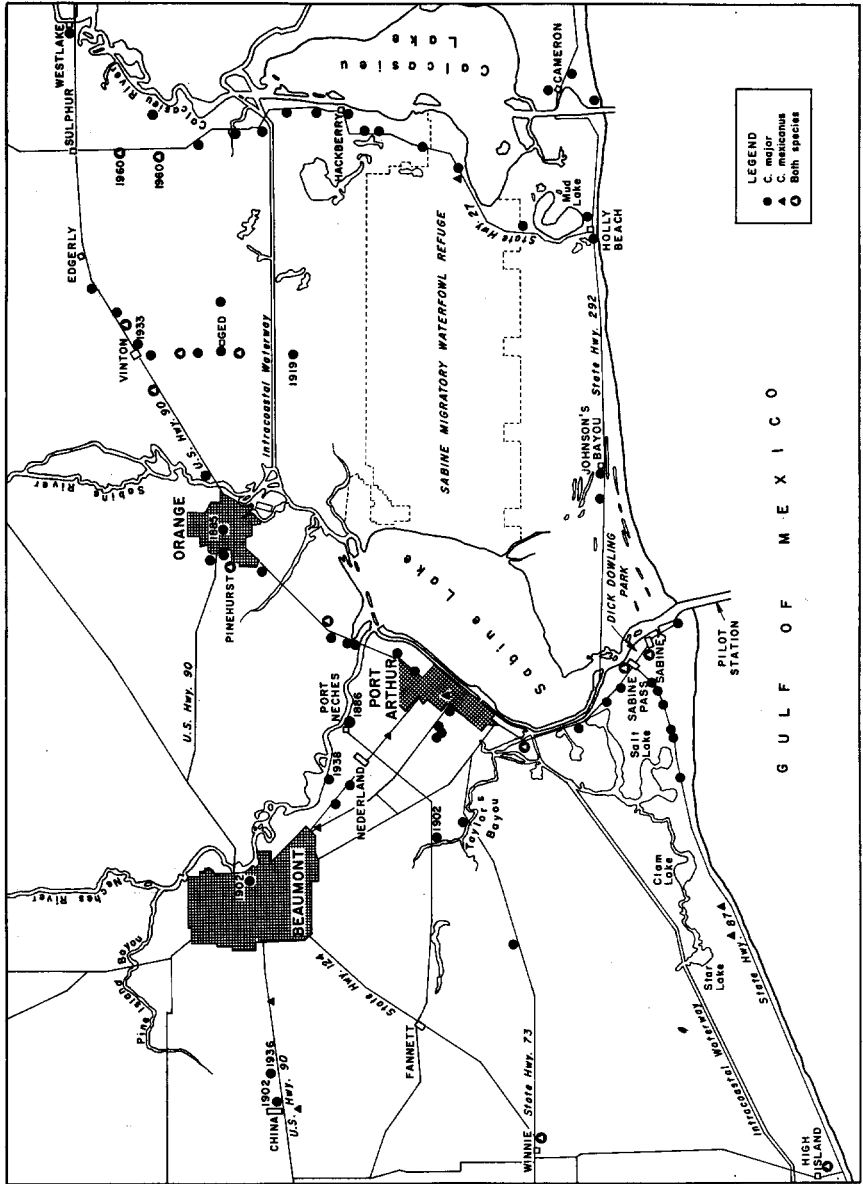
Fig. 3. Eastern part of zone of sympatry between *Cassidix mexicanus* and *C. major*.
All records in late spring and summer are shown.

Louisiana, has been reported (Burleigh, 1944:465), and there is evidence that this grackle occurs, at least in small numbers, southwest of its breeding range along the Texas coast. Possibly there is a general movement of this species from southeastern Texas in the winter, as Nehrling (1896:304) noted that it rarely appears in that area before mid-March. We have examined an adult male of *C. major major* from Sandy Point, 30 miles south of Houston, taken on October 27, 1937; and R. Hauser collected three adult males, one first-year male, and one first-year female of this form 7 and 8

miles north-northwest of Galveston on December 25, 1956, and February 3, 1957. Hellmayr (1937:90) mentions a series of 12 specimens of this grackle collected in February, 1894, by J. G. Parker, Jr., at Port Lavaca, Calhoun County, 140 miles southwest of the breeding range. We have not examined these specimens, but measurements furnished by E. R. Blake indicate that not all are *C. major*. The tails of two of the five adult males in the series measure 207 and 208 mm., which would indicate that they are *C. mexicanus*. Three other adult males have tails 177 to 185 mm. in length and are almost certainly, *C. major*, as is a first-year male with a tail length of 155 mm. Hellmayr's identifications of females in this series have not been checked. Finally, there is a report by Baird (1858:55) of a specimen of *C. major* from Brownsville, Texas, taken prior to 1858.

Recent extensions of range.—In Texas, *C. mexicanus* has extended its range northward in this century, as it has also in Arizona and New Mexico since about 1913 (Phillips, 1950; Ligon, 1926; Compton, 1947). In Texas in 1864, it was not found north or east of the Nueces River (Dresser, 1865:493). According to Strecker (1912:45), the species bred only as far north as San Antonio in 1912, although "stragglers" were seen at Waco as early as 1904 and 1906. By 1925, the northern limit of the breeding range of the species had shifted to Austin, where it was a "rare and local summer resident" from early March to July and reportedly moved southward and eastward to the Gulf coast in winter (Simmons, 1925:185). Local observers claim that *C. mexicanus* became established as a common resident in the Austin region about 25 years ago; and today it is abundant there and breeds at localities several hundred miles to the north (see fig. 1). It reached Fort Worth in April, 1944, and was nesting there by 1952 (Kincaid, 1958). It was first recorded in Dallas in 1947, where nesting records also date from 1952. The species has not yet penetrated the Texas Panhandle as a breeder, but a male was reported near Alva, Oklahoma, on June 29, 1953, and breeding records from that state may be expected at any time. In northeastern Texas, breeding is reported in Van, Smith County, since 1956 or 1957, and it was first noted in Commerce, Hunt County, in 1949. In western Texas, there is also evidence of a northward advance, but the movement is apparently not on a scale equivalent to that occurring in the prairie country of the central-northern part of the state. To date, the species has not become established on the Edwards Plateau in central Texas.

Coincident with the northward advance of *C. mexicanus* in the Blackland Prairie of central and northern Texas, there has been either an actual northeastward extension of breeding range in the prairies along the Gulf coast or a very marked increase in numbers throughout an already inhabited area. Of the two possibilities, the former seems more probable. In 1864, Dresser (1865:494) reported that *C. mexicanus* ranged no farther east or north in Texas than the Nueces River and the Corpus Christi area, where other early naturalists (Sennett, 1878:28, Chapman, 1891, and Rhoades, 1892:109) found it in large numbers in the late 1800's. Strecker (1912:45) indicated Corpus Christi as the northeastern limit of range on the coastal plain in 1912, but at that time it actually occurred somewhat farther northeast, for Carroll (1900:346) had found it "abundant" in Refugio County, about 40 miles northeast of Corpus Christi, between 1896 and 1900; and it was reportedly common in Victoria in 1907. Today, *C. mexicanus* is an abundant resident throughout the Gulf coastal plain of Texas to extreme southwestern Louisiana.

In the same period, 1864–1912, only *C. major* was present in the Galveston-Houston region and in the Beaumont, Orange, Port Arthur, and Sabine area (Nehrling, 1882:168, 1896:304; Dresser, 1865:494; Strecker, 1912:45), where *C. mexicanus* now also breeds. On the basis of these reports, we presume that the two species were not in geographical contact in 1912.
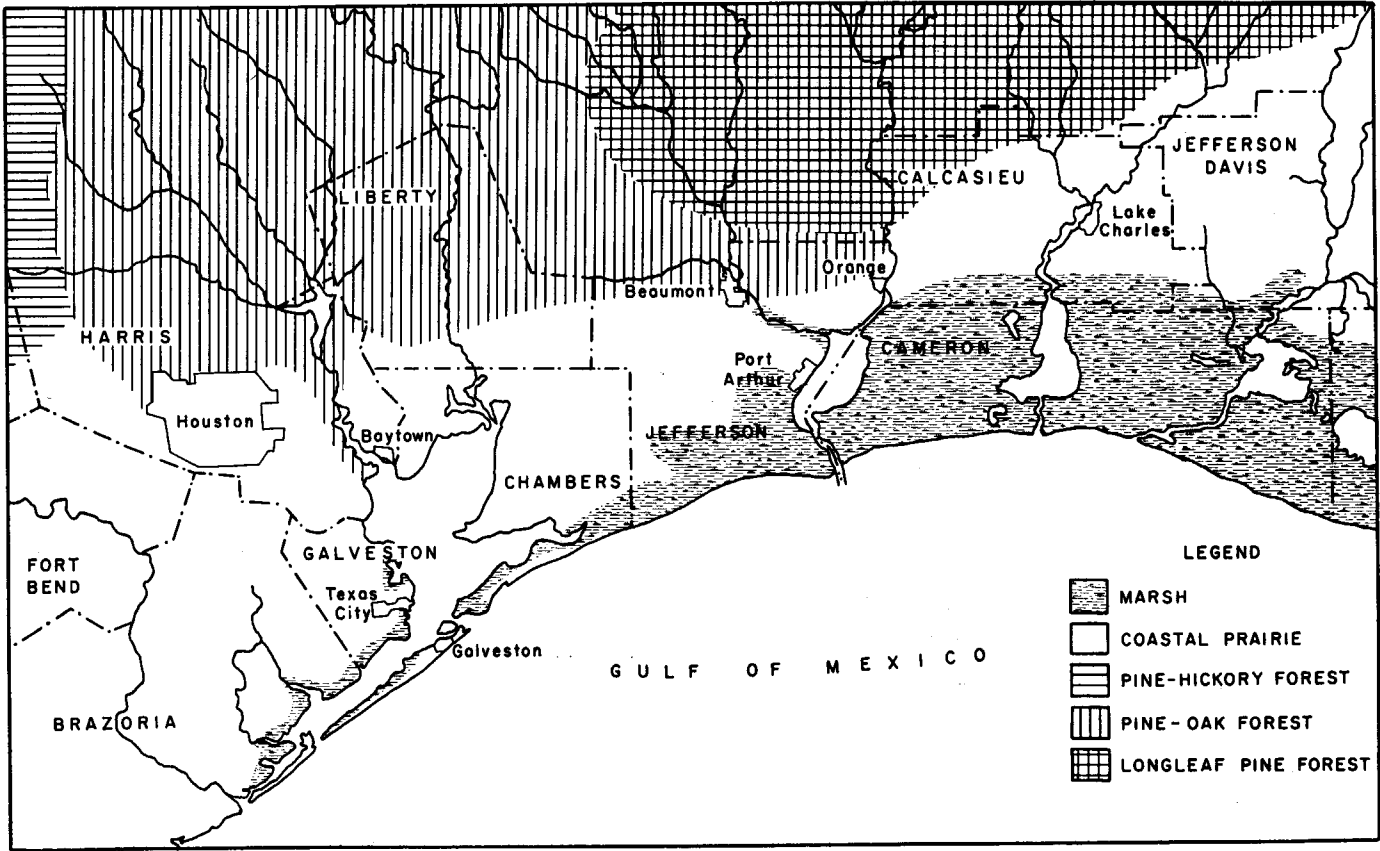
Fig. 4. Distribution of major vegetation types in southeastern Texas and southwestern Louisiana.

LEGEND

▨ MARSH

☐ COASTAL PRAIRIE

▤ PINE-HICKORY FOREST

▥ PINE-OAK FOREST

▦ LONGLEAF PINE FOREST

Specimens taken by Lowery in 1938 demonstrate that *C. mexicanus* had reached the Houston-Galveston region and was nesting with *C. major* at High Island, 17 miles east of Galveston, in 1938. Sometime between 1938 and 1959, *C. mexicanus* moved still farther east and reached Cameron and Calcasieu parishes in southwestern Louisiana. Records for this region were summarized by Oberholser in 1938; of special interest is the fact that he found *C. major* "abundant" in June, 1933, at Toomey, Vinton, and Cameron Farm, 14 miles south of Vinton, but he did not record *C. mexicanus*. In 1959, *C. mexicanus* predominated in that area; and our report constitutes the first breeding record of this species for Louisiana. Because Mr. E. C. Fontenot reported (in conversation) that *Cassidix* markedly increased in numbers in farmland near Vinton, Calcasieu Parish, in 1956, we suspect that *C. mexicanus* may have invaded southwestern Louisiana in the past four or five years.

The northward and eastward extension of range of *C. mexicanus* in Texas occurred in a period of major vegetation changes that have been discussed by Cook (1908), Tharp (1926, 1939), and Price and Gunter (1943). Much of southern Texas, including the coastal region north of the Nueces River, was true prairie until 1870 or 1880. In the decades that followed, mesquite and other elements of the brush or chaparral, together with oaks and other woody vegetation, replaced grassland over large areas, the spread being attributed in large part to intensive cattle grazing, which eliminated prairie fires, and to actual dissemination of seeds by cattle (Cook, *op. cit.*; Tharp, 1939:8). Between 1870–80 and 1943, the area of heavy brush is said to have spread at least from Kleberg County northeast to Matagorda County, a distance of 175 to 200 miles. In more northeastern sections of the coastal plain, large tracts of prairie were occupied by oaks, pines, hackberry, and other woody types (Tharp, *op. cit.*:71–72). In this period, mesquite also is believed to have spread north from southern Texas to the Panhandle (Bogusch, 1950).

The establishment of brush in large areas in southern Texas was undoubtedly beneficial to the grackle populations, principally because it provided elevated nesting sites in areas where none previously existed. However, the northward and eastward extension of range of *C. mexicanus*, together with an increase in abundance throughout its range, was more directly dependent on the establishment of settlements and farms in the prairie country. With irrigation and the planting of shade trees and crops, particularly grain, suitable habitat was provided in previously uninhabitable prairie or brushland in central Texas and along the Gulf coast.

While the recent expansion of range of *C. mexicanus* in the southwestern United States has been facilitated by man's activities, particularly irrigation and planting of trees, in prairie and semi-desert country, additional factors may also be involved, for other subtropical vertebrates, some of which are not clearly dependent on man-made habitats, notably the pigmy mouse (*Baiomys taylori*), show comparable patterns of range extension within the present century (Hunsaker, Raun, and Swindells, 1958).

Sprunt (1958:365–366) has reviewed evidence suggesting a northward extension of range of *C. major torreyi* along the Atlantic coast in recent years, but it is worth noting that there has been no advance of the breeding range of this species westward along the Gulf coast in Texas. *Cassidix major major* has occupied its present range in southeastern Texas since ornithological records for that area first appeared; for example, Dresser (1865:494) found it in the Houston-Galveston area in 1864, Nehrling (1882:168) reported a breeding colony 30 miles northwest of Houston in 1881, and there are breeding records from Beaumont, Orange, and Port Neches in 1885 and 1886. To judge from early reports, it is now less common in the Houston-Galveston area than it was in the 1880's, where it seems to have been replaced to some extent by *C. mexicanus*.

To sum up, *C. mexicanus* apparently first made contact with *C. major* in the Houston-Galveston area sometime between 1912 and 1938, following a range extension of the former species along the Gulf coastal plain from southern Texas. Between 1938 and 1959, the zone of sympatry broadened considerably as a result of an eastward invasion of *C. mexicanus* from the Houston-Galveston region into prairie in southwestern Louisiana. This species may have reached Louisiana as late as 1956, and its eastward advance may be expected to continue.

Data added since completion of the study.—Since this paper was submitted for publication, the supposition that *C. major* breeds no farther southwest on the Texas coast than the Galveston Bay area has proved to be erroneous by the discovery of a small population nesting in marshes bordering San Antonio and Matagorda bays on the central Gulf coast 100 to 140 miles southwest of Galveston and only 70 miles northeast of Corpus Christi. This new finding increases the likelihood that *C. major* was in geographic contact with *C. mexicanus* prior to establishment of the extensive area of sympatry east of Galveston and Houston.

Credit for the extension of the known range of *C. major* is due Mr. Fred Webster and Mr. Edgar Kincaid of Austin, who obtained sight records near Green Lake and Port Lavaca, Calhoun County, in April, 1960. Visiting this area on July 7, 1960, we found a dozen individuals of *C. major*, including two juveniles, in a wet meadow bordering small areas of marsh near the mouth of the San Antonio River between Tivoli and Green Lake. *Cassidix mexicanus* was abundant at this locality and in farmed prairie land all along Texas Highway 35 from Rockport, Aransas County, northeast to Bay City, Matagorda County. We failed to see *C. major* at Port Lavaca, but we collected an adult male, together with a large series of *C. mexicanus*, midway between Port Lavaca and Palacios.

The ecological relationship of the two grackles in this region is similar to that in the more extensive zone of sympatry to the northeast. Whether or not this small population of *C. major* is isolated geographically from that to the northeast remains to be determined, but between Matagorda Bay and Galveston Island there may be a disjunction in range owing to an absence of marshes. At Freeport we found only *C. mexicanus* on July 7.

## COMPARATIVE MORPHOLOGY

SIZE AND PLUMAGE COLOR

Specimens were segregated with respect to age according to criteria previously described for *C. mexicanus* (Selander, 1958) and related icterids (Selander and Giller, 1960), and all comparisons involved birds of similar age.

Adults.—Measurements of adult males and females are presented in figure 5, in which samples from the zone of sympatry are compared with those of *C. mexicanus prosopidicola* from the Austin region, Travis County, central Texas, and of *C. major major* from southeastern Louisiana. *Cassidix mexicanus prosopidicola* averages significantly larger than *C. major major* in all dimensions except length of tarsus, middle toe, and bill. Overlap is minimal in wing length, tail length, and weight, and it is somewhat less marked in males than in females. Comparing body proportions (table 1), and taking percentage difference in cube root of weight as a standard of difference, it is seen that *C. major major* has a relatively shorter tail and a longer tarsus, middle toe, and bill.

Degree of sexual dimorphism in size is greater in *C. mexicanus prosopidicola*. The mean percentage difference between adult males and females for eight characters of size are 21.7 per cent for *C. mexicanus* and 19.5 per cent for *C. major*, using measurements of specimens from the zone of sympatry.

Color differences between adult males of the two species involve distribution of

glossy purple or violet. In *C. mexicanus* this color extends posteriorly from the head and breast over much of the abdomen and flanks and onto the mid-back and humeral coverts; it grades to a greenish blue on the posterior parts of the flanks, abdomen, and back. In *C. major,* the glossy purple is less extensively distributed posteriorly, the mid-back region, humerals, abdomen, and flanks being more conspicuously greenish blue.
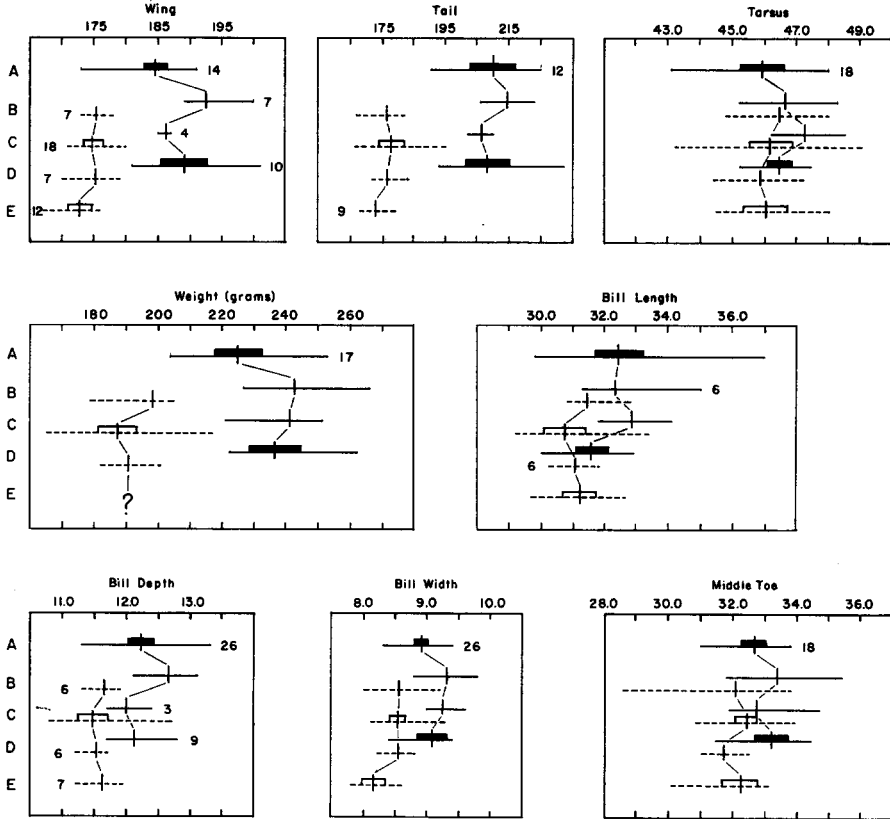
ADULT MALES

Fig. 5. Measurements of *Cassidix mexicanus* and *C. major* from zone of sympatry and adjacent areas, showing sample size, mean, range, and twice standard error of mean. Letters designate localities, as follows: A, Austin region, central Texas; B, Chambers County, Texas; C, Jefferson and Orange counties, Texas; D, Calcasieu and Cameron parishes, Louisiana; E, southeastern Louisiana. Solid horizontal lines and bars, *C. mexicanus*; dashed lines and open bars, *C. major*.

