

FURTHER STUDIES OF THE GENUS *QUISCALUS*

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IN my preceding 'Auk' papers¹ on the genus *Quiscalus*, I treated of the grackles of Louisiana and Mississippi. From those States, thanks chiefly to the cooperation of Mr. E. A. McIlhenny, I have had a sufficient number of breeding males to warrant an attempt to define their ranges and relationships.

Reviewing briefly the theories advanced and results obtained: early in the history of what is believed to be their post-glacial range-extension from Florida and Texas respectively, Stone's and the Bronzed Grackles first met in southern Louisiana and completely merged by interbreeding. The area of intergradation in the State named now averages forty miles in width. North of this zone, which here trends east and west, only *aeneus*² occurs; south of it, only *stonei* and the Florida form, from which it appears to have descended, are found. In the narrow band separating the two typical primary parental forms, complete intergradation occurs. Sometimes this phenomenon is found in a single colony. The relationships of the birds under these conditions seem clear. As we enter Mississippi the problem becomes more complicated. It will be found treated in the fourth of my 'Auk' papers. Here I wish merely to state that the first papers in this series treated of the birds concerned in the most southern area of their intergradation, while in the present paper I consider them in the most northern area of their intergradation.

With the passage of time *aeneus* has extended its range northward through the interior to Slave Lake and from the upper Mississippi valley has swept eastward through New York on a front which now reaches from the lower Hudson valley eastward and northward; while *stonei* has ranged northward through Cis-Alleghenia to the northern limits of the Carolinian Fauna, including Long Island and the Connecticut valley. As we try to picture the original grackle invasion of this territory we must remember that by no means all of the newcomers were typical of either *stonei* or *aeneus*. The study of adequate material from Louisiana, and particularly Mississippi, has given us some conception of the character of the grackle population at the junction of the western with the eastern form. In this area of intergradation pure-blooded individuals are comparatively rare while intermediates

¹ Vol. 52, January and October, 1935; vol. 53, October, 1936; vol. 56, January, 1939.

² For a discussion of the correct name of this bird see Chapman, 'The Auk,' 56: 364, 1939; and Wetmore, *ibid.*, p. 505, 1939.

of mixed blood prevail. As the birds extended their range northward this prevalence of intermediates doubtless continued to mark the area of contact. If this supposition be true it follows that a proportion of the original grackle settlers in the area to which we are here devoting our attention must have been the progeny of *aeneus* and *stonei* and their variants.

Furthermore, without making an attempt to explain the origin of the habit, the fact remains that pure *aeneus* is a regular spring and fall migrant, in large numbers, through the territory of *stonei*. It is therefore more than probable that late spring migrants of *aeneus* occasionally stop in the northern part of the range of *stonei* and breed with that form as they usually, if not invariably, do wherever their breeding ranges meet. We have, therefore, a widespread territory where the northern limits of *stonei* meet the southern limits of *aeneus*, and well within which northbound migrants of the latter doubtless breed with the former. These conditions have been operative over an unknown period and their cumulative results are correspondingly confusing. In the region concerned I have found no stations occupied exclusively by pure *stonei*. Even where that form reaches its full development, specimens occur which show some trace of a remote contact with *aeneus*. But in spite of this irregularity we shall find, I think, that a pattern has been formed which contains for us a lesson in the making of species. Meanwhile, in making available the data I have acquired, I can at least serve the ends of local identification and acknowledge the generous cooperation of my colleagues.

I proceed now to an examination of the specimens, most of which have been collected in the past two nesting seasons, in the area under consideration. With the object of basing this study on breeding males I have used only specimens taken from May 1 to June 15. The resulting short collecting season, added to the difficulty of finding breeding colonies of these highly local birds, has made it impossible to cover even a limited region thoroughly and the inadequacy of my collections will soon be observed.

At the risk of repetition, which I should prefer to call confirmation, I again briefly examine the status of the two forms whose intergradation has produced *ridgwayi* and its subsequent variants. With *aeneus* we have no difficulty. In its own territory, from southern Texas to the limit of trees, it is always *aeneus*. Few wide-ranging birds are more stable. Only when, from Louisiana to Connecticut, its range meets that of *stonei*, does it depart from type and by interbreeding with that form, produce the bird we know as *ridgwayi*.

