HYBRIDIZATION OF GREAT-TAILED AND BOAT-TAILED GRACKLES (*Quiscalus*) IN LOUISIANA

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During the 20th Century, expansion of the breeding range of the Great-tailed Grackle (*Quiscalus mexicanus*) has brought it into sympatry with its sibling species, the Boat-tailed Grackle (*Q. major*), in southeastern Texas and southwestern Louisiana (Selander and Giller 1961, Selander *et al.* 1969, Pratt *et al.* 1977). Because earlier studies (Selander and Giller 1961) that established the specific distinctness of these two forms had been questioned (Phillips *et al.* 1964), I studied interactions of these taxa in Louisiana to determine the extent of hybridization.

Study Area and Methods

My study area is in the southwestern Louisiana coastal marsh and prairie region. The marshes are broken by a number of long, narrow ridges that roughly parallel the coast. These ridges, called cheniers, are the remnants of ancient shorelines and, until recent drainage projects, were the only dry land in southern Cameron and Vermilion parishes (Russell and Howe 1935). All towns and most rural habitations in the area are located on the cheniers. Originally wooded, the cheniers are now much altered by agriculture and grazing. They are ecological islands that provide the only forest and scrub habitat in a largely marshy area. The bulk of my observations were made in April, May, and June of 1972 and 1973. I surveyed grackles along roads throughout Cameron and Vermilion parishes and adjacent portions of other parishes. I attempted no precise population estimates, but rather assessed the ratio of Great-tailed to Boat-tailed grackles and sex ratios for each species. Several mixed breeding colonies were visited frequently and observed for extended periods.

At the end of the breeding season each year, specimens of both species were collected and deposited at Louisiana State University Museum of Zoology (LSUMZ). The iris color of each specimen was noted on the label. Before preparation, the following measurements (see Baldwin *et al.* 1931) were made of specimens: wing length (chord), tail length, bill length from anterior edge of nostril, and tarsometatarsus length. In addition, study skins used by Lowery (1938) in his investigations of *Q. mexicanus prosopidicola* were measured and compared with the new material. Any specimens believed to be hybrids were prepared as study skins, but most others were skeletonized. The following

measurements of the skeletons were made: skull length, skull width, skull depth, frontonasal (nasal bone) width, humerus length, femur length, sternum length, and ilium length. All were taken in the manner of Robins and Schnell (1971) except the ilium length which they did not use. An analysis of variance was conducted for the skeletal data.

The Zone of Sympatry

Boat-tailed Grackles are abundant throughout the coastal marshes of Louisiana and are found only rarely in upland habitats (Lowery 1974). Great-tailed Grackles have been present in the state since the late 1950's, but the earliest colonies were north of the coastal marshes in the prairie region of central and southwestern Louisiana (Pratt *et al.* 1977). Thus the two large grackle species were not truly in contact during the earliest stages of the Great-tailed Grackle's eastward expansion.

Since 1968 Great-tailed Grackles have expanded southward in the prairies just north of the coastal marshes of Cameron Parish. They were present at the Moore-Odom Ranch at Gum Cove, where Boat-tailed Grackles are abundant, on 25 March 1972 and nested there in small numbers in both 1972 and 1973. The residents of the ranch said that the birds had been present for "several years." I also noted Great-tailed Grackles in Hackberry during April 1972, but I found no nesting colonies there.

I first saw Great-tailed Grackles on the coastal cheniers on 10 April 1972. Four males were perched in saltcedar (*Tamarix gallica*) bushes six miles west of Holly Beach. The birds remained at the spot for a week then disappeared. Subsequently on 12 April I observed one male and one female Great-tail at Little Chenier. On 16 April there was a small group of males and females of this species in a grove of live oaks near the Mermentau River bridge on La. highway 82. The birds remained there for several days, but on 23 April I could not find them. On 22 April I had found scattered Great-tailed Grackles along the highway between Oak Grove and Cameron.