In addition, there tends to be less of this glossy color on the abdomen and flanks, as well as on the shanks and under tail coverts. The net effect is that *C. mexicanus* is more uniformly colored, but the difference is subtle and individual variation is such that specimens of the two species are, on the basis of color alone, sometimes indistinguishable. We note in passing that the glossy purple color tends to redden with age, producing rather marked post-mortem changes.

Adult females of *C. major* generally show less metallic or glossy color dorsally and are, on the average, a paler shade of brown ventrally than females of *C. mexicanus prosopidicola.* These differences are most apparent in fresh plumage and tend to become
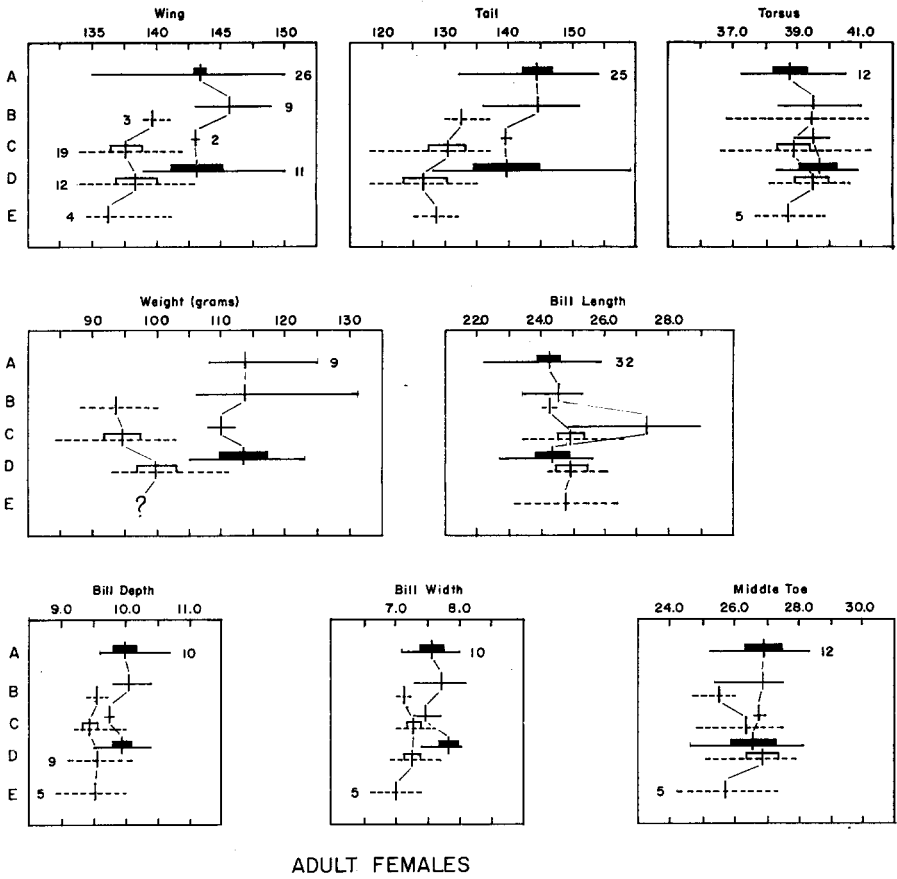
ADULT FEMALES

Fig. 5, continued.

obscured with wear of plumage late in the breeding season. In our material collected in June, approximately 20 per cent of female specimens of either species cannot be identified correctly on the basis of color alone.

First-year birds.—Males of the two species in their first year (table 2) show greater overlap in size than do adult males, but an age difference in this regard is not apparent in females. On the basis of color, we are unable to distinguish first-year males of *C. mexicanus* and *C. major*, but first-year females show approximately the same degree of difference seen in adult females.

Juveniles and nestlings.—Comparing small series of juveniles from the zone of sympatry, we detected no constant differences in coloration, although dorsally the buff feather margins tend to be broader in *C. major*. Careful examination of large numbers of nestlings of all sizes failed to reveal any differences between the species with respect to color, distribution of natal down, pterylography of the incoming juvenal plumage, and such other features as arrangement of barbs on the palate and tongue.

Comparison of C. major with races of C. mexicanus.—In figure 6, average dimensions of *C. major major* and several subspecies of *C. mexicanus* are compared. The former is closely matched in size by *C. mexicanus obscurus* of Nayarit, and populations

TABLE 1

COMPARISON OF SIZE IN TWO SPECIES OF GRACKLES

(Percentage deviation of average measurements of *C. major major* from those
of *C. mexicanus prosopidicola*)

Item	Male adult	Male first-year	Female adult	Female first-year
Wing	—6.8	—5.0	—4.0	—4.0
Tail	—16.0	—12.1	—9.8	—9.7
Bill length	—3.8	—2.7	+1.7	+1.1
Bill depth	—5.8	—6.4	—4.8	—5.3
Bill width	—6.6	—14.4	—6.0	—5.2
Tarsus	—0.4	+1.4	—0.6	—0.6
Middle toe	—2.2	—5.2	—1.5	—3.4
Weight (cube root)	—6.6	—3.0	—5.3	—5.7
Mean, all items	—6.03	—5.93	—3.79	—4.10

of *C. mexicanus* from Sinaloa (*C. m. graysoni*) and Sonora (*C. m. nelsoni*) are in most dimensions even smaller than *C. major major*. Moreover, in the races *C. m. graysoni* and *C. m. nelsoni*, as in *C. major major*, the tail is disproportionately shorter than in *C. m. prosopidicola*. Similarly, in color *C. m. graysoni* and *C. m. nelsoni* show a degree of differentiation from *C. m. prosopidicola* and *C. m. mexicanus* which exceeds that shown by *C. major*. Females from Sinaloa and Sonora are decidedly lighter in color than other races of *C. mexicanus*, those of *C. m. graysoni* being "scarcely distinguishable" from *C. major* (Ridgway, 1902:241–242). In summary, the morphological characters studied provide no clue that *C. major* has diverged from *C. mexicanus* beyond the racial level.

TABLE 2

MEASUREMENTS OF FIRST-YEAR SPECIMENS

Form and locality	Number	Wing	Tail	Bill length	Tarsus	Weight (gm.)
C. mexicanus prosopidicola			Males			
Austin region	75–98[1]	174.5	178.9	30.93	45.89	183.0
		(165–188)	(165–200)	(29.2–34.8)[2]	(41.3–50.0)	(173–188)[3]
SE Texas–SW La.	3	176.3	175.7	31.33	48.37	206.3
		(174–181)	(170–184)	(30.4–32.9)	(47.6–49.2)	(199–214)
C. major major						
SE Texas–SW La.	5	165.8	157.2	30.10	46.54	166.8
		(163–168)	(153–162)	(28.5–31.0)	(44.9–47.6)	(157–171)
C. mexicanus prosopidicola			Females			
Austin region	38–62[1]	140.2	132.4	23.15	38.11	121.6
		(135–147)	(122–145)	(21.3–25.9)[4]	(35.1–40.5)	(117–126)[5]
SE Texas–SW La.	9	141.3	134.2	24.11	39.54	115.2
		(138–144)	(128–141)	(22.8–25.4)	(38.4–40.8)	(108–134)
C. major major						
SE Texas–SW La.	15	135.7	121.2	24.37	39.29	96.3
		(133–142)	(108–131)	(23.3–25.4)	(36.1–41.6)	(90–120)

[1] See Selander (1958:370–371) for standard errors of means.
[2] 7 specimens, June and July.
[3] 3 specimens, June.
[4] 38 specimens, August to March.
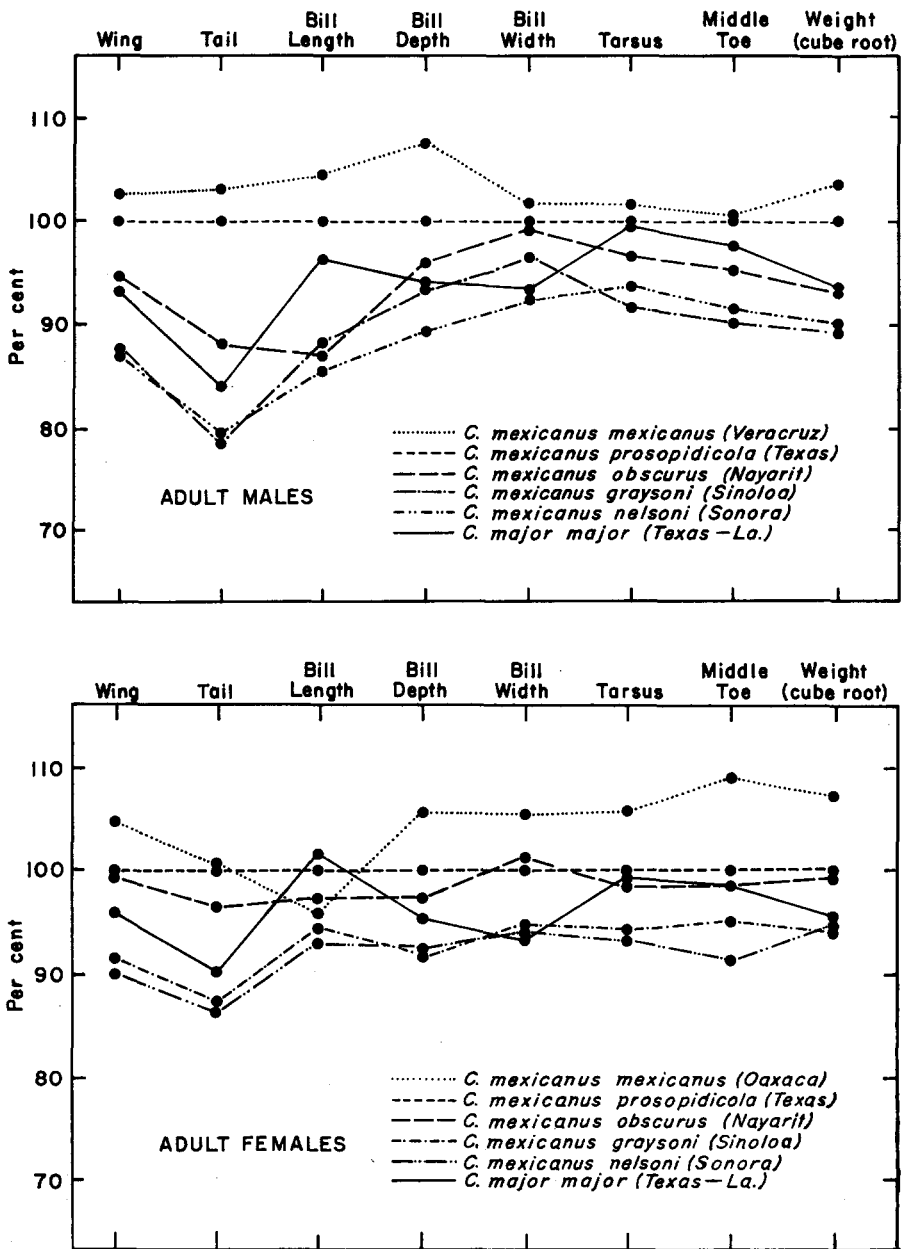[5] 6 specimens, February and March.

Fig. 6. Comparison of size in several races of *Cassidix mexicanus* and in *C. major major.*
Mean measurements of the different forms are plotted as percentages of those of
C. mexicanus prosopidicola.

IRIS COLOR

In all populations of *C. mexicanus*, iris color of adult birds is yellow, being intense or bright yellow in adult males but generally somewhat paler or less intense in adult females. There is some degree of geographic variation in shade, for we have noted that the iris of the race *C. mexicanus nelsoni* is less intensely pigmented than that of *C. mexicanus mexicanus* or *C. mexicanus prosopidicola*.

As described by Selander (1958:368–369), the bright yellow adult iris develops gradually over a period of months from a dull brown condition of juveniles, the transition involving a progressive loss of brown accompanied by an intensification of yellow pigment. In the Austin region, the iris reaches the adult color between January and April of the first year. Transitional stages are variously described as "dull yellowish brown," "pale brownish yellow," "grayish yellow," and "flat yellow of moderate intensity." Typically, yellow pigment first appears in the periphery of the iris, the brown pigment remaining longest around the pupil, where, even in fully adult birds, a few small flecks of brown or dark gray may persist.

In *C. major major*, adult iris color is highly variable but apparently never intense yellow. One typical condition in our material is that described by Lowery (1938:6) in which the inner part adjacent to the pupil is brown but the periphery is pale yellow or tan; but in many other birds the inner ring is definitely gray rather than brown. The iris color of juveniles is brown, as in the other species.

To analyze variation in iris color in adult and first-year specimens, we have established a scale of eight categories, defined as follows:

Category	Description
0	Uniform dark brown
1	Brown with darker brown flecks
2	Brown centrally, tan peripherally
3	Tan or dark gray centrally, very pale yellow peripherally
4	Tan or dark gray centrally, yellow peripherally
5	Pale yellow, often with many brown or gray flecks
5½	Intense yellow (males) or yellow (females), with a few small brown or gray flecks centrally
6	Intense yellow (males) or yellow (females); unflecked

TABLE 3

VARIATION IN IRIS COLOR IN SPECIMENS FROM THE ZONE OF SYMPATRY

	Number of specimens in each category							
	Categories							
Species, age, and sex	0	1	2	3	4	5	5½	6
C. major major								
Adult male	9	1		4	8	1		
Adult female	11	9	12	1		1		
First-year male	1		3	1				
First-year female	4	5	4	1				
C. mexicanus prosopidicola								
Adult male						1	4	16
Adult female						1	8	14
First-year male							1	2
First-year female							4	5

Variation in iris color in the two species is shown in table 3, which demonstrates a small degree of overlap. Because iris color in adult *C. major major* is often suggestive of developmental stages in *C. mexicanus*, we believe that the dark iris of *C. major major* may have evolved from a yellow condition by suspension of development. We wish to note, however, that the condition in which the central part of the iris is dark gray is not duplicated in any stage of development in *C. mexicanus*.

Following a series of notes by Sprunt (1931, 1932*a*, 1932*b*, and 1934), Pennock (1931), Nicholson (1932), and others (Brooks, 1932; Dingle, 1932; Bailey, 1934), it was established that iris color is geographically variable in *C. major*. In the race *C. m. torreyi*, the iris of adults is described as "pale yellow" (Burleigh, 1958:595), "lemon yellow to deep straw yellow," or "bright yellow" (Sprunt, 1931:432; 1958:374), depending on the author. We have not had opportunity to compare iris color in this race with that of *C. mexicanus*.

SKELETAL CHARACTERS

We have carefully compared 12 skeletons of *C. major* from Florida with relatively large series of skeletons of *C. mexicanus prosopidicola* from central Texas and *C. mexicanus mexicanus* from central Veracruz. The racial identity of most of the specimens of *C. major* is in doubt, since only a few were collected in the breeding season; possibly some represent migrants of the race *C. major torreyi*. Unfortunately, we have no skeletal material of *C. major major* from Louisiana or Texas.

The following skeletal measurements were made: length, width, and depth of cranium; frontonasal width; width of occipital muscle scar; and length of humerus, femur, synsacrum, and sternum. Size relationships in adult males are shown in figure 7, in which mean values for *C. major* and *C. m. mexicanus* are plotted as percentages of those of *C. m. prosopidicola*. Measurements of females show a similar pattern. *Cassidix mexicanus mexicanus* is much larger than *C. m. prosopidicola* in all dimensions, but especially in frontonasal width. *Cassidix major* from Florida averages slightly larger than *C. m. prosopidicola* in most dimensions but is significantly smaller in frontonasal width and, perhaps also, in length of the sternum. We have no weights for Florida specimens, but these skeletal measurements would indicate that individuals of *C. major* from that area are fully as large or larger in body size than *C. m. prosopidicola*. Except for greater frontonasal width, skulls of *C. major* do not differ significantly from those of *C. m. prosopdidicola* either in size or configuration. Indeed, as indicated in figure 7, there is greater dissimilarity between skeletons of the two races of *C. mexicanus* than between *C. m. prosopidicola* and *C. major* from Florida.

OTHER MORPHOLOGICAL CHARACTERS

In preparing study skins of males, we experienced greater difficulty in skinning over the head of *C. major* than of *C. mexicanus*, and it was also our impression that in *C. major* it was generally more difficult to free the eyes from the surrounding skin. In females, we noted no difference in this regard.

Comparing plumages of our specimens taken in June, it is apparent that those of *C. major* are, with few exceptions, in a more advanced state of wear. This difference, which is particularly noticeable in females, probably reflects some genetically determined difference in feather structure, for it is shown even in specimens of the two species taken at the same breeding colony. It could result from a marked difference in timing of the fall molt, but, inasmuch as the breeding seasons coincide, it is likely that the molt periods are also the same. A third possible explanation is that *C. major* experiences greater abrasion of the plumage as a result of its more frequent association with marsh
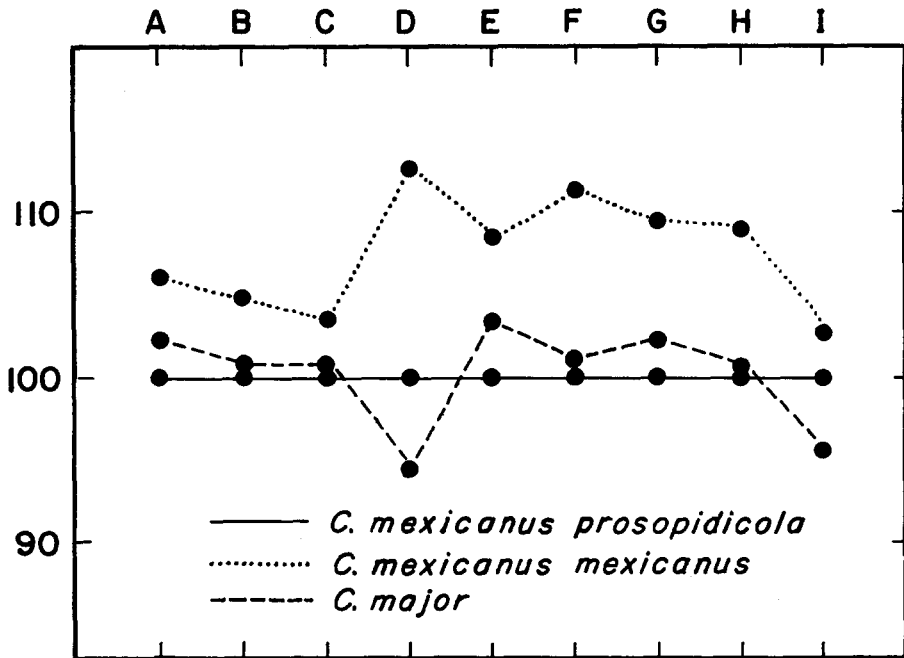
Fig. 7. Skeletal measurements in adult male *Cassidix*, shown by plotting mean values for *C. major* from Florida and *C. mexicanus mexicanus* from Veracruz, México, as percentages of those for *C. mexicanus prosopidicola* from central Texas. Skeletal measurements are indicated by letter, as follows: A, cranial length; B, cranial width; C, cranial depth; D, frontonasal width; E, width of occipital muscle scar; F, length of humerus; G, length of femur; H, length of synsacrum; I, length of sternum. Seven specimens of each form were measured.

vegetation, which is a rather denser vegetation type than those normally utilized by *C. mexicanus*.

Finally, we note that the palatal boss (Beecher, 1951:431) is equally developed in both species, and coloration of the soft parts, other than that of the eye, is identical.