Whether *aeneus* is a species or a subspecies is a question I will not discuss here. It assuredly differs from *stonei* in external appearance more than do many unquestionably distinct forms from each other. On the other hand, the sexual relations of *aeneus* with *stonei* are certainly not those that we expect to find between species. Wherever, when breeding, the two meet, *stonei* accepts *aeneus* and *aeneus* accepts *stonei* with a unanimity which results in their complete fusion and the production of offspring presenting the characters of both parents. This is the first stage in the creation of the "Purple" Grackle complex; that is, a combination, in endless variety, of *aeneus*, *ridgwayi* and *stonei*. To consider these birds in their physical and geographic relation to one another and their environment is the chief object of this study.

Compared with that of *aeneus* the case of *stonei* is not so clear. Additional material and further study strengthen my belief that this form has originated by mutation from the Florida Grackle. The change from that species to *stonei* is apparently not associated with environment and it is completed before the range of *aeneus* is reached. So far as existing conditions go, therefore, neither *aeneus* nor its descendants plays any part in the making of pure *stonei*. Whether we follow the nascent form from Florida westward to southern Louisiana, northward into Alabama or northeastward to New Jersey and Long Island, it passes through essentially the same stages of development and reaches the same end. A series of *stonei* from Louisiana can be duplicated by one from New Jersey.

We go now to Florida in search of the origin of *stonei*. Although the Florida Grackle is the only one of the group in which the head is practically constant in coloration, it is, when compared with *aeneus*, a fairly variable bird. The Bronzed Grackle, as we have seen, through its vast range, presents no constant variation except where it meets *stonei* or their intermediates. But among Florida Grackles individuals are not infrequently found which, in varying degrees, differ from the prevailing type.

The taxonomic ornithologist attributes such departures from type to 'individual variation,' which he expects to find in most large series of birds. By the geneticist these variations, when heritable, are termed 'mutations.' They supply the stuff of which, under favorable conditions, new species are made.

Typical Florida Grackles (*Quiscalus quiscula quiscula*) have the foreback uniform bottle-green, but, on raising the feathers, a faint

iridescent band is found at the base of the broad green tip. It is the growth of this band that constitutes the first observable evidence of variation. In a series of 52 males from the Florida peninsula, nine from seven localities have this band so well developed that it may be seen without lifting the feathers, and in two of these nine birds (Pine Island, Florida, February 10, 1888—F.M.C.; Jupiter, Florida, January 2, 1920—L.C.S.) the back is barred and the feathers tipped with purple. These birds are nearer *stonei* in body color, than they are to the Florida race, and in this respect, they can be nearly matched by specimens from southern Louisiana and also New Jersey. In the color of the head, however, and in size and shape of the bill they agree with the Florida bird, indicating that they are not migrants from the north. Indeed, I have yet to see a northern grackle from Florida.

It seems, therefore, that within the heart of its range, the Florida Grackle exhibits potentialities which, under favorable conditions, may develop into *stonei*. These conditions, which doubtless include partial segregation and new associations, have apparently been found as the bird extended its range from Florida and entered territory before unoccupied by its kind. Thus, removed from the dominating influence of a population overwhelmingly pure *quiscula quiscula*, variations have been perpetuated and in time and space *stonei* has become established. We may imagine history repeating itself when we find that of six grackles from Grady County, Georgia, near the Florida boundary, only four are typical *quiscula* while one exhibits the mutant characters shown by the Pine Island bird above mentioned, and one has the green-blue head so frequently found in northern birds, but never in true *quiscula*.

Our specimens from west of Florida have been recorded in my earlier papers. Here I will state only that of nine specimens from Greensboro, Alabama, four are half way between *quiscula* and *stonei* and five are *stonei*; of ten from Lucedale, southern Mississippi, one is *quiscula*, seven are intermediate toward *stonei*, and two are *stonei*; while of 27 from Avery Island, southern Louisiana, one is *quiscula*, 15 are *stonei* and 11 are between the two.

Northward from Florida to New Jersey, my data are very incomplete. Descendants of the Florida bird range northward through Alabama apparently to eastern Tennessee whence *stonei* has been recorded from Rockwood in the Tennessee Valley and from Washington County still farther north. From Johnson County, in extreme northeastern Tennessee, Dr. Wetmore (Proc. U. S. Nat. Mus. 86: 231,

1939) records a specimen of *ridgwayi* showing that we are here within the influence of *aeneus*. In West Virginia this influence is more pronounced, though pure *stonei* still occurs. Our collection contains two specimens of *ridgwayi* and one of *stonei* from White Sulphur Springs and Mr. J. Lloyd Poland sends us specimens from eastern West Virginia as follows: Monroe County, three *ridgwayi*; Greenbrier County, one *ridgwayi*; Berkeley County, one *ridgwayi*, one intermediate nearer *stonei*; Jefferson County, one *stonei*. From Lewis County, in the north-central part of the State, a single specimen of pure *aeneus* suggests that we are near the boundary of the range of that form.