On 25 April 1972 I discovered several Great-tailed Grackles nesting among a large group of Boat-tailed Grackles in a grove of black willows (*Salix nigra*) about four miles west of Oak Grove. I also obtained evidence of limited breeding by Great-tailed Grackles at other localities on the cheniers after this date, but I estimated that no more than 20 nests altogether of this species were active in colonies on the cheniers in 1972.

The following year the situation had altered dramatically on the cheniers with regard to the occurrence of Great-tailed Grackles. As early as 30 March I found a male Great-tailed Grackle in the willows west of Oak Grove and a foraging flock of both sexes in Cameron. Both males and females were setting up a nesting

colony on 31 March in a residential area east of Cameron in trees they had occupied the year before in small numbers. On 6 April I saw Great-tailed Grackles at several places along the highway between Oak Grove and Cameron, and in Cameron 12 male Great-tails had by then established territories in a row of large live oaks. That new colony remained active throughout the breeding season. In 1972 there had been no Great-tailed Grackles as far west on the coastal ridge as Johnsons Bayou. In 1973 I saw a male there on 31 March and found active nests of the species behind the Johnsons Bayou School on 8 June. The number of Great-tailed Grackles on the cheniers in 1973 was approximately three times as large as in 1972.

Before 1973, Great-tailed Grackles were largely absent from Louisiana in winter. A few birds had been reported during the winter months from widely scattered localities, mostly outside the study area. Although most of the Great-tailed Grackles had departed from Cameron Parish by the end of September 1973, I saw single individuals in the area throughout that winter. The winter of 1974-75, however, showed a dramatic increase in the wintering population of Great-tailed Grackles in the Cameron area. Several flocks of ten or more birds were present near the sites of nesting colonies throughout the nesting season. I noted one male bird at the Gum Cove Ranch in January 1975, the first winter record for that locality. I also noted several birds in the industrial area west of Lake Charles that winter.

The Great-tailed Grackle's range expansion mirrors previous expansions in Texas. When the species first became established as a breeding bird in Austin, it was migratory (Simmons 1925); but as its numbers increased in the area, it became a permanent resident (Selander and Giller 1961).

In both grackle species discussed here, previous studies have shown that the sex ratio in adults is unbalanced, with females greatly outnumbering males. McIlhenny (1937) claimed that this unequal ratio was a primary one present in the nestlings; but Selander (1958, 1961), by dissection of nestlings, showed the sex ratio at that stage of the life cycle to be 50:50 in both species. Thus the unbalanced tertiary sex ratio must be due to differential mortality (Selander 1966, Davis and Arnold 1972). I was surprised then to find that during the early years of this study the sex ratio of Great-tailed Grackles on the cheniers, when unbalanced at all, favored males. This imbalance was particularly noticeable in 1972, when approximately 70% of the Great-tailed Grackles I saw on the cheniers were males. This fact strongly suggests that the impetus for range expansion in this species comes from surplus males that have been unsuccessful in setting up nesting territories in the main centers of

population. That such surplus males exist in Texas was clearly pointed out by Selander and Hauser (1965).

Comparative Morphology

Both Great-tailed and Boat-tailed grackles possess a promiscuous mating system that makes determination of the parentage of any individual difficult. Furthermore, the two are very similar morphologically, but can nevertheless be readily distinguished in the field (Pratt 1974). The two are similar in most mensural characters, with the Great-tail averaging slightly larger in most dimensions than the Boat-tail in the zone of sympatry. External mensural differences between the two are no greater than the differences among the subspecies of each (Selander and Giller 1961). I examined a series of specimens from the most recent area of sympatry to determine whether intermediate birds were present that might indicate that introgression was occurring. In Table 1, alongside my data, I give ranges and arithmetic means from Selander and Giller (1961) and Selander *et al.* (1969). If allowance is made for my small sample size, my data generally agree with those of previous researchers. Most of my specimens, collected late in the breeding season, are very worn. Thus my sample has somewhat smaller means for feather measurements. The consistently smaller tarsometatarsus length in my data may be the result of differences in the technique of measurement.