POSSIBLE PROTEROGENESIS

It is interesting to note that the distinctive morphological characters of adult *C. major* show greater resemblance to characters of immature individuals than do those of adult *C. mexicanus prosopidicola* (see Selander, 1958, for comparisons of adult and first-year plumages). Thus, the adult male *C. major*, as compared with adult male *C. mexicanus*, resembles in greater degree first-year individuals of either species in brown iris color, relatively short tail, and tendency to have less extensive distribution of glossy color on the posterior under parts. In the same category are the relative reduction of metallic color dorsally, the pale ventral coloration, and the brown iris of adult female *C. major*. Finally, the apparent lesser degree of resistance to wear of feathers of *C. major* also suggests a more juvenal-like condition. We are not necessarily suggesting that *C. major* evolved from *C. mexicanus*; rather we wish merely to indicate that all of the distinctive morphological characteristics of *C. major*, including, incidentally, small size, could be derived from those of *C. mexicanus* by retardation of somatic developmental rates or proterogenesis (Rensch, 1960:260).

FIELD IDENTIFICATION

Interspecific differences of value in field identification in Texas and Louisiana are summarized in table 4. The songs and certain calls of adult males are unmistakable, and the very distinctive "wing-flip," part of the ruff-out display of males of *C. major*, permits identification at long distances; but, unfortunately, the most distinctive vocalizations and displays are given regularly only in the breeding season. At other times of the

TABLE 4

SUMMARY OF DIFFERENCES USEFUL IN FIELD IDENTIFICATION

Item	*C. major major*	*C. mexicanus prosopidicola*	Relative value in field iden- tification
	Adult males		
Size	Smaller	Larger	Fair
Tail	Shorter and narrower	Longer and wider	Good
Color	More greenish posteri- orly on abdomen, flanks, and back	More purplish posteriorly	Poor
Iris color	Brown or gray brown; usually darker or duller	Almost invariably intense yellow	Very good
Head and neck	Often appear to be larger or thicker	Usually appear to be smaller or thinner	Fair
Posture	Wings often drooped and held out from body	Wings infrequently held out from body	Fair
Displays and vocalizations	See text	See text	Excellent
	Adult females		
Size	Smaller	Larger	Poor
Metallic sheen dorsally	More conspicuous	Less conspicuous	Poor
Ventral color	Paler	Darker	Fair
Iris color	Brown or dull yellow	Yellow	Good
Vocalizations	See text	See text	Poor

year, iris color is the most valuable character for identification. This is also the best field character for adult females, but the smaller size and paler ventral coloration of *C. major* are often apparent when birds of the two species are compared at close range.

Until early spring, at which time the iris of immature *C. mexicanus* becomes yellow, first-year birds cannot be identified in the field. Unless one allows for the fact that the iris of first-year *C. mexicanus* is brown in the fall and winter, birds of this species will be misidentified as *C. major*.

THE QUESTION OF HYBRIDIZATION

We have been especially concerned with possible hybridization and introgression because of two previous claims of intergradation of *C. major* and *C. mexicanus*. Ridgway (1901:237) noted simply that there is a "grading" of the two forms on the Texas coast; but Lowery (1938:3–4) was more specific, reporting that "specimens from southeastern Texas at Matagorda, Virginia Point, Sandy Point (30 miles south of Houston), and High Island (17 miles east of Galveston) are definitely intermediates between *prosopidicola* and *major*. Birds of a series from Lake Charles in southwestern Louisiana . . .

are not typical *major* because they show a perceptible tendency toward *prosopidicola* by reason of their more purplish color and, on the average, longer tail." With this background, we have carefully examined our own collections and other museum specimens, including most of those which were previously designated as "intergrades," for evidence of hybridization. Specimens of *C. mexicanus* from the zone of sympatry are no smaller than those of the same species from the Austin region, central Texas; in fact, they appear to be slightly larger on the average (fig. 5). This is a significant finding, since introgressive hybridization with *C. major* would be reflected in smaller size. In the case of
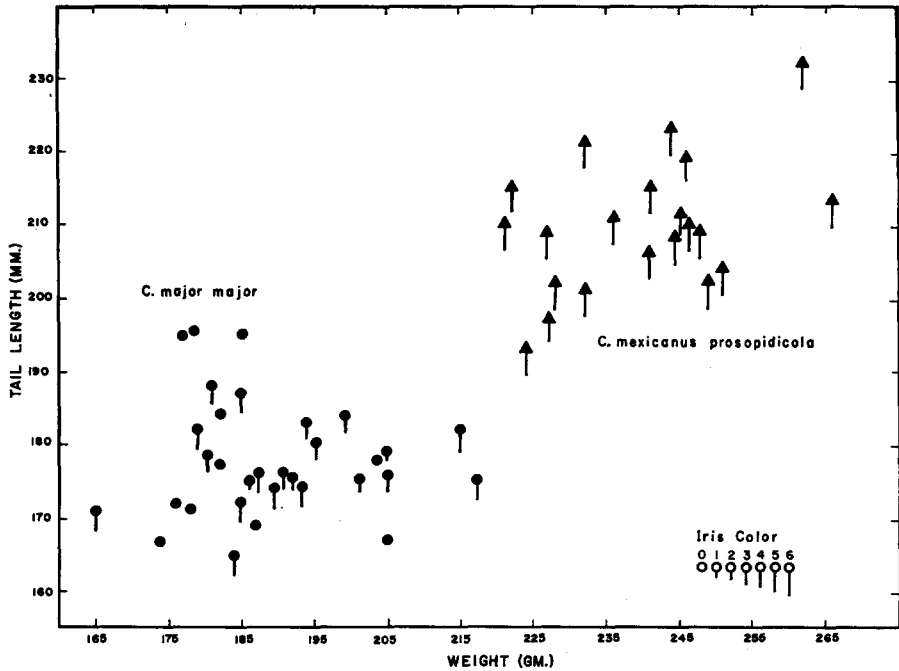

Fig. 8. Scatter diagram showing tail length, weight, and iris color in adult male specimens of *Cassidix* from the zone of sympatry. Specimens of *Cassidix mexicanus* are represented by triangles, those of *C. major* by dots. Categories of iris color range from dark brown (0) to intense yellow (6), as described in text.

C. major, our data suggest that birds from the zone of sympatry are no larger, on the average, than those from localities in Louisiana east of the zone. Similarly in color, we have found no obvious indications of introgression in our material.

In summary, from comparisons of specimens from the zone of sympatry with samples of *C. mexicanus* and *C. major* from localities west and east, respectively, of this zone, it is at once apparent that there is no conspicuous intergradation of characters. This is not to say, however, that hybridization does not occasionally occur, for the detection of hybrids is, of course, difficult when two forms are similar morphologically and show overlap or close approach in ranges of variation of characters. Since correlation of intermediacy of several separate characters may be indicative of hybridization (Anderson, 1949), we have prepared a scatter diagram (fig. 8) showing weight, tail length, and iris color in adult males from the zone of sympatry. There is in *C. mexicanus* some suggestion of relationship between weight and tail length, but in neither species is iris color correlated with either of these characters.

Of all adult males examined, R.K.S. 4284 from 12 miles east of Anahuac, Chambers County, Texas, June 10, 1959, most strongly suggests hybrid ancestry. This individual is referable to *C. major* on the basis of linear dimensions (wing, 178 mm., and tail, 182 mm.), but it approaches *C. mexicanus* in iris color (class 5, described as "yellow—not intense—with some gray flecks"), plumage color, and weight (215 gm.). Whether this specimen is merely a variant of *C. major* or an actual hybrid is, of course, problematical, but we favor the former interpretation. Other adult males of *C. major* which resemble *C. mexicanus* in plumage color are as follows: R.K.S. 4027, 6 miles south-southwest of Sabine Pass, Jefferson County, June 4, 1959 (weight, 181 gm.); R.K.S. 4035, same locality and date (165 gm.); R.K.S. 4081, Pinehurst, Orange County, June 6, 1959 (182 gm.); and L.S.U. 2256, Cameron Parish, April 11, 1938 (weight not recorded). Significantly, none of these specimens shows any particular approach to *C. mexicanus* in linear dimensions, weight, or iris color.

In females, occasional hybridization would be even more difficult to detect than in males, owing to their greater morphological similarity. We can only state that we have found no correlation of intermediacy of characters or other evidence of hybridization in females from the zone of sympatry. The fact that specimens of one species may resemble those of the other in certain characters we attribute to individual variation. It is our view that previous claims of intergradation, with the implication of interbreeding between the species, may in large part be attributed to a lack of appreciation of the full range of character variation in the two species. Thus, although the possibility of occasional hybridization exists, it is clear that the two grackles co-exist without extensive exchange of genes, interbreeding being prevented by intrinsic isolating mechanisms, the nature of which is discussed beyond.

COMPARATIVE ECOLOGY

ECOLOGICAL DISTRIBUTION

Along the Gulf coastal plain and elsewhere in their respective ranges, *C. mexicanus* and *C. major* exhibit significant average differences in habitat occurrence. As an aid to understanding the relationships of the two species in the zone of sympatry, it is desirable to review data on ecological distribution.

Cassidix mexicanus.—This species inhabits such a great variety of climatic regions and utilizes such a diversity of plant types for nesting that it is difficult to characterize its ecological distribution in any but general terms. Basic habitat requirements include standing water and open ground for foraging (fig. 9). Hence, this grackle is not found in forests or at any great distance from the ocean, lakes, ponds, or streams; and, in desert or prairie country, it is confined to water courses or to irrigated agricultural areas where trees are available. In Costa Rica, *C. mexicanus* is restricted to mangrove swamps on the Pacific coast (Skutch, 1954:321), but it occurs widely through the interior from Nicaragua north through México and into the southwestern United States. In México, grackles of this species are found abundantly in both the humid and arid divisions of the Tropical Zone and also in the Temperate Zone on the Central Plateau. The altitudinal range in Guatemala and El Salvador extends from sea level to 7000 feet (Skutch, 1958:335, and Dickey and van Rossem, 1938:538), and the species exhibits a similarly wide range in México, although it is most common at lower elevations.

With respect to nesting sites, *C. mexicanus* shows great flexibility. Palm and shade trees in town plazas are favorite nesting and roosting locations throughout tropical México and Central America, but clumps of bamboos and riparian trees or bushes and marsh vegetation are also used. Dickey and van Rossem (1938:539) report it as nesting in pines and thorny hedgerows in El Salvador. In the lower Rio Grande Valley and
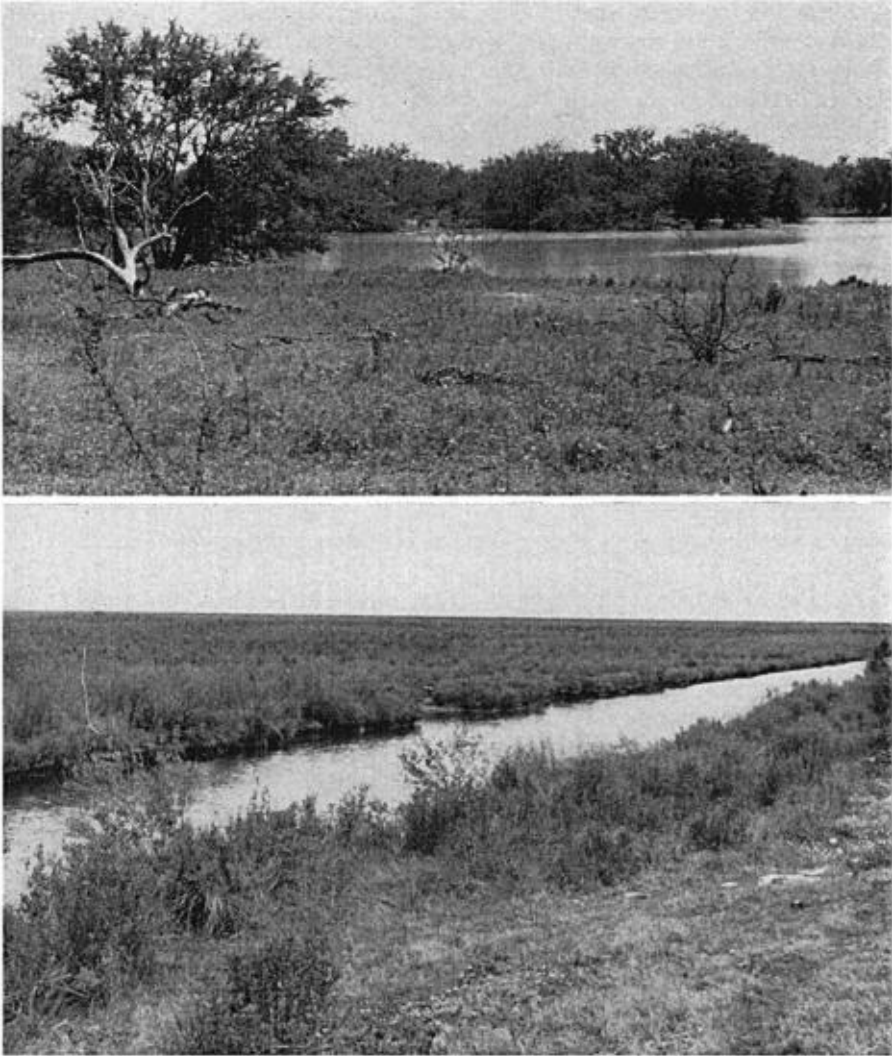
Fig. 9. Above: typical habitat of *Cassidix mexicanus* near Brookshire, Waller County, south-
eastern Texas, near the zone of sympatry. Large nesting colonies occurred in acacia and
other trees in this area. Photograph taken June 2, 1959.
     Below: marshland habitat of *C. major* on the Sabine National Wildlife Refuge, south-
western Louisiana. Photograph taken June 9, 1959.

on the Gulf coastal plain of southern Texas, nesting colonies occur most commonly in
mesquite (*Prosopis juliflora*) but they also occur regularly in huisache (*Acacia farnesi-
ana*), hackberry (*Celtis* sp.), prickly ash (*Zanthoxylum clava-herculis*), oak (*Quercus*
sp.), cottonwood (*Populus* sp.), prickley pear cactus (*Opuntia lindheimeri*), Texas
ebony (*Pithecolobium flexicaule*), willow (*Salix* sp.), yucca, and even in tall grass
(Sprunt, 1958:353). Bendire (1895:505) reports nesting in canebrakes bordering la-
goons and lakes and in rushes in salt water marshes on the Gulf coast; and Sennett
(1878:28) reported nesting "in great numbers" in a "heronry" in salt marshes between

Brownsville and the coast. Rarely, fresh water marsh vegetation is used for nesting, as on the Welder Wildlife Refuge, near Sinton, San Patricio County, Texas, where a large breeding colony was located in bullrushes at the edge of a shallow lake in 1959. In prairie land of central and southeastern Texas, nesting colonies are placed almost exclusively in trees in towns or about farm and ranch houses, where cedar elms (*Ulmus crassifolia*) and live oaks (*Quercus virginiana*) are most commonly used. Where trees are not available, the grackles may resort to telephone poles or other man-made structures for nesting.

Nest height may vary from two feet above water in marshes to about 50 feet above ground in tall live oaks, and there is a marked tendency for birds to place nests as far above ground as the available vegetation will permit. Marsh vegetation is used only when there are no suitable trees or tall shrubs in close proximity to a water source.

Cassidix major.—Unlike *C. mexicanus*, this species is characteristically coastal in distribution, selecting for nesting sites mainly marshes (fig. 9), an ecological characteristic shared with *C. palustris* and, presumably, with *C. nicaraguensis*. The northern race, *C. major torreyi*, is reported to show such a decided preference for salt water habitats that it is rarely seen elsewhere, although it occasionally follows up the margins of large tidal rivers for short distances inland (Sprunt, 1958:370). In South Carolina, it has not been recorded more than 40 miles inland from the coast, even in the winter; and, in Georgia, a breeding record 29 miles inland is considered exceptional (Burleigh, 1958: 593).

In ecological distribution, *C. major major* apparently differs little from *C. major torreyi*, except that it goes farther inland from the coast, frequenting streams, ponds, and other aquatic situations. Even so, it is only in Florida that it penetrates the interior any considerable distance (Sprunt, 1958:360). There it occurs along both coasts and is also found scattered through the interior of the peninsula wherever there is swampy or river-lake habitat. In Mississippi, it breeds only about the larger stretches of open salt marsh on the narrow coastal plain and on offshore islands (Burleigh, 1944:465). Discussing the ecological distribution of *C. major* in Louisiana, Lowery (1955:466) notes that it "is primarily a resident of coastal marshes . . . ." For a description of the Louisiana marshland, see Penfound and Hathaway (1938).

Nesting colonies in marshes are located over water in a variety of plant types, including, most commonly, sawgrass (*Cladium effusum*), cattail (*Typha latifolia*), and *Spartina alterniflora*. Both fresh and salt water marshes are utilized.

Despite a general restriction to marshy areas in the breeding season, nesting of *C. major* is not confined to aquatic vegetation. *Cassidix major torreyi* is an abundant breeder in many towns and cities on the Atlantic coast, as at Charleston, South Carolina (Wayne, 1910:112), where it nests, always near water, in wax myrtle (*Myrica carolinensis*), palmettos, pines, and, occasionally, up to 80 feet above ground in live oaks. Nesting in cedars and pines is reported in Virginia (Bailey, 1913:213). Brooks (1928) claimed that *C. major major* is less prone than *C. mexicanus* to become established in the vicinity of human habitations, but, according to Sprunt (1931:432, and 1954:44), this apparently is not the case. In Florida, *C. major major* nests in towns and cities, as in Jacksonville, and is reported to nest at many small farms on the east coast. Nests are placed in sawgrass, willows, buttonwoods (*Platanus occidentalis*), and maiden cane about lakes and marshes, and in live oaks on high land (Sprunt, 1954:444). In Louisiana, the same race occurs commonly in city parks in New Orleans, along the Mississippi River (Lowery, 1955:466), and it was found nesting not only in marshes but also in oaks, hackberry trees, willows, cane and other non-aquatic vegetation in the zone of sympatry with *C. mexicanus* (see beyond).

In winter, *C. major* is less restricted to marshy or other coastal habitats than in the

breeding season. For example, in Louisiana it wanders short distances inland along waterways and has been recorded occasionally at Baton Rouge, on the Mississippi River, 90 miles from its breeding range near the coast. There is also a record in January, 1949, near Anchor, Pointe Coupee Parish, 70 miles inland (Miles, 1950). In July, 1959, we found only a few small flocks in marshes near Grande Isle, Jefferson Parish, Louisiana, where the species breeds commonly; but large flocks were found in agricultural fields at Golden Meadow, a few miles inland from the marshes. And in southeastern Texas and southwestern Louisiana, *C. major* was decidedly less common in marshes in July, following the breeding season, than in June.

In the zone of sympatry in Texas and Louisiana, the distinction between habitats of *C. mexicanus* and *C. major* in the breeding season is as follows: In marshy areas where there is no dry ground, only *C. major* breeds; but either or both species may be found where marshland is interrupted by considerable areas of dry land supporting oaks or other trees. Inland from the coastal marshes, *C. mexicanus* predominates in prairies and agricultural areas, with *C. major* showing a more marked tendency to occur in wet meadow areas. *Cassidix mexicanus* is more likely to occur in towns and cities than is *C. major*, although both are sometimes present, as at Sabine Pass, where marshes are adjacent. For nesting, *C. major* shows a strong preference for marsh vegetation, frequently selecting this type even when trees are available, as at Avery Island, whereas *C. mexicanus* was not found nesting in marshes in the zone of sympatry and, elsewhere within its range, it seems to utilize marshes only when more elevated nesting sites are not available.

FORAGING

In the zone of sympatry, both species were frequently seen feeding together in rice fields and marshy areas, on lawns and mudflats, and along roads, where not the slightest difference in foraging behavior was apparent. If in fact there are any differences between the species in methods of foraging or in types of food items taken within any one area, they are extremely subtle and could be demonstrated only by the most extensive quantitative studies. Referring to *C. mexicanus* in Central America, Skutch (1954:324) notes that "few birds, I imagine, subsist on a greater variety of food . . . or display greater ingenuity in procuring nourishment. Everything is grist for their mill." Much the same type of comment is made by Sprunt (1958:369) with reference to *C. major*. A detailed analysis of 116 stomachs of *C. major torreyi* is available (Beal, 1900), but comparable data are lacking for *C. mexicanus*. However, unless stomach contents of individuals of the two species from the same locality were analyzed, any existing species difference in food would be completely masked by geographical and habitat differences in availability of food items.