We follow now the more direct route of the Florida form and its derivatives northward through the Atlantic States. Georgia, as possibly free from the influence of *aeneus*, should have an interesting story to tell, but unfortunately, except the Grady County birds above recorded, I have no specimens from that State. Along the coast the Florida form extends at least to Charleston whence I have seen nine specimens, all referable to *quiscula*; one, however, has the head greenish blue as in many specimens of the Bronzed-Purple group. From the rest of South Carolina, and from North Carolina, we have no material. Four specimens in worn plumage from Newport News, Virginia, are apparently between *quiscula* and *stonei* but additional and better material is required to determine the status of the grackles of this district.

The National Museum collection, Dr. Wetmore reports, contains two May males between *quiscula* and *stonei*, four *stonei* and one *ridgwayi* from the District of Columbia. From Worthington Valley, Baltimore County, Maryland, we have two *stonei*, two *ridgwayi* and two intermediates. A single specimen of *stonei* from Jefferson, Frederick County, Maryland, in connection with our West Virginia records, suggests the occurrence of that form in Pennsylvania west of the Alleghenies.

The capture of two specimens of *stonei* and one intermediate toward *quiscula* in Cecil County, Maryland, northeast of the head of Chesapeake Bay, arouses a special interest in the grackles of eastern Maryland and eastern Virginia which may be removed from the influence of *aeneus* derivatives by the waters of Chesapeake Bay. Possibly also, we may find there the northern limits of pure *quiscula quiscula*.

We now enter the southern limit of what may be called the New York region, which I have previously defined as including the northern

limits of *stonei* and the southern limits of *aeneus*. The accompanying table lists all our presumed breeding males from this grackle 'melting pot.' Note that with the exception of one specimen from Old Westbury in western Long Island, no intermediates between *stonei* and *quiscula* have been found north of Princeton, New Jersey.

An April 23 bird from Penns Grove, New Jersey, is practically *quiscula quiscula* but has the head bluish green. Ten specimens from Princeton are almost equally divided between *stonei* and *ridgwayi* and their intermediates in both directions; thus, from the same station, we have specimens near *quiscula quiscula* and also near *aeneus*, an unusual association. From Rye, New York, on the Sound near the Connecticut line, our series contains specimens of both typical *stonei* and *aeneus* and all the stages between them.

Proceeding northward up the Hudson and northeastward into New England we will, in due time, enter the territory of pure *aeneus* where evidences of its contact with *stonei* are unknown. Crossing to Long Island, which has claimed our especial attention, we encounter an exceptional environment which apparently has produced highly significant results. Here, in extending their range, grackles have entered a partially insulated region removed from direct contact with pure *aeneus* and nearly out of touch with *stonei*. In western Long Island we are still within the area of the 'melting pot.' Thus of twenty specimens from Oyster Bay, four are *stonei*, four intermediates toward *ridgwayi*, seven *ridgwayi* and five intermediates toward *aeneus*, one of which, indeed, is almost *aeneus*. As we proceed eastward we find a pronounced increase in the numbers of *ridgwayi*, with a corresponding decrease in the numbers of other forms. For example, from Jericho seven of eleven, from Plainview seven of twelve, and from Central Islip eight of eleven specimens are *ridgwayi*.

Without at least ten specimens one should not attempt to determine the grackle complex of any one station. I therefore leave the presentation of further local details in Table 1 in the belief that the facts I wish to emphasize will be more impressively shown in this summary. The decrease in *stonei* and increase in *ridgwayi* on Long Island are the significant features of this comparison. The latter, with its intergrades toward *aeneus*, number, indeed, 65 out of a total of 72 specimens, as compared with a total of 11 out of 46 in New Jersey, thus showing to what extent the *ridgwayi* type prevails in eastern Long Island. In view of this fact it may well be asked, if *ridgwayi* is the offspring of *aeneus* and *stonei*, how do we account for its presence where