Clearly, external measurements alone are not sufficient for identification of all specimens. Even though the arithmetic means are distinctly different for some characters such as wing length and tail length, there is overlap in the range of all measurements. Therefore, evidence of introgression cannot be obtained by a search for specimens intermediate in external measurements.

To explore the possibility that introgression might be revealed by skeletal characters, I examined a series of skeletons of the two species from the zone of sympatry. No skeletal specimens from this area were available to previous workers, but Selander and Giller (1961) pointed out that skeletal differences are greater among Great-tailed Grackle subspecies than between Boat-tailed Grackles from Florida and Great-tailed Grackles from Texas. Most of the skeletal measurements show overlap (Table 2), and in many cases the means for the two species fall within one millimeter of each other. Nevertheless, T-tests revealed statistically significant interspecific differences for the following measurements: skull depth, frontonasal width, humerus length, illium length, femur length, and sternum length. The differences are somewhat more pronounced in males than in females. Two characters, sternum length and illium length, appear to be diagnostic for the two species, at least for males, but the

small size of the sample dictates caution in making generalizations. I found no obvious qualitative differences between the skeletons of the two species.

Clearly, external measurements of these birds are of only limited use in the search for possible introgression, even though they are useful for identification of specimens in the hand. Larger samples of skeletal specimens are needed to assess properly the value of osteological features in this regard. Unfortunately, the diagnostic characters, iris color and vocalizations, are impossible to preserve in museum specimens.

Hybridization

On 14 April 1973 while observing a colony of large grackles in a grove of live oaks approximately five miles east of Cameron, I heard vocalizations of males of both species and assumed that the

Table 1. Means and ranges of measurements of Great-tailed and Boat-tailed grackles from the zone of sympatry with the results of this study (Column A) compared with those (Column B) of Selander and Giller (1961) and Selander *et al.* (1969). All measurements are in millimeters.

		Quiscalus major		*Quiscalus mexicanus*	
	Measurement	**A**	**B**	**A**	**B**
Adult Males	Wing length	171.2 (161.5-181.0)	174.3 (170-180)	184.1 (176.5-192.0)	188.2 (181-202)
	Tail length	171.3 (151.0-185.5)	176.8 (171-195)	198.6 (191.0-210.5)	208.2 (190-233)
	Tarsometatarsus length	42.6 (41.0-44.5)	46.5 (43.2-49.1)	43.1 (37.5-48.5)	46.9 (45.2-48.5)
	Bill length	31.1 (29.5-33.0)	30.8 (29.2-33.3)	31.5 (30.0-34.0)	31.8 (30.0-34.1)
	Bill depth	12.8 (12.5-13.0)	11.5 (10.8-12.7)	13.4 (13.0-14.0)	12.2 (11.7-12.8)
Adult Females	Wing length	133.9 (131.0-137.5)	137.2 (133-144)	143.0 (138.5-147.5)	144.5 (139-150)
	Tail length	127.4 (123.0-137.5)	130.0 (118-137)	139.8 (133.5-144.5)	145.6 (128-159)
	Tarsometatarsus length	34.8 (33.5-37.0)	39.0 (36.6-41.2)	34.0 (31.5-38.0)	38.9 (38.2-40.9)
	Bill length	25.5 (25.0-26.5)	25.0 (23.1-26.6)	24.1 (23.0-25.5)	24.6 (22.7-29.0)
	Bill depth	10.5 (10.0-11.0)	9.5 (8.9-10.1)	10.7 (10.5-11.5)	10.0 (9.5-10.4)