Like other grackles, both species of *Cassidix* obtain most of their food on the ground, where they characteristically forage by walking along, probing (often by gaping) into mud and litter or turning over leaves, shells, flat stones, and papers with the bill. Typical foraging sites include grain fields, cattle pens, marshes, and the margins of ponds, sloughs, lakes, and streams. It is significant that both species exhibit a similar range of "special" feeding habits. Thus, both are known to wade into shallow water to "fish" for minnows, amphibians, and aquatic arthropods (Coues, 1870:377; Sprunt, 1958:369; Skutch, 1954:324); and both are reported to snatch food from the surface of deep water while hovering, petrel-like, or, occasionally, to plunge like a tern below the surface of the water to obtain fishes (Anthony, *in* Griscom, 1932:400; Sprunt, 1958:371; D. J. Nicholson, personal communication). Additionally, both species are adept at "flycatching" and have a reputation for preying on the eggs and nestlings of other species of

birds; both are said to pursue, attack, and sometimes kill other species of birds, especially when the latter are injured (McIlhenny, 1937; Lamb, 1944; Johnston, 1960:20; Nicholson, 1960); and both are scavengers and rob other species of birds of food (Sprunt, 1941).

In reviewing the literature, we note that most of the "special" feeding habits of *Cassidix* also are practiced by the Common Grackle (*Quiscalus quiscula*); these include "flycatching" (Bartlett, 1956), wading into shallow water or hovering over water (Cottam, 1943; Follett, 1957; Beeton and Wells, 1957; Ernst, 1944), eating eggs of other species, and killing and eating birds of other species, notably the House Sparrow, *Passer domesticus* (Terres, 1956; Taylor, 1958; see Bent, 1958, for review of older literature).

NESTS

Nest building in both species is performed entirely by the female. Nests have been described by Bendire (1895), Skutch (1954:326–328), Sprunt (1958:367), and others. In mixed colonies of the two species, we were unable to distinguish the nests. Composition and, to a considerable extent, structure depends on the available nest materials. Those in marshes are usually composed largely of rushes, cattails, and marsh grasses and may have only a general resemblance to those located in oaks or other trees in farm land or cities, where twigs and weed stalks typically form the foundation, into which are incorporated Spanish moss, string, rags, paper, feathers, and other material. Both species frequently use mud or cow dung as a "cement" for the foundation material.

EGGS

Size and color.—Comparing eggs of the two species from the zone of sympatry, mean differences in color, pattern, size, and shape are apparent. Those of *C. mexicanus prosopidicola* average about 1 mm. longer and tend to have a less rounded appearance because they are, on the average, no wider than those of *C. major major* (table 5). Appar-

TABLE 5

MEASUREMENTS OF EGGS IN MILLIMETERS

Form and locality	Number of eggs	Length Mean	Range	Width Mean	Range
C. major torreyi					
Eastern U. S. Coast[1]	98	31.60	27.9–34.3	22.49	21.6–24.6
C. major major					
SW Louisiana-SE Texas	21	31.28±0.28	28.9–33.7	22.23±0.17	20.8–23.8
C. mexicanus prosopidicola					
SW Louisiana-SE Texas	29	32.56±0.28	29.1–34.8	22.49±0.12	20.5–23.6
Texas[2]	93	32.18	28.2–36.6	21.75	20.6–22.6
C. mexicanus nelsoni					
Southern Sonora	43	30.05±0.20	27.3–33.6	21.39±0.10	20.0–23.2
C. mexicanus graysoni					
Culiacán, Sinaloa	8	29.09	26.9–31.6	20.79	20.0–21.9
C. mexicanus obscurus					
Acaponeta, Nayarit	29	31.08±0.32	28.3–35.3	21.07±0.26	19.8–22.7
C. mexicanus mexicanus					
"Alsacia," Guatemala[3]	62	33.6	31.0–36.5	23.0	21.4–24.6

[1] Sprunt (1958:367); localities not indicated.
[2] Bent (1958:352); localities not indicated.
[3] Skutch (1958:342).

ently there are no differences in egg dimensions between the two races of *C. major*; but in the other species there is geographic variation in correlation with body size. Note that the eggs of *C. mexicanus nelsoni* and *graysoni* are somewhat smaller than those of *C. major*.

Bendire (1895) has already described color and pattern differences between eggs of the two species that are apparent in our material from the zone of sympatry. All available sets of eggs can be readily identified to species on the basis of a combination of the following characters:

	C. mexicanus prospodidicola	*C. major major*
Blue ground color	Averages darker	Averages paler
Vinaceous and umber "clouding"	Invariably present; most pronounced at smaller end of egg but often widely distributed and dark enough to obscure ground color over whole surface of egg	Often absent; if present, more pronounced on, if not confined to, larger end of egg
Black and brown lines, tracings and splotches	More numerous and more prominent at small end of egg	Less numerous and often finer; more prominent on, and sometimes confined to, larger end of egg

In eggs of *C. mexicanus prosopidicola*, individual variation in pattern is somewhat greater than in those of *C. major major*. A description of the eggs of the nominate race of *C. mexicanus* by Skutch (1958:342) also calls attention to great individual variation, such that "if all the eggs in a populous colony were mixed together, each bird might conceivably be able to recognize her own by its distinctive markings."

We have not examined eggs of *C. major torreyi*, but Sprunt (1958:359) states that they are identical with those of *C. major major*. Pattern and color of eggs vary geographically in *C. mexicanus*, as suggested by the data in table 6; both in distribution of markings and in ground color, many eggs of *C. mexicanus nelsoni* show a close resemblance to those of *C. major*. Thus, the conspicuous average differences in color and pattern seen in the zone of sympatry are bridged by geographic variation in *C. mexicanus*.

TABLE 6

VARIATION IN DISTRIBUTION OF DARK MARKINGS ON EGGS

		Percentage with lines, tracings, and splotches:		
Form and locality	Number of eggs	More conspicuous at small end	More or less uniformly distributed	More conspicuous at large end
C. mexicanus				
Texas	24	79.2	16.7	4.1
Nayarit	16	75.0	12.5	12.5
Sonora	18	22.2	50.0	27.8
C. major	21	4.8	14.3	80.9

Clutch size.—A mean clutch size of 3.45 was previously reported (Selander, 1960) for *C. mexicanus prosopidicola* in central Texas, and clutch size is the same in the zone of sympatry with *C. major*, as indicated by data obtained between June 2 and 10, 1959, at colonies near Vinton, Calcasieu Parish, and near Anahuac, Chambers County (table 7). For *C. major major*, we do not have adequate information on clutch size, but the available data support McIlhenny's claim (1937:282), based on observations of hundreds of nests at Avery Island, Louisiana, that clutch size is almost invariably three; he recorded only one clutch of four and none of five. Between June 3 and 9, we obtained

TABLE 7

CLUTCH SIZE IN GRACKLES

Form and locality	Date	Number of clutches	Mean	Standard deviation
C. major major				
SW Louisiana-SE Texas	June 3–9, 1959	8	2.88	
C. mexicanus prosopidicola				
SW Louisiana-SE Texas	June 2–10, 1959	22	3.45±0.16[1]	0.74
Austin, central Texas	April 29, May 6, 1959	31	3.45±0.11	0.62
C. mexicanus nelsoni				
30 mi. N Obregón, Sonora	June 8, 1960	11	3.91±0.25	0.83
C. mexicanus obscurus				
Acaponeta, Nayarit	June 10, 1960	12	2.83±0.22	0.78
C. mexicanus mexicanus				
"Alsacia," Guatemala[2]	March (?)	49	2.71±0.07	0.50

[1] Selander (1960); erroneously reported as 4.45.
[2] Skutch (1958:342).

eight completed clutches of *C. major* in the zone of sympatry, two at the Sabine Wild-life Refuge, two near Vinton, three near Port Arthur, and one near Sabine Pass. Seven clutches were of three eggs and one consisted of two eggs; hence, mean clutch size is 2.88. We may note also that we found no indication of clutches larger than three in an additional 20 nests of this species containing nestlings or a combination of nestlings and unhatched eggs.

Geographic variation in clutch size occurs in both species of grackles, and the significant species difference found in the zone of sympatry is not evident when we compare clutch size from certain other parts of these species' ranges. Following a trend shown by many bird species (Lack, 1954:37), clutch size in *C. mexicanus* decreases from north to south, from extremes of 3.91 in Sonora to 2.71 in Guatemala (table 7). *Cassidix major* apparently also shows a north-south decrease in clutch size, with four eggs being found in most clutches of *C. major torreyi* in South Carolina and Virginia (Bailey, 1913: 214; Sprunt, 1958:367).

Percentages of infertile and addled eggs.—Unusually large losses of eggs due to "infertility" have been reported for *C. major* by McIlhenny (1937:283) and Sprunt (1958:359). The latter author notes that "on many an occasion, when investigating the home life of this bird and examining nests of young, I have found at the bottom an un-hatched egg or even two; and now and then a search of the nests after the [breeding] season has revealed these lonely reminders of an unborn progeny." McIlhenny (*loc. cit.*) reported a progressive increase in percentage of "infertile" eggs with each nesting at-tempt of the breeding season, as follows: in the first nesting, there were no infertile eggs; in the second an occasional one; while in the third, the majority of nests contained one or more infertile eggs. In a count of 19 nests containing young late in the breed-ing season (June 11, 1936) at Avery Island, Louisiana, one unhatched egg was found in each of 12 nests, and three nests contained two eggs each that did not hatch. These data would indicate that approximately 30 per cent of all eggs laid in the 19 nests were "infertile."

Because McIlhenny's data were obtained by a count of unhatched eggs "in nests in which the young had just hatched" and since he failed to mention whether or not the supposed "infertile" eggs were broken open and examined, Selander (1960:40) ques-

tioned the validity of his claim. Hatching is asynchronous in *Cassidix*, and it seemed possible that some of the supposed "infertile" eggs would have hatched a day or two later. Also, in 39 nests of *C. mexicanus prosopidicola* in the Austin region, each of which contained young, the percentage of undeveloped eggs was only 6.7 (Selander, *op. cit.*:41).

In the present study, special attention was given to this problem, and all unhatched eggs were broken or "blown" to determine their condition. The resulting data tend to support the earlier reports by McIlhenny and Sprunt. In 14 nests of *C. major* containing young ·or a combination of recently hatched young and eggs that were ready to hatch, a total of six dead eggs was found; four held partly decomposed advanced embryos and two showed no visible embryonic development. The latter were judged as infertile but it is possible that embryonic development had proceeded to a very early stage before death occurred. Taking a value of 2.88 as mean clutch size for this species, we calculated that 15 per cent of all eggs laid were infertile or addled. In addition, we found one nest of *C. major* which held three decomposed eggs showing no embryonic development; but these were not included in our calculation, since their failure to develop may have resulted from abandonment by or death of the female parent.

By way of contrast, in 23 nests of *C. mexicanus* containing young, or a combination of young and eggs which were ready to hatch, we found only a single dead egg; this showed no embryonic development. From these data, it is calculated that only 1.3 per cent of the total of 79 eggs laid in these nests were infertile or addled. Considering our findings and the reports of other workers, we therefore conclude that there is a significant difference between the two species with regard to loss of eggs in late nestings due to infertility and addling, assuming, of course, that *C. mexicanus* is not more prone to remove unhatched eggs from the nest than is *C. major*. We are unable at present to suggest an explanation for the unusually high mortality rate of eggs of the latter species.

COMPARATIVE ETHOLOGY

The behavior of *C. mexicanus* is well known to us from studies in the Austin region (Selander, MS) and Central America (Skutch, 1954). Although comparably detailed studies are not available for *C. major*, we are able to make a preliminary evaluation of species differences and similarities on the basis of our own observations in 1959 and 1960 and the reports of McIlhenny (1937) and other naturalists (summarized by Sprunt, 1958). For present purposes, we are especially concerned with displays and vocalizations because of their significant role in mechanisms of reproductive isolation.

ANNUAL CYCLE

Following is a brief summary of major events in the annual cycle of *C. mexicanus*, as determined in large part from investigations in central Texas. Most of these comments apply equally well to *C. major*, but some apparent specific differences are discussed beyond.

In fall and winter, grackles forage and roost in flocks, often in association with other icterids and with Starlings (*Sturnus vulgaris*). Most foraging groups are composed largely of one sex. In late February or early March, adult males establish small breeding territories in which several females will build nests in mid-March or later; nesting is colonial, with over 100 nests being found in large trees (Selander, 1960). Females, attracted to the colony site by the displays and vocalizations of the males, build nests within the territory of a male and defend a small area around the nest site against the intrusions of other females; minimal distance between nests is about two feet. The sex ratio at the breeding colonies is strongly unbalanced in favor of females, and the mating relationship is promiscuous. This results in intense competition among adult males both for territories and for the attentions of the females at the time of mating. Males take

no part in nest-site selection, nest building, incubation, or care of the young. Copulation usually occurs near the nest site or elsewhere at the nesting colony, but it may take place at some distance from the nesting colony, in which case the particular male in whose territory a female has built her nest may not be involved.

TABLE 8

TESTIS LENGTH IN MILLIMETERS OF ADULT MALES TAKEN JUNE 2 TO 10, 1959

Species	Number	Mean±Standard error	Range	Standard deviation	Coefficient of variability
C. mexicanus prosopidicola	16	16.43±0.17	14.9–17.3	0.68	4.12
C. major major	18	15.84±0.26	13.5–18.3	1.09	6.86

First-year females normally breed but first-year males do not. Spermatogenesis occurs about one month later in first-year males than in adults, and, although the former visit the breeding colonies, solicit females, and make brief attempts to establish territories, they are completely dominated and driven off by the adult males. Adult males continue to roost communally, usually at some distance from the breeding colony, with first-year males and with non-breeding females throughout the breeding season. Breeding females remain at the breeding colony at night only when they are incubating or brooding. As the young fledge, they gather into flocks with females and soon leave the vicinity of the nesting colony.

Attendance of adult males at the breeding colonies.—In *C. mexicanus*, adult males remain at the breeding colonies throughout the day; and our color banding work at Austin has shown that individual males hold more or less fixed territories at the colony for a period of at least several weeks. On territory, a male alternates almost continuously between agonistic interactions with other territorial or intruding males and courtship displays directed to the females. Frequently the male displays from a perch a few inches above a nest site as the female builds; and males fly down to solicit copulation with females that are searching for nesting material on the ground. Often males chase females in long sexual flights above and around the nesting colony or roost. Thus, males of *C. mexicanus* are conspicuous at the nesting colonies and undoubtedly play an important role in stimulating the female's nest building and other reproductive activities.

In most colonies, the activities of the females are not closely synchronized, so that some late-comers are nest building while other females are feeding nestlings or fledglings (Selander, 1960). The males remain at the colonies as long as nest building and egg laying are in progress; but many of the males leave the colony, sometimes moving to other, more "active" ones, when there is no longer mating opportunity. However, even at colonies in which all the young have hatched and no further nesting is in progress, it is usual to find one or two males in attendance.

In *C. major*, it would seem from comments of McIlhenny (1937) that adult males differ somewhat from those of *C. mexicanus* in attendance at large breeding colonies. He notes that adult males gather and display or chase females in the vicinity of sites where nests will be built but that only an occasional male actually visits the colony itself. Perhaps this is due to the fact that colonies studied by him were located in marsh vegetation, in which adult males would find it difficult to remain perched on vertical bulrushes or sawgrass blades where the nests were constructed. On April 7, 1936, he visited a colony of 200 nests in sawgrass at which 250 females were present; nest building and laying were in progress at the time. No males were in attendance and only an occasional male flew over the colony. On April 12, however, most of the nests contained full sets of eggs and 20 males were present at the colony. At a second large colony in
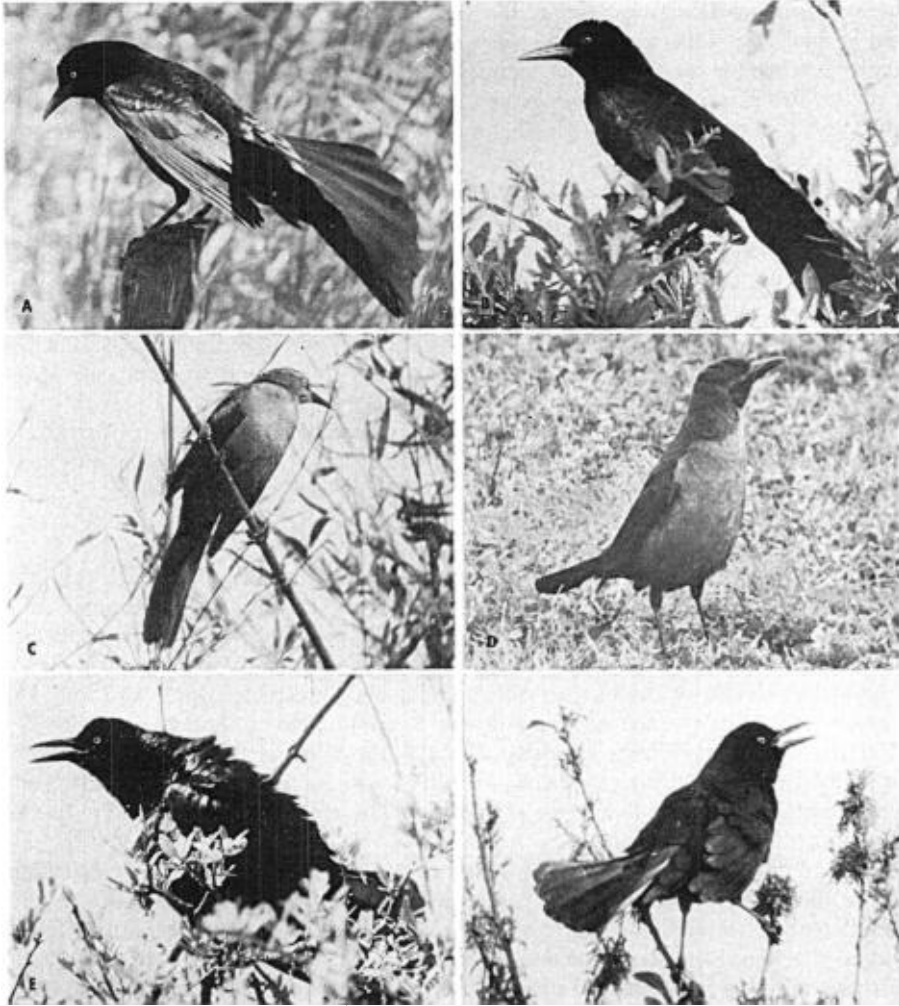
Fig. 10. Displays of *Cassidix*. A, adult male *C. mexicanus* in cock-posture on territory; B, adult male *C. major* in same posture—note thick-headed appearance; C, female *C. mexicanus*; D, female *C. major*; E, ruff-out display of male *C. mexicanus*; F, ruff-out display of male *C. major*.

which most of the 160 nests held full sets of eggs, McIlhenny found only 15 to 20 males on April 12; and, visiting a third large colony (150 nests) on May 28, he found only a single male in attendance. At the latter colony, the nests were all newly built and many lacked complete sets of eggs. On May 28, he studied a colony of 34 nests, all of which contained newly hatched young or eggs; again, only a lone male was in attendance.

At small colonies (six to 20 nests), most of which were established late in the breeding season, McIlhenny found that one male, never two, remained throughout the day. His account of the establishment of small colonies, in which a male holds a territory to which he attracts females, is essentially similar to that given previously for *C. mexicanus*. He also notes that these lone males showed concern over his handling of the nestlings, whereas at large colonies the males were indifferent under similar circum-

stances. At all small colonies studied by us, males of *C. major* were territorial and be-haved in much the same way as males of *C. mexicanus*, except that they spent less time actually perched in the immediate vicinity of the nests (see beyond). Since we have not yet studied large nesting colonies of *C. major* early in the breeding season, we can neither corroborate nor refute McIlhenny's statements concerning male behavior at large colonies.

PRINCIPAL DISPLAYS AND VOCALIZATIONS

The major ritualized behavior patterns, or displays, and the vocalizations of the two species of *Cassidix* have obvious counterparts in the Brewer Blackbird (*Euphagus cya-nocephalus*) studied by Williams (1952), in grackles of the genera *Quiscalus* and *Holo-quiscalus* (Selander, MS), and in other related icterids, including the cowbirds of the genus *Molothrus* (Friedmann, 1929; Laskey, 1950) and the Redwinged Blackbird, *Agelaius phoeniceus* (Nero, 1956). Our major aim at this time is to emphasize species-specific patterns in *Cassidix* rather than to attempt a comprehensive analysis of behavior in these species. To denote probable homologous behavioral elements in *Cassidix* and *Euphagus*, William's terminology of displays is sometimes employed, and names applied by Nero to similar displays in *Agelaius phoeniceus* are given in parentheses.