TABLE 1

	Florida Grackle No. 1	Intermediates	Stone's Grackle No. 2	Intermediates	Ridgway's Grackle No. 3	Intermediates	Bronzed Grackle No. 4	Total
New Jersey and Staten Island		5	19	11	8	3		46
Eastern Long Island			3	4	48	17		72

one parent is unknown and the other comparatively rare? The condition which inspires this query is emphasized by the occurrence of *aeneus* and *ridgwayi* and complete absence of *stonei* on the island of Nantucket, showing that *ridgwayi* may exist with only one or the other of the original parents. From this stage it is but a step to its existence without either of the original parents. The conditions favorable for this step are evidently provided by the partial insulation found in eastern Long Island where, in my belief, it is only a question of time when *ridgwayi* will be the only form of grackle regularly breeding there. In this connection it should be remembered that *aeneus*, one of the original parents of *ridgwayi*, is an exceptionally stable, virile form, adapting itself to the widely varying conditions of a breeding range that extends from the Rio Grande valley to the limit of trees. Note that in the accompanying table no adequately represented station is without evidences of the influence of *aeneus*. Hence it may be presumed that, by inheritance, *ridgwayi* is well equipped to hold its own, and possibly more.

It appears, therefore, that removed from contact with one parent and in a large measure from the other, the descendants of both have become the dominant type of grackle in a definite area where they promise fully to establish their independence as a well-marked, self-perpetuating form wholly deserving of recognition in zoological nomenclature.

This conclusion, with my earlier remarks on the origin of *stonei*, I submit in support of the belief that of the two post-glacial grackles constituting the *stonei-ridgwayi* complex, the former originated by mutation, the latter through the interbreeding of allied forms.

TABLE 2

	Florida Grackle No. 1	Intermediates	Stone's Grackle No. 2	Intermediates	Ridgway's Grackle No. 3	Intermediates	Bronzed Grackle No. 4
<i>New Jersey</i>							
Penns Grove		1					
Lakehurst		1	3	2	1		
West End (near Long Beach)			3				
Crosswicks, 12 mi. s. Princeton		2	4	1	1		
Princeton		2	1	3	2	2	
Raritan						1	
Morristown			1		1		
North Plainfield			3	1	2		
<i>New York</i>							
Staten Island (Butler Estate)			4	4	1		
Central Park, New York City				2			
West Farms				1	1		
Rye			4	4	3	1	1
White Plains			1		3		
Ossining			1				
<i>Connecticut</i>							
Westville (near New Haven)					1	2	1
Simsbury (n. of Hartford)					1	2	1
Litchfield					1		
<i>Long Island</i>							
Floral Park			1				
Old Westbury		1			3	1	1
Jericho			1	2	7	1	
Locust Valley			1	1		1	
Mill Neck			1		1		
Bayville			1	1	3	1	
Oyster Bay			4	4	7	5	
Cove Neck					3		
Plainview				2	7	3	
Farmingdale					1		
Greenlawn			1		1		
Seaford			1				
Cold Spring Harbor				1	1		
Brentwood					1		
Bay Shore				1	1	1	
Central Islip					8	3	
Smithtown					1		
Lake Ronkonkoma					1		
Brookhaven			1	1	1		
Moriches					1		
Eastport					1	1	
Speonk			2	2	3	2	
Westhampton						1	

TABLE 2—Continued

	Florida Grackle No. 1	Intermediates	Stone's Grackle No. 2	Intermediates	Ridgway's Grackle No. 3	Intermediates	Bronzed Grackle No. 4
<i>Long Island</i>							
Hampton Bays					1		
Easthampton					5		
Amaganset					1		
Shelter Island				1	24	10	
Greenport					2	1	
Orient					2		
Orient Point			1		8		
Gardiner's Island				1	1	2	
<i>Massachusetts</i>							
Martha's Vineyard						5	4
Nantucket					3	2	3

I append a list of those to whom I am indebted for the birds recorded in the preceding table, together with a statement of the localities represented. Specimens from the remaining localities were collected by Mr. Sven Raven, of the Museum staff. Dr. Stanley C. Ball, near New Haven; Dr. Thomas Barbour, Nantucket, Martha's Vineyard; Mrs. Gladys Gordon Fry, Oyster Bay; Mr. John Galm, Central Park; Mr. Winston Guest, Gardiner's Island; Dr. W. T. Helmuth, Easthampton; Mr. Roy Latham, Orient, Orient Point; Mr. Charles H. Rogers, Crosswicks, Princeton; Dr. Eugene Swope, Oyster Bay; Mr. Leroy Wilcox, Speonk; Mr. W. W. Worthington, Shelter Island.

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