colony was mixed. A male, which I identified as a Great-tail on the basis of his yellow eyes, was defending a teritory near the highway. However, calls of the Boat-tailed Grackle type, that I had assumed were being given by an unseen dark-eyed bird, were being produced by the yellow-eyed bird. The bird's posture resembled that of typical male Boat-tailed Grackles. The call most frequently given by the bird was the harsh *jeeb-jeeb-jeeb* call characteristic of the Boat-tails. Occasionally this call was followed by the distinctive ascending whistle of the Great-tailed Grackle. (For a discussion of vocal differences in these birds, see Selander and Giller 1961, Pratt 1974.) On subsequent visits to the colony, I repeatedly heard mixed vocalizations from a bird, presumably the same individual. On 20 May it gave the *jeeb* call followed by the ascending whistle. After moving to another perch, the bird repeated the *jeeb* call, but this time followed it with the peculiar *chewechewe* vocalization of the Great-tail. I collected the bird (study skin LSUMZ 73334).

The bird had a wing length of 176.0 mm and a tail length of 184.0 mm. Thus, in the only two measurements that do not show wide overlap between the species (Table 1), the specimen falls within the range of the Boat-tailed Grackle and well outside that of the Great-tailed Grackle. Therefore, this individual was the size of a Boat-tail with the eye color of a Great-tail and gave vocalizations characteristic of both species. The most likely explanation for such anomalies is that the bird is a hybrid.

On 2 June 1973, I collected a first-year male grackle among several birds from a colony 10 miles south of Sulphur, Calcasieu Parish. I identified it at the time of collection as a Great-tail on the basis of eye color. Its linear dimensions (wing 169.5 mm, tail 161.0 mm), however, fall within the range of measurements for first-year male Boat-tails as given by Selander and Giller (1961). Earlier in the season I had observed a first-year bird at this locality that gave vocalizations of the Boat-tailed Grackle type, but had bright yellow irises. I also thought that the bird was the source of some whistles of the Great-tailed Grackle type, but I was unable to confirm this suspicion. Attempts to collect the bird when first observed were futile, and I did not see it again at the site prior to 2 June. Whether the bird shot on that date was the bird with the unusual vocalizations could not be ascertained.

On 9 June 1973 I collected several individuals of both species at a colony three miles west of Oak Grove. Among them was an adult male with clear yellow eyes with a wing length of 172.0 mm and a tail length of 173.0 mm. Both measurements were well within the range for the Boat-tailed Grackle. Also, in a series of specimens prepared as skeletons in 1972, I discovered another male with

Table 2. Means, standard deviations, and ranges of skeletal measurements of Great-tailed and Boat-tailed grackles from the zone of sympatry. All measurements are in millimeters.

	C. mexicanus (male) n=4	*C. major* (male) n=13	*C. mexicanus* (female) n=9	*C. major* (female) n=9	Hybrid (male)
skull length	74.9 {1.49} (72.8-76.0)	73.7 {1.45} (71.9-76.7)	62.7 {0.77} (61.3-63.8)	62.9 {2.65} (56.3-65.7)	70.7
skull width	25.1 {0.70} (24.5-26.0)	24.5 {0.44} (23.7-25.0)	22.8 {0.77} (22.3-23.5)	22.5 {0.55} (16.7-18.9)	24.6
skull depth	19.5 {0.43} (19.1-20.1)	18.6 {0.35} (18.0-19.0)	17.7 {0.59} (16.7-18.9)	17.1 {0.31} (16.5-17.4)	18.6
frontonasal width	15.2 {0.84} (14.4-16-0)	14.6 {0.67) (13.4-15.8)	12.8 {0.45) (12.1-13.5)	12.1 {0.65} (10.7-12.9)	15.4
humerus length	43.6 {0.50} (42.9-44.1)	41.1 {0.67} (39.9-42.2)	34.8 {0.83} (33.1-33.5)	33.6 {0.59} (32.8-34.8)	40.6
femur length	40.2 {0.79} (39.1-41.0)	38.9 {0.95} (37.1-40.2)	32.6 {1.10} (30.8-33.7)	32.3 {0.58} (31.4-33.2)	37.1
illium length	39.8 {0.69} (38.9-40.5)	37.2 {0.74} (35.6-38.3)	31.7 {0.46} (30.7-32.3)	30.6 {0.18} (30.3-30.7)	37.2
sternum length	47.5 {1.14} (46.1-48.7)	43.3 {0.93} (41.8-44.9)	38.3 {1.11} (36.7-39.9)	34.9 {0.69} (34.0-36.2)	46.6