DISPLAYS OF MALES

Ruff-out (song-spread).—In *C. mexicanus*, the head is thrust forward, the plicate tail is fanned but not depressed, the contour feathers, including the marginals of the wing, are elevated, and the bill is opened; the head is often held up at a slight angle above the horizontal, but it may be arched down or up at a considerable angle, depend-ing upon the position of the bird to which the display is directed (figs. 10E and 11A). In low intensity displays, the wings are drooped and are held motionless or weakly quiv-ered at the tips; but, in high intensity displays, they are partly opened and held out from the body on a level with the back. This display is sometimes initiated with a slight forward lunge or step and is usually accompanied by the song (see beyond). Its dura-tion varies from 2 to 8 seconds.

When one male gives ruff-out to another at his side, the display may be asymmet-rical, the tail being displaced to that side. This feature was first called to our attention by Dr. Peter Marler, and it was later noted by us in the ruff-out displays of other icterids, including the Brown-headed Cowbird (*Molothrus ater*).

In its beginning and terminal phases, the ruff-out display of *C. major* (fig. 10F) is similar to that of *C. mexicanus*, but, whereas the wings are motionless or only weakly quivered in the latter species, in *C. major* the wings suddenly flutter rapidly to an almost vertical position above the back midway in the display in synchronization with a peculiar "rolling" or "rattling" part of the song (see fig. 11B and beyond). Following this "wing-flip" part of the display, the wings return to their former position. Thus there are three phases in the full display, a ruff-out with the wings drooped or level with the back, a short but very conspicuous second phase in which the wings flutter almost vertically above the back, and a third phase identical with the first.

The ruff-out display is given in full intensity only in the breeding season. It has strong threat function and is much used in proclaiming territory. Most frequently it is directed to other adult males, but it is also given to females both at the nest site as the female builds and elsewhere. Lone males on territory frequently give the display when no other birds are in sight, in which event it is undirected. The display may pass rap-idly at any stage into other displays, especially head-up and solicitation.

Cock-posture.—In the breeding season, males assume a distinctive posture, shown in figure 10A and B, which suggests the attitude of a strutting rooster. This is the
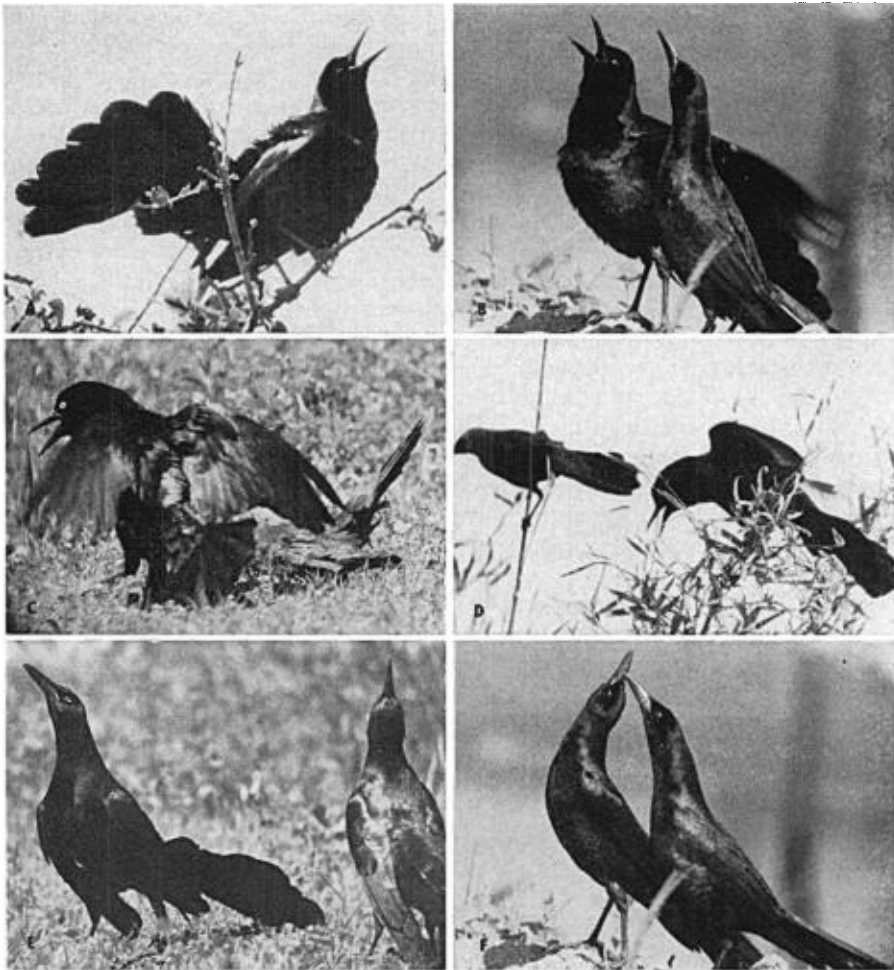
Fig. 11. Displays of *Cassidix*. A, ruff-out of male *C. mexicanus* directed to another male at close quarters; B, a male *C. major* in ruff-out display begins a wing-flip as another male returns head-up display from cock-posture; C, solicitation display of male *C. mexicanus* directed to a female dummy; D, male *C. major* soliciting a female of the same species; E, head-up display of *C. mexicanus*; F, two males of *C. major* exchanging head-up display.

typical posture of adult males that are not engaged in other displays and is most intense in dominant individuals holding positions at breeding colonies. First-year males may assume this posture but only in the absence of adult males. The posture resembles the ruff-out in that the tail is conspicuously fanned and the wings are drooped; the body feathers are fluffed to some extent, thus increasing the apparent size of the bird, but the body contours are smooth, unlike the situation in ruff-out. From the cock-posture, there are smooth transitions to ruff-out, solicitation, and head-up displays.

The cock-posture of *Cassidix*, which is identical in the two species, is possibly related to the "exposed epaulets" display of male *Agelaius* (Nero, 1956:9) and to the "generalized" or elevated tail display of *Euphagus*, which is directed to females and functions as "an invitation or indication of receptive state" (Williams, 1952:8). Conspicuous

features of this display in *Euphagus* are the fanned tail and the spread and slightly drooped wings. In watching males of *C. major* perched on wires or posts, we often noted that the wings are held farther out from the body than in *C. mexicanus* and in a position more nearly approaching that seen in the "generalized" display of *Euphagus*.

Head-up (bill-tilting).—This is a very frequent short-range hostile display used throughout the year. It occurs in many icterids, but it is more highly ritualized in male *Cassidix* than in *Euphagus* and other related genera. It is essentially identical in the two species of *Cassidix* but a bit more "stylized" in *C. mexicanus*.

At low intensity, the head is merely flicked to, or held momentarily at, a nearly vertical position, with the feathers of the head, neck, and body sleeked and the bill closed. At higher intensity, the neck is stretched upward and the bill is held vertically for periods up to 20 seconds, with only an occasional accenting flick of the head (fig. 11E and F). At highest intensity, the neck is flexed strongly and the top of the head touches the back; then the head and neck return to a vertical position. During the display, the eye is frequently squinted and the niciitating membrane may be drawn over the eye.

Sexually active males usually give the head-up display in cock-posture, but with the body feathers sleeked; but, in the nonbreeding season, the display is given without any special posture and is less intense in form. Head-up displays of males are rarely directed to females, except in winter disputes over food or to adjust spacing at the communal roosts.

Two or more males disputing territory frequently perch or stand a few inches apart and exchange displays, alternating between head-up and ruff-out with song. In this situation, the head is directed vertically during ruff-out, and almost invariably the typical head-up display follows (see fig. 11A and B).

Solicitation or pre-coitional (courtship).—Males invite copulation with a distinctive display resembling the ruff-out but differing as follows: the feathers are fluffed to greater degree, the tail is usually more widely fanned, the bill invariably is directed downward, and the wings, which are extended in a half-open position slightly above the horizontal, are violently quivered (but not flapped or fluttered as in ruff-out of *C. major*). The display (fig. 11C and D) is directed to females and may be given from perches, on the ground, or in flight. On the ground, the male runs or lopes toward the female and usually circles her once. Solicitation may begin on the wing as a male flies toward a female, in which event the wing movement is a compromise between the quivering of the display and the normal strokes required to maintain flight. During solicitation display, a characteristic call is given; but, when the male's aggressive tendency is strong, as it often is when a male first approaches a female, the special solicitation note is preceded by the first part or the first and second parts of the song. On occasion the complete song accompanies solicitation display, particularly in *C. major*.

DISPLAYS OF FEMALES

The displays of females are much less dramatic and frequent than those of males and have not previously been mentioned in the literature. Among the female displays, most of which appear to be identical in the two species, are the following.

Ruff-out (song-spread).—In disputes over nest sites, females of *C. mexicanus* occasionally give brief low intensity ruff-out displays that are similar in form to those of males. In females of *C. major*, ruff-out displays are more frequent and their intensity is generally higher. Moreover, they are used not only in territorial disputes but also in hostile encounters among females away from the nest sites. Another specific difference involves the vocalizations given during ruff-out; females of *C. mexicanus* give a chattering call, whereas those of *C. major* give a song which is closely similar in all respects

to that which accompanies male ruff-out (see beyond). In *C. mexicanus*, females apparently never direct their ruff-out displays to males, but females of *C. major* may occasionally do so. In *Euphagus* (Williams, 1952) and *Quiscalus* (Selander, MS), mutual exchange of ruff-out displays by male and female is a conspicuous feature of the early stages of pair formation, but this ceremony does not occur in either species of *Cassidix*.

Head-up (*bill-tilting*).—This display, which is used less frequently by females than by males, consists of a brief pointing of the bill in a more or less vertical position. The neck is never flexed over the back as in the male, and females do not posture in head-up display for more than a few seconds. As it is manifest in female *Cassidix*, this display resembles that of male *Euphagus* (Williams, 1952:8, figs. 9 and 10) or *Molothrus ater* (Friedmann, 1929:164; LaRue and Selander, MS). It is most often seen early in the breeding season, usually in connection with disputes over nest sites or material, but it is also given in winter in squabbles over food. As in the male, this is a short-range threat display.

Generalized.—This display in *Cassidix* and the corresponding display of female *Euphagus* (Williams, 1952:5) are apparently identical. The bill is held at an angle of 30° above the horizontal, the tail is cocked but not spread, and the wings are held out from the body, drooped, and may or may not be quivered rapidly; the feathers are not fluffed. A chattering series of notes often accompanies the display, especially when the latter is given at high intensity.

Females give this display only in the breeding season, when it is most evident at the time of nest building and laying. Then, the approach of a soliciting male evokes the display in the female; or the display may be initiated independently by the female, in which case it almost invariably serves to attract one or more males in the vicinity.

Solicitation or pre-coitional.—As in *Euphagus*, the pre-coitional display seems to be an intensified version of the generalized display. Frequently a female alternates between generalized and solicitation displays, and the two may grade into one another completely; perhaps it would be more realistic to regard the two displays as one, the difference being one of intensity. At low intensity (generalized) the wings are held out from the body but not quivered; at moderate intensity, the wings vibrate and chattering *kit* notes are given; at high intensity (solicitation), the tail is cocked at a greater angle, the body tips forward, and the bird gives a series of high-pitched *che* notes similar to but weaker than the solicitation notes of the male.

Solicitation display is not given by females before the nest is constructed. As in *Euphagus* (Williams, 1952:5–6), the display and accompanying call serve to indicate the female's readiness to copulate; but males do not mount until the female's wing quivering ceases and she assumes a rigid pose with head and tail elevated.

VOCALIZATIONS OF MALES

Many of the vocalizations of males of *C. major* and *C. mexicanus* differ markedly, yet previously only Townsend (1927) and Brooks (1928) have commented on this fact. This is perhaps not surprising considering the variety of factors which complicate the description and analysis of vocalizations in this genus: (1) Both species of grackles have unusually large vocal repertoires. (2) Incomplete versions of the song and some of the more complex calls are very often given; thus, the casual listener has the impression that the variety of sounds is almost unlimited. (3) First-year males, singing and calling for the first time in the spring, perfect their vocalizations, especially the song, over a period of weeks or months; and they may, in this long developmental period, give versions of the song or calls which have little resemblance to the same vocal-

izations of adults. (4) At least in *C. mexicanus*, and perhaps also in *C. major*, there is considerable geographic variation in the quality of the vocalizations. In the races *C. m. mexicanus* (studied in Veracruz, Oaxaca, and elsewhere in eastern México), *C. m. monsoni* (Las Cruces, New Mexico, and Zacatecas, México), and *C. m. prosopidicola*, the same basic repertoire of sounds is represented but there are conspicuous differences in pitch and distribution of harmonics. And in the races of *C. mexicanus* along the west coast of México (*C. m. obscurus* and others) many of the vocalizations, particularly the song, are distinctly different from those of other subspecies (Selander, MS).

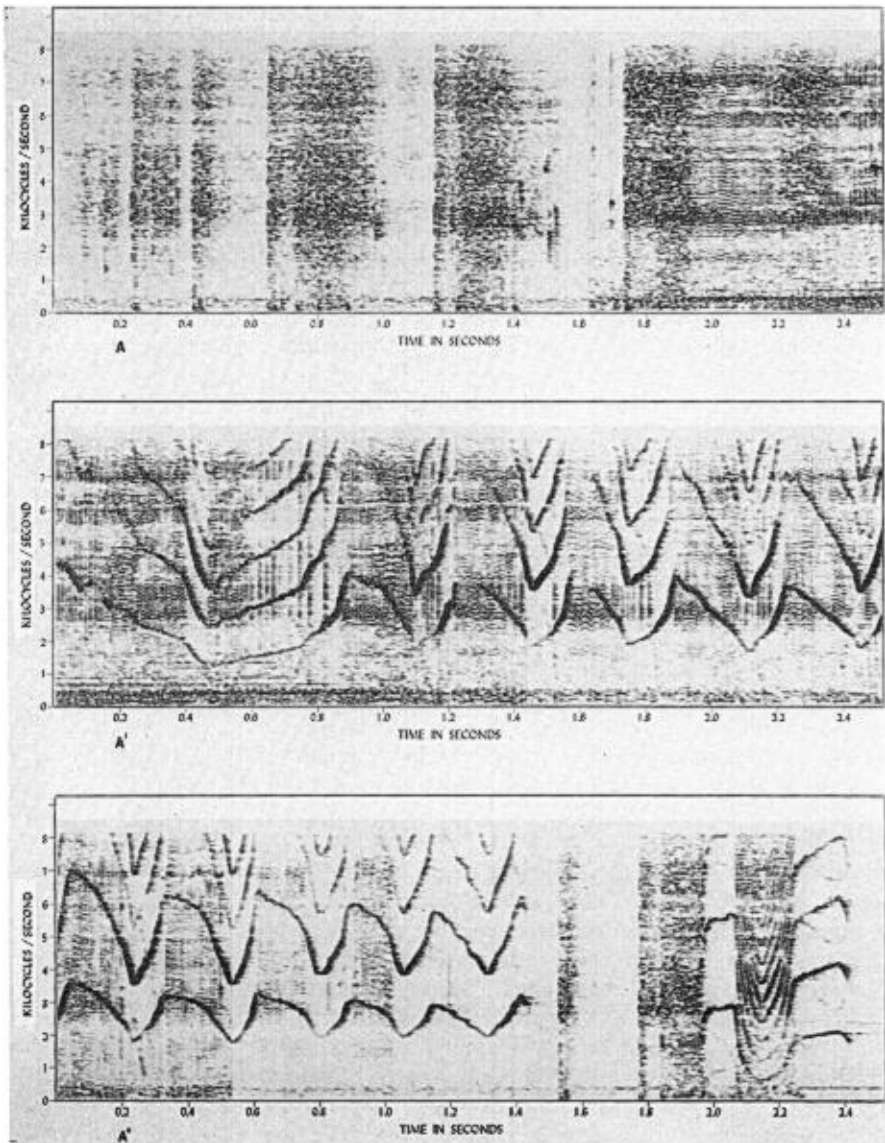*Song.*—Grackle vocalizations of this designation fall in the category of "territorial

Fig. 12. Sound spectrographs of vocalizations of *Cassidix*. A–A″, song of adult male *C. mexicanus*.

song" as generally defined by ethologists (Tinbergen, 1939:80; Armstrong, 1955:72). Songs of male *Cassidix* are accoustically complex and function to intimidate and repel rival males, to attract females, and to indicate the location, identity, and vigor of the singer. Song in complete form is given with regularity only in the breeding season and, by some individuals, in the period of fall recrudescence of the gonads. Generally it is accompanied by ruff-out display and is delivered from a conspicuous position.

In *C. mexicanus* song is limited to the male. Complete versions are divisible into four distinctive parts or phrases (fig. 12): (a) a low, untuned introductory phrase which suggests "the crackling of twigs" (Friedmann, 1925:550), "brush-breaking" (Simmons,
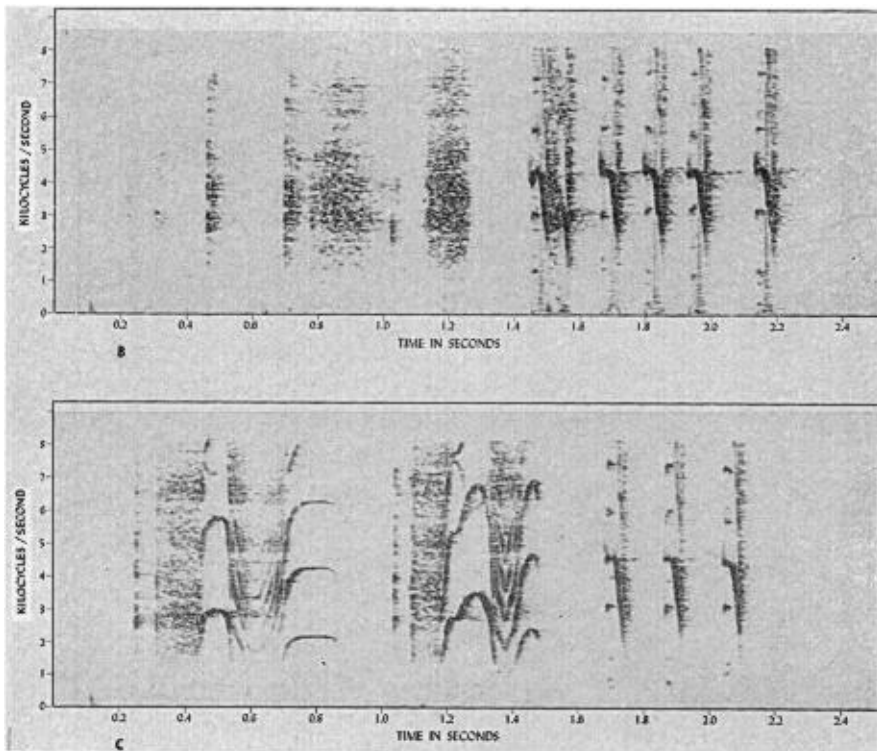

Fig. 12, continued. B, first part of song and *cheat* notes of male *C. mexicanus*; C, last part of song and three *cheat* notes of male *C. mexicanus*.

1925:186), or "tearing the dry husk from an ear of corn" (Baird, Brewer, and Ridgway, 1905:227); (b) a finely tuned undulatory *chewechewe* (repeated) phrase which is accompanied by an untuned hissing sound; (c) a short clacking repetition of the harsh sound of phrase (a); followed by (d) a terminal series of one to five (usually two) loud, piercing *cha-we* notes, which are described by other authors as *"may-ree, may-ree!"* (Peterson, 1960:234), "a high falsetto squeal, *quee-ee, quee-ee*" (Bailey, 1902:303), or a "clear almost Flicker-like *week-it, week-it*" (Townsend, 1927:553). Phrase (b) is highly variable in length, and phrase (c) is often very short and soft. All sounds of the song are vocal, none being produced, as erroneously suggested by Allen (1944:693), by wing movement.

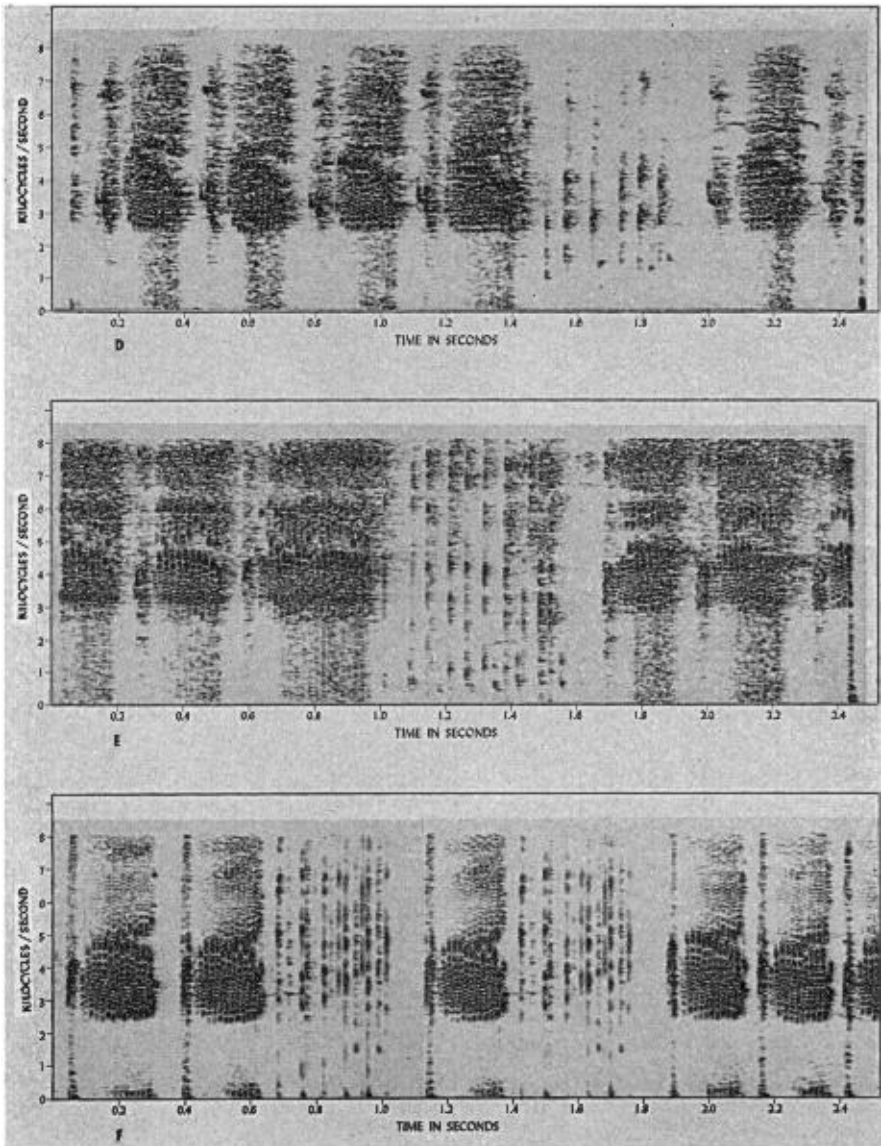The loud terminal phrase of the song is very often given alone, and any of the other

Fig. 12, continued. D, song of adult male *C. major* recorded in southwestern Louisiana; E, song of male *C. major* recorded in Florida (Cut 4, Cornell Library of Natural Sounds; recorded by P. P. and B. J. Kellogg at Paradise Key, Everglades National Park, on February 2, 1950); F, song of female *C. major* recorded in southwestern Louisiana.

phrases may also be given separately (fig. 12B and C). Early in the breeding season, first-year males frequently omit phrase (a) and give atypical versions of the terminal phrase in which the notes ascend rather than descend in pitch.

The song of *C. major* (fig. 12D and E) has no particular resemblance to that of *C. mexicanus*. In complete form it consists of three parts: (a) a variable number of harsh *tireet* or *shireet* notes; (b) a peculiar, rapid series of weakly ascending notes accom-

panying the "wing-flip" part of the ruff-out display; and (c) a second series of *tireet* notes similar to those of phrase (a). The song was accurately described by Townsend (1927:551) and has been mentioned in part by numerous authors, including Chapman (1912:368), Dingle (1932:357), Harper (1920), Howell (1932), Torrey (1894), and Wayne (1910:112). Most of these authors' comments pertain to phrase (b), which is variously described as a "curious rolling noise," a "singular rolling call, which bears a close resemblance to the sound produced by a coot pattering over the water," a "gut-
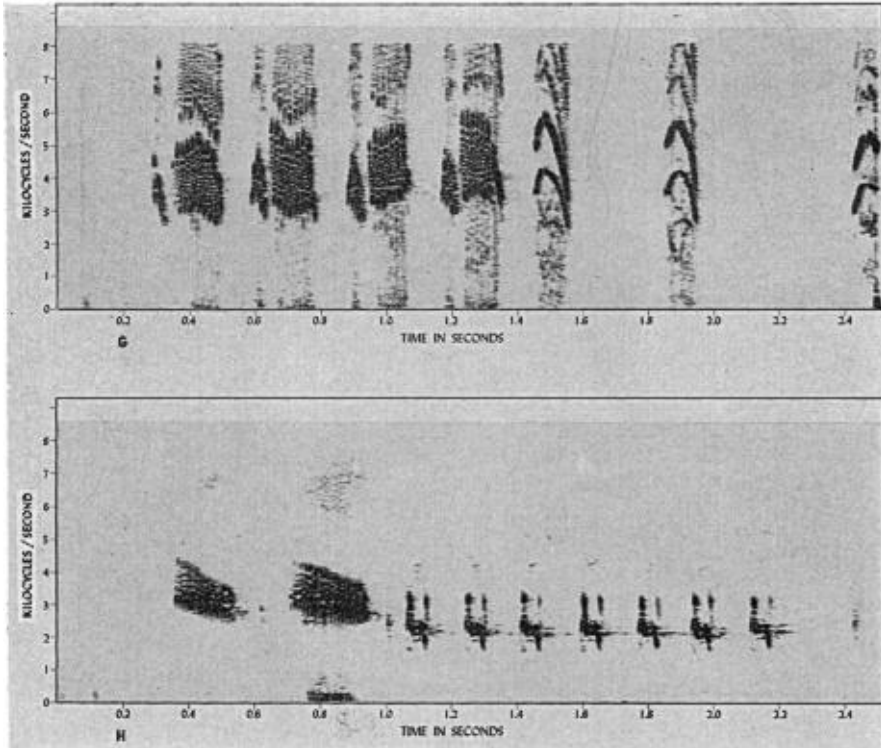

Fig. 12, continued. G, first part of song and *cheat* notes of male *C. major*; H, vocalization of *C. major* of undetermined function recorded in Florida (Cut 1, Cornell Library of Natural Sounds; recorded by A. A. and E. G. Allen on the west side of Lake Okeechobee on January 11, 1954.

tural, clattering sound," and a "guttural rattle" similar to certain parts of the song of the Purple Martin (*Progne subis*). There has been considerable controversy concerning the source of this sound, some observers claiming that it is produced by the wings and others suggesting that it is caused by rapid striking together or vibration of the mandibles (see review of opinions by Sprunt, 1958). However, our observations support the view, originally advanced by Townsend (1927:553), that the sound is strictly vocal. He says that "on several . . . occasions I noticed that during the rattle the wings were sometimes moved but little or were motionless . . . I also heard the rattle many times given in flight, and there was no perceptible modification of the action of the wings at the time. I think it can be definitely stated, therefore, that the evidence eliminates the wings from any causative action of the rattle, although the vibratory movement is gen-
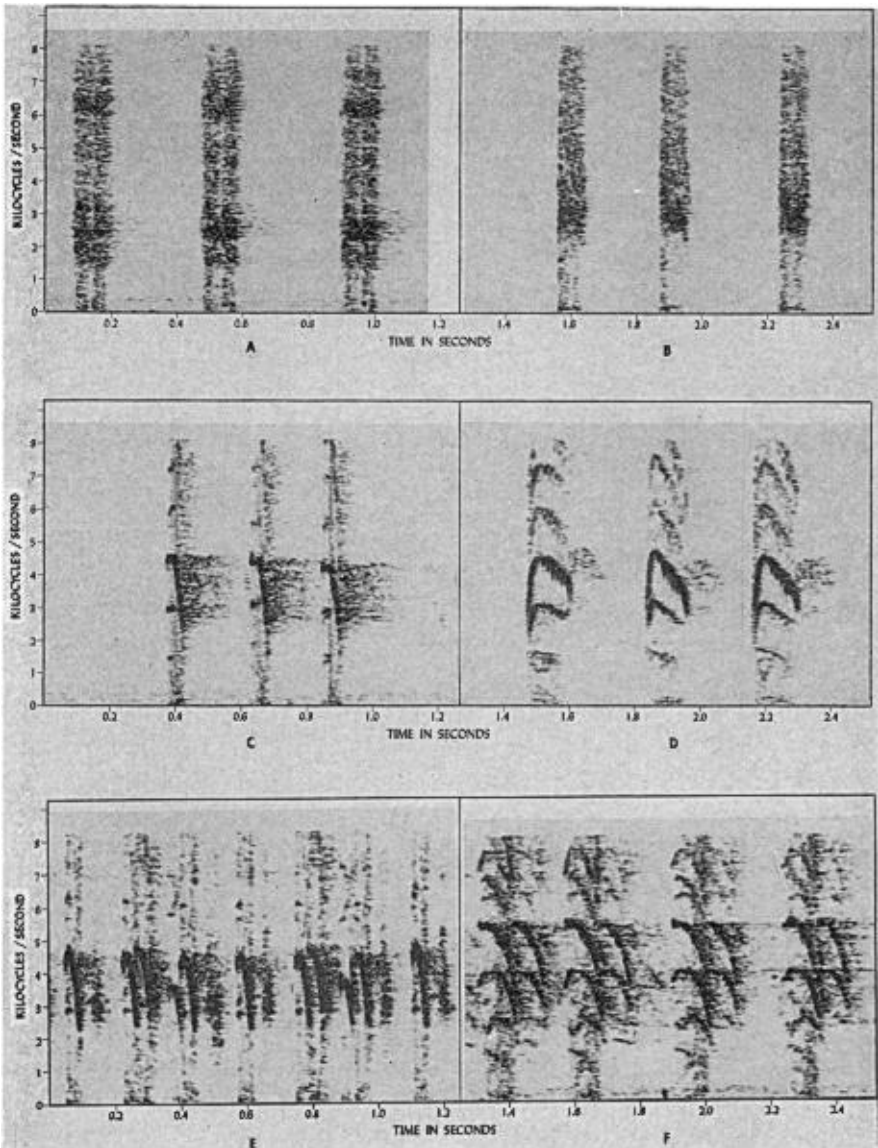
Fig. 13. Sound spectrographs of vocalizations of *Cassidix*. A, clack of male *C. mexicanus*; B, same, male *C. major*; C, *cheat* notes of male *C. mexicanus*; D, same, male *C. major*; E, double-note version of *cheat* call of male *C. mexicanus*; F, same, male *C. major*.

erally present and exactly synchronous with it." Elsewhere Townsend concluded that the sound may be modified by throat vibrations but is not made with the bill.

Solicitation calls.—Males of both species indicate their readiness to mate by giving solicitation display accompanied by series of notes which vary from a medium-pitched *cheat* through intermediate forms to a high-pitched *che*. The latter version is indicative of a high level of intensity of the mating "drive" and is almost always given from solicitation posture, whereas the lower-pitched notes may not be accompanied by the display.

The solicitation calls of the two species are similar but differ as follows: the high-intensity notes of *C. mexicanus* (fig. 13G) are higher pitched and have a "strained" or "whimpering" quality that is rarely if ever achieved by *C. major*; moderate-intensity notes of *C. mexicanus* have a flat *cheat* sound (fig. 13C), whereas those of *C. major* were usually recorded as a softer *cheep* (fig. 13D); the calls of *C. major* are more frequently preceded by the first part of the song (fig. 12G).
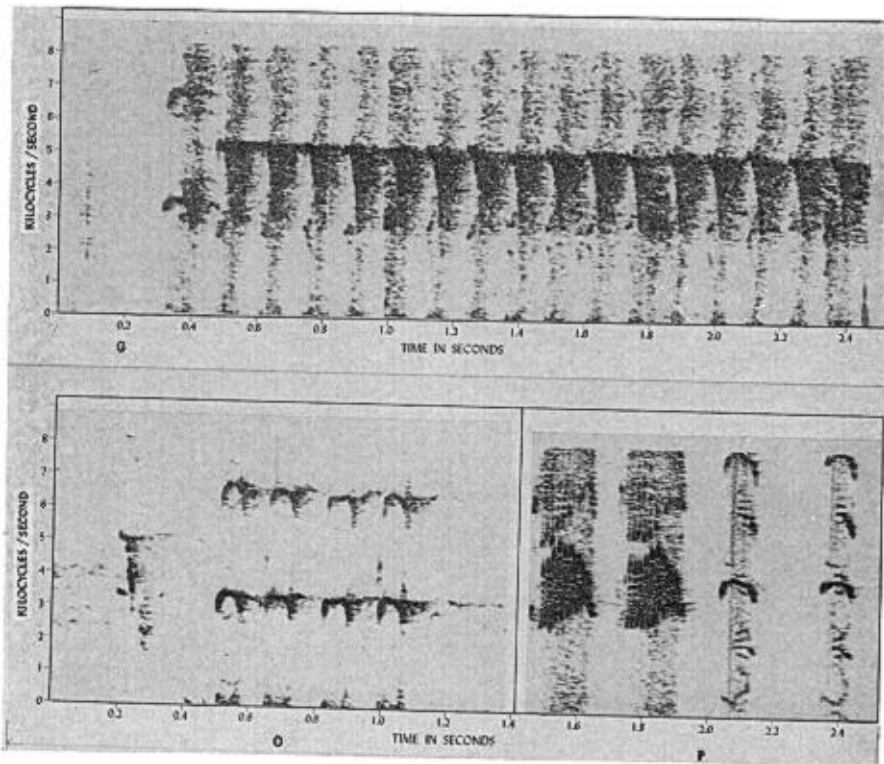

Fig. 13, continued. G, high, "pleading," solicitation *che* notes of male *C. mexicanus*; O, high peeping notes of male *C. mexicanus*; P, peeping notes of male *C. major*, introduced by first part of song.

Warning notes.—Males of both species give low *chut* notes indicating unrest and a tendency to fly, particularly from a source of danger (fig. 13K and L). Those of *C. mexicanus* have most of their energy between 1.2 and 3.2 kilocycles, but those of *C. major* are higher pitched, with significant energy between 2.0 and 3.8 kilocycles. Similar notes are given by many other related icterids.

A second warning note of *C. mexicanus* is a loud, low *clack* or *clock* given at the approach of a human or other potential predator to the nesting colonies and roosts. Most of the energy of the call is distributed between 1.2 and 3.4 kilocycles (fig. 13A). A comparable call of males of *C. major* is a higher pitched *kle-teet* or *teet-teet* (2.5–5.2 kilocycles) having only a suggestion of a clacking quality (fig. 13B). This two-note call grades into a single *teet* version, the sound of which suggests a small tin horn. The single-note call apparently has the same warning function as the two-note call and may be used exclusively in its stead by some individuals.
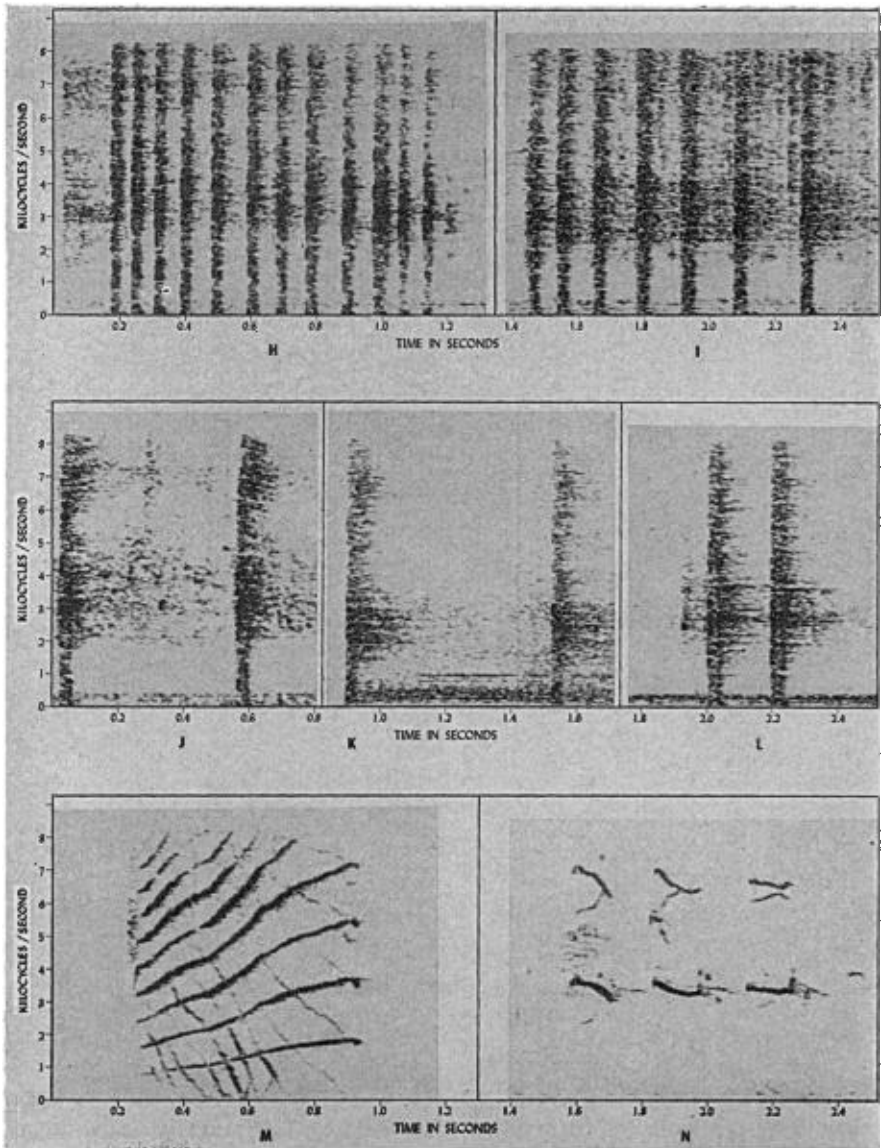
Fig. 13, continued. H, chatter of female *C. mexicanus*; I, same, female *C. major*; J, harsh *chut* of female *C. mexicanus*; K, *chut* of male *C. mexicanus*; L, same, male *C. major*; M, ascending *weet* call of male *C. mexicanus*; N, *klee* call of male *C. major*.

It is noteworthy that neither species of *Cassidix* has a clear, whistled "predator note" of the type given by most related genera, including *Euphagus* (Williams, 1952:4), *Sturnella* (Lanyon, 1957:11), *Agelaius* (Nero, 1956:130), *Holoquiscalus*, and *Molothrus* (Selander, MS).

Other calls.—Males of *C. mexicanus* have a finely-tuned ascending whistle (fig. 13M) given from ruff-out or cock-posture and almost invariably followed by intense

head-up display. The call functions to warn off other males which are approaching the nesting colonies. This call as such is lacking in *C. major*, which in comparable situations gives the song or a series of four to seven strained and poorly tuned *kloo* or *klee* notes (fig. 13N); these do not ascend in pitch and bear some resemblance to the *tireet* notes of the song or to the low-intensity solicitation notes.

Each species possesses other notes in addition to those described above; but, since we have not thoroughly analyzed variation in those of *C. major*, further detailed comparison will be postponed. Apparently *C. mexicanus prosopidicola* has a larger repertoire of sounds than does *C. major*, as previously noted by Townsend (1927); and, in this respect, there is a parallel with the two species of meadowlarks studied by Lanyon (1957:14), in which *Sturnella magna* has *"zeree"* and *"dzert-tut"* complexes of calls not represented in *S. neglecta*.

VOCALIZATIONS OF FEMALES

We have already noted that females of *C. major* occasionally give songs which are closely similar to the male song (see fig. 12F), whereas females of *C. mexicanus* do not sing. Even under sustained treatment with testosterone, females of *C. mexicanus* do not produce the male song, although they are induced to give full-intensity versions of ruff-out display and to perform other characteristically masculine behavior.

Other vocalizations of females of the two species are similar, showing only minor differences in pitch and distribution of harmonics. Both species give *chut* warning notes like those of the males. Apparently the repertoire of females of *C. major* does not include *kle-teet* or *teet* warning notes of the males; and our work with female *C. mexicanus* has conclusively demonstrated that the male *clack* call is lacking. Females of both species also give similar chattering calls (fig. 13H and I) as they move to and from their territories and as they engage in agonistic encounters with other females. These calls are also given at the close approach of a soliciting male. The chattering of female *Cassidix* apparently corresponds to the *kit-tit-tit-tit* call of female *Euphagus cyanocephalus* (Williams, 1952:4), the "rattle," "roll," and "chatter" calls of *Sturnella* (Lanyon, 1957:12), and the chattering call of female *Molothrus ater*, which is given in response to the courtship display and song of the male (Selander, MS).