mixed characteristics. The specimen was taken on 21 June 1972 in a mixed-species grackle colony near the Lake Charles Airport. It had been identified as a Great-tail on the basis of its yellow iris, but the wing length (174.0 mm) and tail length were those of a Boat-tail. The skeletal measurements of this specimen are given in Table 2 as "Hybrid male." These measurements reveal a mosaic of parental characteristics, with a sternum length in the range for the Great-tailed Grackle and an ilium length within the range for the Boat-tailed Grackle.

Among older specimens at the Louisiana State University Museum of Zoology is another bird with probable hybrid characters. The specimen, taken on 22 October 1937 in Jefferson County, Texas, was identified as a Great-tail, but its wing (172.0 mm) and tail (177.5 mm) lengths are within Boat-tail range.

My only female specimen that is not clearly referable to one species or the other is a bird taken in the colony west of Oak Grove on 9 June 1973. The bird had a pale yellow iris in life, but the specimen is very small, the smallest in fact of either species that I have examined (wing 133.0 mm and tail 117.0 mm). The plumage is very worn, partially accounting for the small measurements, but the asymmetrical scattering of white feathers through the plumage suggests some genetic abnormality.

All six of these birds show a consistent pattern: Great-tail iris color combined with Boat-tail external dimensions. I interpret their heterospecific combination of characters to hybridization between Great-tailed and Boat-tailed grackles. Selander and Giller (1961) found several specimens suggestive of mixed ancestry. In my opinion, however, only one of these could not be easily interpreted as an individual variant. The bird (RKS 4284) is described as having a Great-tailed iris color but Boat-tailed linear dimensions. Because they had no other evidence of hybridization, Selander and Giller did not think that this represented a mixed parentage, but my recent observations indicate that it may well be a hybrid.

With a single exception, none of the seven birds just described was thought to be a hybrid when collected. All were taken in random collecting in several colonies, and thus I have no data on their vocalizations other than those previously mentioned. Their status as hybrids is based on a comparison with one relatively certain hybrid and on the fact that they cannot be unequivocally identified to species.

Only a few examples of interspecific hybridization have been reported in the Icteridae, e.g. (Gray 1958; Lanyon 1966; Selander and Dickerman 1963). The only previously reported case of hybridization involving a large grackle was that of a "nondescript blackbird" from Arizona (Selander and Dickerman 1963). That bird was shown to be a hybrid between a small subspecies of

Great-tailed Grackle and the Red-winged Blackbird (*Agelaius phoeniceus*). This mixed mating was attributed to local mate shortage. The Great-tailed Grackle was expanding its range and was rare in Arizona at the time the hybrid was collected. Any pioneering individual would have had difficulty finding a conspecific mate.

The mating system of larger grackles contributes to the likelihood that individuals will mate with other species, because promiscuous birds are more prone to hybridize than those with more restrictive mating habits (Mayr 1964). Male Great-tailed Grackles are not very selective: Selander and Dickerman (1963) found that these birds will attempt to mate with receptively postured dummy females of other species. Phillips (in Phillips *et al.* 1964) stated that male Great-tailed Grackles are so vigorous in their sexual activities that isolating mechanisms between them and Boat-tailed Grackles must surely break down in sympatry. Thus, the existence of hybrids of these two species is not unexpected.