Solicitation calls of females, high-pitched series of *tee* or *che* notes (the "pleading peeps" of Skutch, 1954:320), appear to be identical in the two species of *Cassidix*. This call and the chatter are given only in the breeding season.

OTHER BEHAVIORAL DIFFERENCES

Comparing the behavior of the two species of grackles at mixed breeding colonies, we noted that males of *C. mexicanus* tend to hold smaller territories and to spend greater percentages of their time perched near the nests. This was especially apparent at a colony near Bridge City in April, 1960 (see beyond). On their territories, males of *C. mexicanus* also remain in one position for longer periods; those of *C. major* more often move from perch to perch and they are more prone to chase females or to fly down to the ground to solicit. We also noted that males of *C. major* more frequently sing as they fly to and from the colony. Despite the fact that males of *C. major* are less regular in their attendance at the colonies, we have noted that they show greater readiness to join the females in "mobbing" defense of the colony against a potential predator.

In males of *C. major* in resting or "alert" postures, the head and neck feathers are fluffed out to a greater degree than in *C. mexicanus*, thus producing a characteristic thick-headed appearance.

TERRITORIAL AND OTHER INTERRELATIONSHIPS IN THE BREEDING SEASON

Much of our field study was devoted to the behavior of the two species in mixed breeding colonies or in areas in which they were nesting in close proximity. Following are summaries of information on the territorial and other social interrelationships at several study areas.

Port Arthur area, Jefferson County.—A large colony of *C. mexicanus* was located on the grounds of St. Mary's Hospital in Port Arthur, where nests were placed in tall live
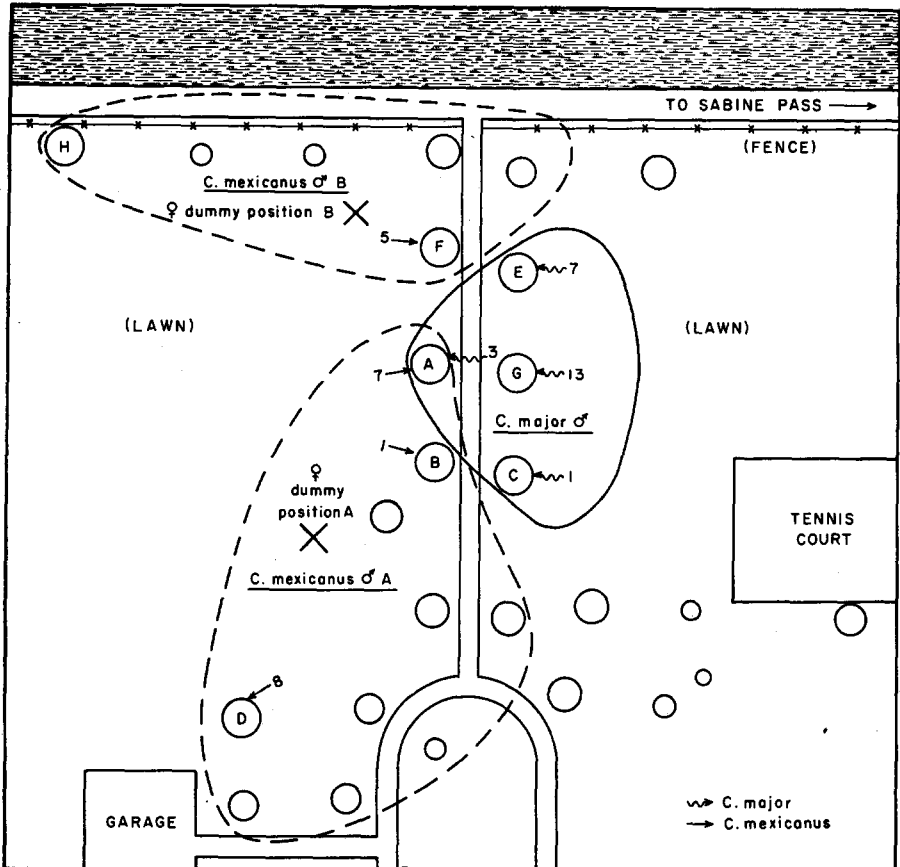

Fig. 14. Territories of male *Cassidix* at mixed nesting colony on grounds of Sabine Coast Guard Station, Jefferson County. Texas. Numbers and arrows indicate numbers of feeding trips made to nests in trees by females of *C. mexicanus* (straight arrow) and *C. major* (undulating arrow).

oaks and other shade trees. *Cassidix major* was not seen in the city, but at the western edge of Port Arthur we observed a single adult male and six to ten females of this species in a cattail marsh on June 2 and 3, 1959; and a few individuals were seen in the northeastern outskirts on April 4, 1960. One and one-half miles west of Port Arthur, a small colony consisting of one adult male and six females of *C. major* was located in willows along a canal, and numerous females and juveniles were seen foraging in marshes and fields adjacent to the canal. It is likely that several large breeding colonies of *C. major*

were located in the extensive marshland west of Port Arthur and along the Neches River between Port Arthur and Beaumont.

Sabine and Sabine Pass area, Jefferson County.—In this area, *C. major* was abundant in marshes and agricultural fields, as our records, shown in figure 3, indicate. Breeding colonies were found in 1959 at the following localities: 3 miles north of Sabine Pass (colony of four males and approximately 15 females in low bushes in a marshy area); 2 miles south of Sabine (colonies in cattail marsh, and males singing from tamarix, *Tamarix gallica,* along a road adjacent to the marsh); 6 miles west-southwest of Sabine Pass (small colony in hackberry trees between pastures); and 4 miles south-southwest of Sabine Pass (small colony in grove of live oak trees). Lone individuals or small groups of *C. major* were seen feeding at many localities in this area, and males were frequently noted singing and displaying from telephone poles and wires adjacent to marshland.

Cassidix mexicanus occurred only in the town of Sabine Pass and on the grounds of the Coast Guard Station at Sabine; and in both localities it was closely associated with *C. major.* At the Coast Guard Station, two adult males of *C. mexicanus* and an adult male *C. major* held territories in small live oak trees (fig. 15). The activities of these birds and of several other individuals of *C. major* in the adjacent Dick Dowling Park were studied from June 3 to 5, 1959. Territories of the three adult males are indicated in figure 14; lines encompass areas in which the males spent most of their time and from which other males were driven. Territorial defense was uncommon, but this is the normal situation late in the breeding season when territories have been established for a considerable period of time. On one occasion, male B of *C. mexicanus* flew to tree A and was driven away by strong hostile display of male A of *C. mexicanus.* Later the same day, male B of *C. mexicanus* was chased from tree E by the male of *C. major.* Once the male of *C. major* flew to tree H and was threatened by male B of *C. mexicanus* and by another male of *C. major* which held a territory beyond the limits of the study area. After a few minutes, the male of *C. major* which we were observing returned to tree G within his own territory.

Tree A was held jointly by male A of *C. mexicanus* and the male of *C. major.* When the two birds frequented the tree simultaneously, they often exchanged threats, although neither attempted to chase off the other. Other studies of territoriality in *C. mexicanus* (Selander, MS) have shown that two males often hold some part of their territories in common, reaching an agonistic stalemate, at least temporarily.

Adult and first-year males which entered one of the territories were immediately approached and driven off by the resident male, either by hostile display at close range or, less frequently, by actual attack. Male A of *C. mexicanus* remained within his territory most of the time, but male B of *C. mexicanus* often left the study area to forage in the adjacent marsh; and the male of *C. major* frequently foraged on the lawn by the tennis court or flew to feed in Dick Dowling Park and in the marsh across the Sabine Pass road.

At the time of our study, females were feeding young, some of which had recently left the nests but were unable to fly and remained near the nests. Females foraged singly or in small groups, which were often composed of both species, on the grounds of the station, along the road, in the marsh, and in fields a quarter-mile from the colony. In the study area, they freely perched and foraged in trees within the territories of males of their own and the other species, where they were never threatened or attacked by the males. By recording feeding visits made by females definitely identified to species, we were able to determine the spatial arrangement of nests, with significant results, as shown in figure 14. Females of *C. major* brought food to trees A, C, E, and G, all of
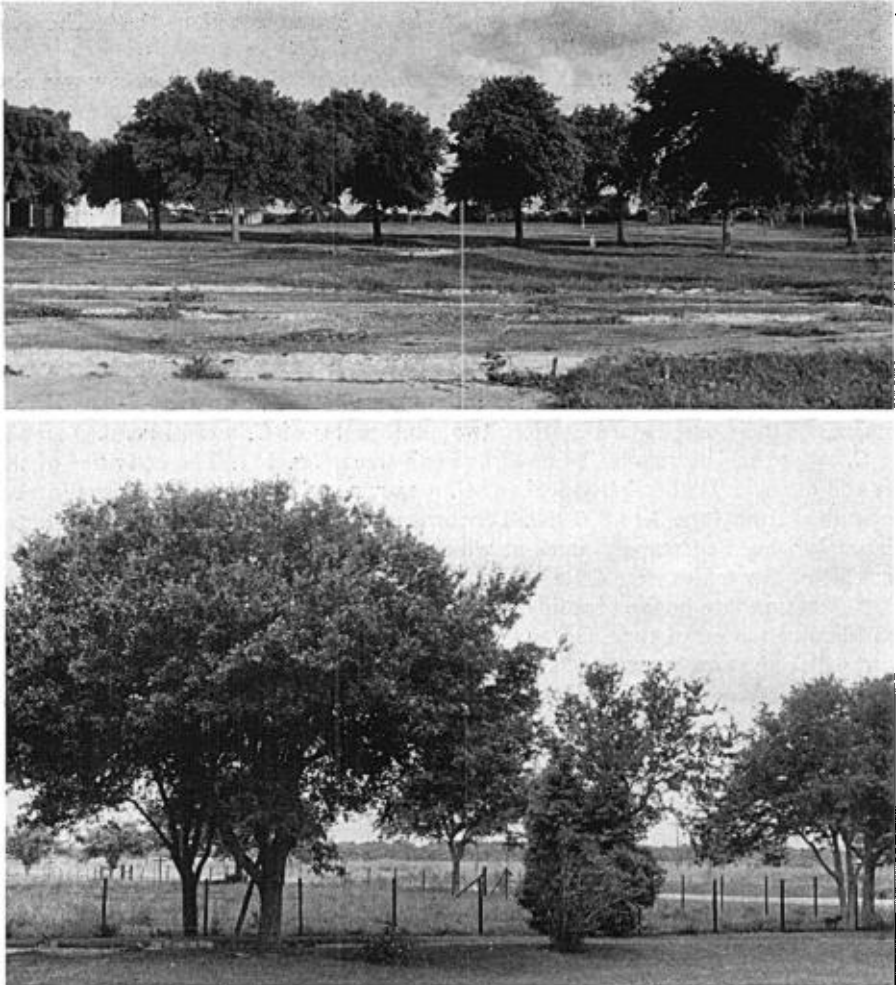
Fig. 15. Above: grounds of the Coast Guard Station at Sabine, Texas, where *Cassidix major*
and *C. mexicanus* nested in a mixed colony in 1959.
     Below: location of a mixed nesting colony at the farm of Edwin C. Fontenot in farmed
prairie near Vinton, Louisiana.

which were within the territory of the male of *C. major*; and females of *C. mexicanus*
were seen carrying food only to trees within the territories of males of *C. mexicanus*.
Both species nested in tree A, but we were unable to determine the spatial relationships
of nests in that tree. We estimated that at least five females of *C. major* and six females
of *C. mexicanus* were feeding young in the study area; probably a few others were still
incubating. On June 5, the resident males and several females and juveniles were col-
lected to verify our field identifications of species.

     Bridge City, Orange County.—A mixed colony attended by 10 adult males of *C. mexi-
canus* and two adult males of *C. major* was studied at this locality, between Orange and
Port Arthur, on April 3 and 4, 1960. Males of *C. mexicanus* occupied positions in the
top of a tall clump of canes, where their territories in some cases did not exceed three

feet in diameter. From 15 to 20 females of *C. mexicanus* were building or incubating in the cane. The territory of male A of *C. major* included the northern tip of the cane clump and an adjacent small oak tree; four females of *C. major* were nesting in positions indicated in figure 16. The other male of *C. major* (B) seemed to be attempting to establish territory in the center of the cane clump, where he had many lengthy disputes with males of *C. mexicanus,* and he also spent much time in a neighboring large pecan tree. Females of *C. major* were not nesting in the central part of the cane clump and neither species was nesting in the pecan.
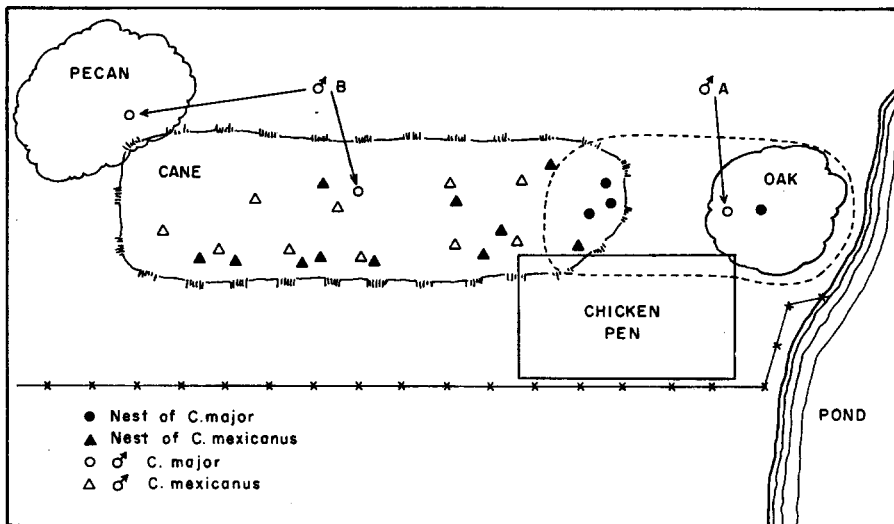

Fig. 16. Spacing of *Cassidix* at mixed nesting colony near Bridge City, Orange County, Texas.

Male A of *C. major* repeatedly defended his territory against males of *C. mexicanus,* but, in his absence, one or two of the neighboring territorial males moved over to occupy his area. Whereas it was estimated that individual males of *C. mexicanus* remained on their territories 80 per cent of the time, male A of *C. major* was present in his territory only about 25 per cent of the time; often he flew after passing females or ranged out to surrounding fields to solicit females or to sing in trees. Male B of *C. major* was even less constant in his attendance at the colony; on his return he usually flew to the cane to solicit females of *C. mexicanus* or he displayed to females of either species in the pecan tree. Females of *C. major* did not often range into territories of *C. mexicanus,* but a female of *C. mexicanus* nested in the territory of male A of *C. major,* where she had several minor squabbles with females of the other species and a long fight with another female *C. mexicanus.* Other females of *C. mexicanus* often perched within the territory of male A of *C. major* and were solicited by him.

Pinehurst area, near Orange, Orange County.—On June 6 and 7, 1959, the two species were found nesting in close proximity in meadowland near the settlement of Pinehurst. In one area (fig. 17) an adult male *C. major* held a territory centering on two sweetgum trees (*Liquidambar styraciflua*). This bird threatened or pursued all males of either species which flew over, and on three occasions he engaged in vigorous song and display bouts with an adult male *C. mexicanus* in tree C; finally the latter retreated to tree F. Two females of *C. major* collected in tree A had brood patches, and another
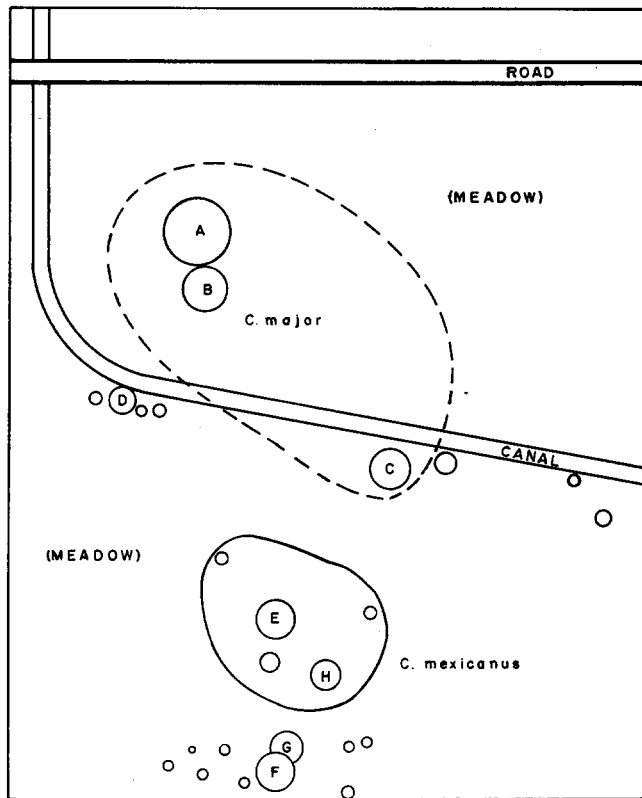
Fig. 17. Territories of *Cassidix* near Pinehurst, Orange County, Texas.

female was seen carrying nesting material to tree A. Of the trees regularly frequented by the male of *C. mexicanus*, only E held active nests.

Winnie, Chambers County.—In farmland near Winnie both species were nesting in a tall cottonwood tree and a live oak in a farmyard on June 10.

12 miles east of Anahuac, Chambers County.—Along Texas Highway 73 west of Winnie, both species were common in rice fields on June 10, 1959, and we found one adult male and two females of *C. major* in a very large nesting colony of *C. mexicanus* in a farm yard. At least 100 females of *C. mexicanus* were attending nests in a row of six trees, at the end of which two nests of *C. major* were located in a large sycamore within a territory defended by the lone male of the same species. The two nests were placed six feet apart and were only six feet from nests of *C. mexicanus* in an adjacent tree.

High Island, Chambers County.—On April 17, 1938, Lowery obtained specimens of the two species at a mixed breeding colony on the Bolivar Peninsula, 10 miles west of High Island. In 1959, we found only *C. mexicanus* between Galveston and High Island.

Vinton area, Calcasieu Parish.—The largest mixed colony studied was located in farmed prairie along U. S. Highway 90 near Vinton, about 10 miles west of Sulphur, Louisiana (fig. 3). Here approximately 30 females of *C. major* and 90 females of *C. mexicanus* were nesting in oaks and elms in the front yard of the home of Mr. Edwin C. Fontenot and in small oaks planted along the highway west of Fontenot's residence (fig. 15). Our observations and collections were made in this area on June 8 and 9, 1959.

TABLE 9

CONTENTS OF NESTS OF CASSIDIX MEXICANUS FROM THE FONTENOT COLONY

Contents	Oak A	Oak B	Oak C	Combined
Nest empty	4	14	3	21
1 egg	1	3	2	6
2 eggs		4	2	6
3 eggs	3	5		8
4 eggs		4		4
Small nestlings	1	6	3	10
Large nestlings		6	5	11
Totals	9	42	15	66

The activities of *C. mexicanus* centered in the large trees near Fontenot's house. In one oak (B in fig. 18) we examined 42 nests of *C. mexicanus*, 28 of which held eggs or young. The contents of these nests and of nests located in oaks A and C are shown in table 9 to demonstrate the lack of synchrony of breeding activities of the females, a feature previously noted in the Austin region (Selander, 1960:34). Asynchrony is also characteristic of breeding colonies of *C. major* in the zone of sympatry, but close synchrony has been reported in nesting colonies of this species in marshes at Avery Island, Louisiana (McIlhenny, 1937).

Three active nests of *C. major* were found in an oak just north of oak A, and both species were nesting in close proximity in a row of 17 small oaks along the highway. By watching females incubating or making trips to nests with food, we were able to determine the ownership of many but not all nests in these trees, as indicated in figure 18. Note that most trees held nests of one species only but that both nested in trees 10 and 14. The majority of nests held well-incubated eggs or young, and most of the empty nests appeared to have been used; at least none was in construction.

Several territorial squabbles between females of the same or different species were noted, but agonistic interactions were at a minimum since territories were well established and all females were busy incubating or caring for young. Undoubtedly, many males had deserted the colony, for we estimated that only 25 *C. mexicanus* and 5 *C. major* were present, and these birds spent relatively large proportions of their time in fields away from the colony.

The colony was visited again on April 1, 1960, at which time the breeding season was just beginning. Several adult males of *C. mexicanus* had established territories near the house but females were not yet building there. In four hours of observation along the highway west of Fontenot's residence, we recorded the following territorial and other behavior of interest.

Tree 10 was held by a male of *C. mexicanus*. Once as he returned to the tree from a foraging trip, two females of the same species which had been perched in tree 9 joined him; and later, a female of *C. mexicanus* left a passing flock to join him briefly before flying on.

Tree 11 was held by a male of *C. major* which moved over to tree 10 in the absence of the resident male of *C. mexicanus* but retreated upon his return.

Trees 12, 15, 16, and 17 were defended by a particularly vigorous male of *C. major*, which, in passing between trees 12 and 15, flew low to the ground, apparently to avoid arousing a male of *C. mexicanus* holding trees 13 and 14. The following extracts from our notes reflect the pace and variety of the activities of this male of *C. major*:

"Solicits a female *C. major* which came to tree 12. Flies to a pole across highway but hurries back to tree 16 to drive off an adult male *C. mexicanus* which had stopped there; the latter retreats to tree 13 and is followed and again driven off by the male *C. major* (despite the fact that the latter
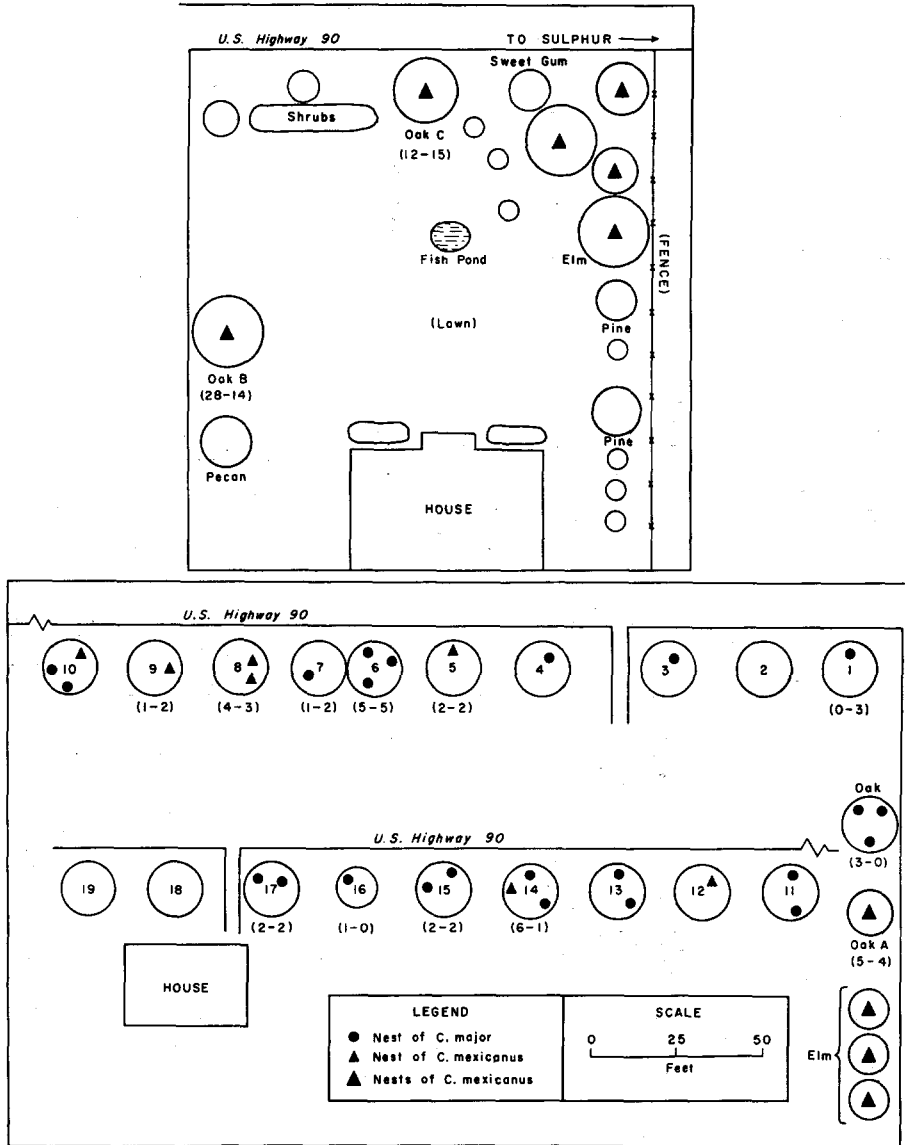
Fig. 18. Distribution of nests in large mixed nesting colony of *Cassidix* near Vinton, Calcasieu Parish, Louisiana, in June, 1959. Upper part of figure adjoins right side of lower segment. Most trees (indicated by circles) are numbered or lettered for identification; numbers of nests containing eggs or young and numbers of empty nests are indicated in parentheses. For example, tree 14 held six nests containing eggs or young and also held one empty nest. (Error: numbers below oak C should read 12–3.)

does not hold tree 13). Drives another adult male *C. mexicanus* from tree 12. Engages in a long hostile display bout with the male *C. mexicanus* in tree 13 but breaks off to return to tree 12 where he drives off another "transient" male *C. mexicanus* which had stopped there. Flies singing on the wing to the base of tree 17 to solicit two female *C. major*; notices a male and female *C. mexicanus* in tree 16 and flies up to threaten the male; gives solicitation display to the female *C. mexicanus* after the male had

flown to tree 13; in a moment the female also flies to tree 13. Threatens off a "transient" adult male *C. major* in tree 15; the latter flies to tree 13 and is immediately chased away by the resident male *C. mexicanus*. In tree 16 gives head-up display to a first-year male *C. mexicanus* which soon flies. Gives strong solicitation to a female *C. major* which is beginning to build a nest in tree 17."

Tree 18 and two trees to the west (not shown in fig. 18) were held by a male *C. major*; three female *C. major* were building nests in tree 18.

DISCUSSION

ISOLATING MECHANISMS

The absence of demonstrable hybridization between the two grackles in their zone of sympatry indicates the existence of one or more effective biological isolating mechanisms (Mayr, 1942:247). In the present case, seasonal isolation is not operative and habitat differences serve only to limit rather than to exclude contact between individuals of the two species. Also, physical inconformity of the copulatory organs (mechanical factors) is unlikely. In the absence of laboratory experiments on hybridization and data on viability and fertility of hybrids that might result from interspecific matings, we can only speculate concerning possible genetic or physiological barriers to interbreeding. It is apparent, however, that in the present situation the first, if not the only, "line of defense" against hybridization is an ethological barrier. Our thesis is that the females have the selective role in mating and distinguish between males of the two species, largely on the basis of their behavioral differences, both at the time of nest site selection and at the time of mating. Males, on the other hand, show no obvious preference for females of their own species. Our interpretation is similar in many respects to that proposed by Lanyon (1957) in his study of sympatric species of meadowlarks.

The behavioral tendencies in courtship.—To appreciate the function of species discrimination by the females as an isolating mechanism, it will be instructive to consider the "motivation" or complex of tendencies (Hinde, 1955–1956) underlying courtship and mating behavior in *Cassidix*. This brief account summarizes the results of observations and experimental studies of *C. mexicanus* which were undertaken by Selander largely within the theoretical framework developed by European ethologists (see Hinde, 1959, for a recent review). We refer particularly to numerous recent studies demonstrating that the nature of courtship behavior depends on the absolute and relative strengths of conflicting tendencies to attack, flee from, and behave sexually toward a potential mate.

Adult males of *Cassidix* solicit females and are ready to mate at the first appearance of the females at the nesting colonies. The courtship behavior of the male, which includes both ruff-out and solicitation displays with accompanying vocalizations, is of the fAM type, as characterized by Morris (1956), in which aggressive (A) and mating or sexual (M) tendencies are relatively strong and there is little suggestion of a fleeing (f) tendency among the component movements and postures (Marler, 1956:4) of his displays. As the male approaches in display, the female normally flees, either running or flying, in which event, the male may (1) discontinue courtship, (2) fly to the female and continue courtship display, or (3) chase her in flight, in which case temporary dominance of the aggressive tendency is often shown by song and, occasionally, by an outright attack on the female. Under no circumstances do females of *C. mexicanus* attack or show other hostile behavior toward adult males; but, in *C. major*, an aggressive tendency probably underlies the ruff-out displays that are occasionally directed to males.

As the female finishes nest building, she becomes more receptive to the males and tends to flee shorter distances as they approach; she now gives generalized or solicitation display and calls to the displaying male, or she may attract males to her by giving these

displays. Only when her fleeing tendency has been reduced relative to her mating tendency does she display at high intensity in a fixed position at the approach of the soliciting male. This change in her behavior presumably is caused by a combination of factors, including the displays of the males, hormones, and, possibly, the actual performance of her own generalized and solicitation displays.

Feminine solicitation display resembles in some respects the begging posture of young birds and is perhaps "designed" to reduce, or at least not to increase, the aggressive tendency of the approaching male (Marler, 1956:143). When presented with female dummies in solicitation posture, males attempt copulation then often attack, presumably because stimuli from these inanimate females do not effectively reduce the aggressive tendencies of the males.

Experiments on species recognition by males.—In the course of our studies, we often witnessed males of one species giving solicitation displays and vocalizations to females of the other species. And in mixed breeding colonies, females of one species freely perch or forage in trees located within territories of males of the other species, where they are often solicited but never threatened or attacked by the males. These observations suggest that males show no particular preference for females of their own species; and, indeed, it seems probable that they do not distinguish between them. To test this hypothesis, on June 4, a female dummy of *C. major*, which was mounted in copulatory solicitation posture with the head and tail elevated and which had a white cotton "eye," was placed on the lawn within the territory of male A of *C. mexicanus* (position "A" in figure 14) on the grounds of the Coast Guard Station at Sabine Pass. A few minutes later, the male *C. major* that occupied an adjacent territory flew to the dummy and, without preliminary display, mounted and attempted copulation. Almost immediately, male A of *C. mexicanus* flew down from tree D, drove the male of *C. major* from the dummy, and copulated with the dummy, also without preliminary display.

The dummy was then moved to position "B" within the territory of male B of *C. mexicanus*. After several females had approached the dummy, male B of *C. mexicanus* flew down from tree F, walked to the dummy, and mounted. After attempting to copulate, he walked away, foraging and giving *chut* warning notes. Five minutes later, the male of *C. major* flew to the dummy from tree G, solicited briefly, and mounted. At once he was driven from the back of the dummy by a vigorous attack by male B of *C. mexicanus*. A long bout of head-up display followed, in which male B of *C. mexicanus* seemed to dominate. He then again mounted the dummy, but he was attacked and knocked from the dummy by the male of *C. major*. This activity attracted male A of *C. mexicanus*, who arrived on the scene just as the two other males were beginning a second bout of head-up display. The three males displayed for about a minute, at which time the male of *C. major* and male A of *C. mexicanus* returned to their respective territories. The other male remained within ten feet of the dummy for several minutes but did not mount again.

This experiment demonstrates that males of *C. mexicanus* will mount and attempt to copulate with female dummies of the other species. The fact that the "eye" of the dummy was white, rather than brown or yellow, is probably without significance, since our earlier work has shown that males of *C. mexicanus* will solicit and attempt to mate with dummies of their own species having brown eyes. They will also react to headless dummies of their own species and to female dummies of other species, including *Quiscalus quiscula* and *Euphagus cyanocephalus*. We also have records of males attempting copulation with brown-eyed juveniles and first-year males of their own species. Further, experiments performed in March, 1960, show that males of *C. major* will readily solicit, mount, and copulate with female dummies having bright yellow eyes (Selander, MS).

Conclusions.—Considering the type of courtship and mating pattern shown by *Cassidix*, it is clear that the actual time of mating is determined to large degree, if not entirely, by the female. It is also obvious that the female has every opportunity to select her mating partner from a number of males that direct solicitation display to her. The fact that males show no obvious species discrimination or selectivity leads us to conclude that heterospecific mating is prevented by the females' consistent choice of mates of their own species at the time of mating. And since females in mixed nesting colonies usually build their nests within the territory of a male of their own species, it is also apparent that the females actually recognize and choose males of their own species before mating occurs. Probably all of the many behavioral differences between males that we have described in a previous section have significance as a basis for species recognition by the females, although the marked species differences in song and ruff-out display undoubtedly are of paramount importance in this regard.

TIME OF SPECIATION

The present distribution of *C. major* and *C. mexicanus*, with a narrow zone of sympatry in Texas and Louisiana, exemplifies a pattern common to a considerable number of species- and race-pairs of vertebrates in the Gulf region and suggests a history of secondary contact of populations following Pleistocene disjunction. A large body of paleontological and zoogeographical evidence examined by Deevey (1949, 1950) and Blair (1952, 1958a) supports the thesis that climatic and ecological changes in the Pleistocene, particularly during glaciation stages in the north, were sufficiently drastic to force withdrawal of warmth-adapted coastal-plain species into separate eastern (Floridian) and western (Mexican) refuges, where differentiation of populations proceeded in geographical isolation. Secondary contact was later established by post-Wisconsin spread from these isolated centers of differentiation.

The Pleistocene disjunction theory has the added advantage of offering a plausible explanation for the present-day restriction of *C. major* to coastal habitats. Notwithstanding major climatic changes in the southern United States, coastal marshes would doubtless have persisted throughout the Pleistocene in Florida and, probably, elsewhere along the southern Atlantic and Gulf coasts. Possibly with the elimination of favorable inland habitat situations by changing climatic conditions, the ancestral form of *C. major* became largely confined to coastal marshes, where there evolved special adaptations which continue to limit the ecological range of its modern representative. In contrast, the population represented today by *C. mexicanus* may have escaped enforced restriction of ecological range by retreating into México, where it continued to occupy diverse habitat types.

In considering causes for the relatively narrow ecological range of *C. major*, the possibility of restriction through competition with the Common Grackle should be examined, but there are as yet no concrete data bearing on this problem. We note, however, that *Quiscalus* occurs abundantly throughout the range of *C. major*, where it occupies a variety of habitats, some of which are not unlike those utilized by *C. mexicanus* (see Bent, 1958). Sympatry of *C. mexicanus* and *Quiscalus* occurs only locally in central and northern Texas.

Although we are suggesting, as the most likely hypothesis, that *C. major* and *C. mexicanus* reached the species level of differentiation in geographical isolation in the Pleistocene, it is, of course, possible that the two grackles had actually evolved effective isolating mechanisms in pre-Pleistocene times. Indeed, it is possible that *C. major* is actually less closely related phylogenetically to *C. mexicanus* than to another marsh-dwelling species, *C. palustris*. Following this line of argument, one could speculate that

C. major and *C. palustris* evolved from a common ancestral population, the range of which was divided and restricted by the invasion of a second stock, represented today by *C. mexicanus*, moving northward into México from Central and South America. It is also possible that the restricted distribution of *C. nicaraguensis* may be explained on this basis, and a study of this species may be expected to provide data of value in reconstructing the phylogeny of the genus *Cassidix*.

THE QUESTION OF CHARACTER DISPLACEMENT

Where closely related species are sympatric, selection may cause a divergence or displacement of characters (Brown and Wilson, 1956) that facilitates species recognition (reinforcement of isolating mechanisms; Blair, 1958b; Sibley, 1957), reduces interspecific competition, or serves both functions simultaneously (Moore, 1957). This process is perhaps most likely to occur when selection against hybrids of inferior viability or fertility is operative, but, according to our view (see also Sibley, 1957:101), accentuation of differences in characters having significance in species recognition or in reduction of competition might be expected even in the absence of hybridization.

With respect to behavior, we find in *C. mexicanus prosopidicola* no clear evidence of reinforcement of species characteristics in the zone of sympatry; vocalizations and displays of birds in this zone do not differ significantly from those of individuals in central Texas. In the case of *C. major*, we cannot comment on reinforcement, since we have not compared the behavior of sympatric and allopatric populations of this species. Incipient displacement of morphological characters in males is perhaps indicated by the fact that males of *C. mexicanus* tend to be slightly larger in the zone of sympatry than in the Austin region, yet these minor variations could represent merely normal geographic variation unaffected by reinforcing selection. It is noteworthy that females show no evidence of displacement. All things considered, we are inclined to believe that the two species underwent such strong behavioral differentiation in geographical isolation that there was no necessity for reinforcement of isolating mechanisms after sympatry was established. Even if there is selection for character displacement in the very narrow zone of sympatry, it is probably being effectively countered by gene-flow from adjacent allopatric populations that are not subject to this selection.

Assuming that the eastward expansion of range of *C. mexicanus* continues, it will be interesting to observe the ecological relationships of the two grackles as the ecologically more restricted species *C. major* becomes sympatric with *C. mexicanus* over an increasingly large area. Since the ecological range of the latter species includes marshland, there is every reason to believe that it has the potentiality to invade the extensive areas of this habitat in coastal Louisiana that are now occupied by *C. major*. Yet *C. mexicanus* has not managed to displace *C. major* from marsh habitat in the present zone of sympatry, and it seems probable that *C. major*, with a long history of adaptation to this habitat, will hold its own in competition with the other, ecologically more versatile species. We are planning experiments to test the hypothesis that the superior adaptation of *C. major* to coastal marshes is due, at least in part, to a greater tolerance to salt in water which it drinks. This is likely in view of a recent demonstration (Cade and Bartholomew, 1959) of inter-racial differences in salt tolerance in the Savannah Sparrow (*Passerculus sandwichensis*).

SPECIES LIMITS IN CASSIDIX

The discovery that *C. major* is not conspecific with *C. mexicanus* naturally raises questions as to the evolutionary status of certain other grackle populations currently regarded as subspecies of *C. mexicanus*, particularly the forms *graysoni* and *nelsoni* of the coastal plain of northwestern México. These forms have distinctive vocalizations,

and, as we have shown in an earlier section, they show degrees of morphological differentiation from the races of the Mexican plateau that are at least equivalent to that existing between *C. mexicanus prosopidicola* and *C. major major*. However, current field studies of these populations (Selander, MS) indicate that they are only racially distinct from the plateau forms of *C. mexicanus*. South of the Sierra Madre Occidental, *graysoni* intergrades, through the form *obscurus*, with *C. mexicanus monsoni* in Jalisco. In southern Arizona, where *nelsoni* and *monsoni* have recently come into secondary contact following extensions of range north from México, the relationship is not entirely clear at the present time. It has been claimed (Phillips, 1959) that the two forms are sympatric without interbreeding, but material collected in December, 1959, at Tucson suggests at least limited hybridization in that area. Analysis of this situation will be presented elsewhere.

It is noteworthy that the form *peruvianus*, which is currently considered a race of *C. mexicanus* (Hellmayr, 1934), parallels *C. major* both in color and, as noted earlier, in its apparent restriction to coastal habitats throughout its range, which extends from northwestern Perú and the Santa Marta region of Colombia north to Costa Rica (Todd and Carriker, 1922; Chapman, 1926). Mainly because field notes of Dr. Paul Slud on Costa Rican grackles suggest that the vocalizations of *peruvianus* are recognizably similar to those of *C. mexicanus* in Texas and México, we believe that intergradation between *peruvianus* and *C. mexicanus mexicanus* may be expected where the two forms meet in Nicaragua; but, in any event, the situation warrants careful investigation.

The present study should serve to emphasize the need for continuing re-examination of the decisions of the morphological taxonomists regarding species limits and relationships of allopatric or contiguously allopatric differentiates, particularly where no concrete evidence of intergradation is available. Speculative "lumping" of allopatric populations on morphological evidence alone has admittedly been of value in indicating probable evolutionary relationships, but we suggest that a stage in systematic ornithology has been reached in which there is no longer any particular merit in opinions unsupported by ecological or behavioral data.

SUMMARY

This study is a detailed comparative analysis of the morphology, ecology, and ethology of the morphologically similar Great-tailed Grackle (*Cassidix mexicanus*) and Boat-tailed Grackle (*Cassidix major*) in a 100-mile-wide zone of sympatry on the coastal plain of the Gulf of Mexico between Houston, Texas, and Lake Charles, Louisiana. Here their failure to interbreed indicates that they are good species, notwithstanding the fact that they have long been considered conspecific by morphological taxonomists.

Sympatry of the two species is believed to have been established in the present century as a result of a northeastward extension of range by *C. mexicanus* along the Gulf coast from southern Texas.

In the zone of sympatry, and, also, elsewhere in its range, *C. major* is largely confined to coastal marshland in the breeding season, whereas *C. mexicanus*, which has a greater ecological range, occurs mainly in farmed prairie and other man-made habitats.

Both species commonly nest in mixed breeding colonies, where males hold mutually exclusive territories and solicit mating with females of either species.

The mating system is promiscuous in both species, and it is suggested that hybridization is prevented by an ethological isolating mechanism involving the females' selection of homospecific mates on the basis of major differences in the displays and vocalizations of the males.

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