All the hybrid Great-tailed x Boat-tailed grackles taken in Louisiana came from localities where the Great-tail was a recent arrival. Most were collected on the chenier near the coast. Because of the preponderance of males in the Great-tailed Grackle population there in 1972 and 1973, these birds very likely experienced difficulty in attracting conspecific females, a situation that closely parallels the one in Arizona that produced the "nondescript blackbird." That hybrids are rare or nonexistent in areas of longer contact between the two large grackles indicates that the zone of hybridization is a moving one and that isolating mechanisms are again effective when the usual sex ratios in both species are established. Similar patterns of temporary hybridization associated with range expansion have been found in two palearctic tits (Vaurie 1957), Sharp-tailed Grouse and Prairie Chickens (Johnsgaard and Wood 1968) and the Blue-winged/Golden-winged Warbler complex (Ficken and Ficken 1968).

Most avian hybrids are intermediate between the parental types in many, if not all, characters. Intermediacy may be apparent in qualitative characters such as coloration (Short 1965; Sibley 1958; Sibley and Short 1959 and 1964; West 1962) or measurements (Johnston 1971; Lanyon 1966; Selander and Dickerman 1963). Some hybrid characters, however, appear to be inherited through a Mendelian system of dominance. Such features are usually color patterns, as in the Blue-winged and Golden-winged Warblers (*Vermivora*) (Parkes 1951; Short 1963 and 1969a; Ficken and Ficken 1968), some icterids (Lanyon 1966; Selander and Dickerman 1963), and in terns (Hays 1975). Rarely, morphometric characters may be inherited in this manner (Short and Robbins 1967).

Characteristics of hybrid Great-tailed x Boat-tailed grackles suggest such

a Mendelian system. These hybrids are not intermediate in the usual sense but rather are composites of parental characters. A dominant-recessive inheritance scheme could partly explain why hybrids between the two grackles have not been readily detected in the past. Unless an observer is careful to note which birds produce which vocalizations in a mixed grackle colony, the mixed vocalizations of a single individual can be easily overlooked. Without vocalizations as a cue, the observer would likely mistake a hybrid for a normal Great-tailed Grackle on the basis of eye color, because differences in measurements are not readily apparent in the field.

Most mixed matings of large grackles in Louisiana probably result from pairing of male Great-tailed Grackles with female Boat-tails. As pointed out by Selander and Dickerman (1963), such matings could occur whether or not the females were receptive to the courtship displays of the males of the other species. In such a situation, a female might assume the receptive posture in response to the displays of a conspecific male but then be mounted by a nearby male of the other species. Nevertheless, the hypothesis advanced by Selander and Giller (1961) that correct mate selection by females is the most effective isolating mechanism between Great-tailed and Boat-tailed grackles is probably still valid. Song is probably the most important stimulus for the release of mating behavior in females, because plumages and displays of the two species are rather similar, but vocalizations are markedly different. Perhaps noteworthy is that all females attracted to the first known hybrid male were typical *Q. major* females. Boat-tailed Grackle-type vocalizations were much more frequent in that male's repertoire than were the calls of the Great-tailed Grackle type.

Discussion

My observations support the currently accepted taxonomic treatment of Great-tailed and Boat-tailed Grackles as separate species (e.g. American Ornithologists' Union 1983). In Louisiana the two established what Short (1969b) would call a zone of overlap and hybridization: hybrids are infrequent when compared to the number of pure parental types in the area. Avise and Zink (1988) found diagnostic differences in the mitochondrial DNA of the species. My interpretation of the situation with these two grackle species is as follows. The zone of overlap and hybridization between the two grackles is dynamic and moves eastward as the range expansion of the Great-tailed Grackle continues in that direction. This movement is shown not only by the present distribution but also by the two older hybrid specimens mentioned previously, which also came from areas where, at the time, Great-tailed Grackles were a recent arrival.

Hybridization decreases in an area when sufficient numbers of conspecific females are available for males of both species. Consequently, little or no introgression is apparent between populations in areas of long contact. Thus Great-tails and Boat-tails stand in contrast to the smaller Common Grackle (*Quiscalus quiscula*) whose two color forms ("Purple" and "Bronzed") were long considered separate species. In that case, the two types lack vocal and other behavioral isolating mechanisms, differ only in plumage color, and interbreed freely in a hybrid zone that includes Louisiana (Huntington 1952).

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