FURTHER REMARKS¹ ON QUISCALUS WITH A REPORT ON ADDITIONAL SPECIMENS FROM LOUISIANA.

BY FRANK M. CHAPMAN.

THANKS to the continued cooperation of Mr. E. A. McIlhenny I can now speak with some definiteness of the distribution and relationships of the forms of the genus *Quiscalus* in Louisiana. I present these data not alone as a contribution to a wider study of our Grackles but for their bearing on the problem of the methods of intergradation of representative forms.

My first paper on this subject has been so long out of print that I make no apology for again presenting a map which, semidiagramatically, shows the distribution of Grackles when nesting and thereby illustrates the important position Louisiana occupies in an attempt to define their relationships and breeding ranges. In a word, all four forms of Grackles breed in that state and it is obvious that whatever we can learn about their intergradations there will be of value in their study elsewhere.

It will also promote a clearer understanding of our problem if I restate briefly the facts which have developed thus far:

First.—The Florida Grackle (No. 1) and the Bronzed Grackle (No. 4), within the limits of their respective ranges, are stable forms, but in the area between their ranges there is wide variation which eventually results in their complete intergradation.

Second.—Both to the northward and westward the Florida Grackle gradually changes into the purple-backed bird for which the name Quiscalus quiscula stonei (No. 2) has been proposed.

Third.—The Bronzed Grackle (No. 4) breeds from southern Texas to Newfoundland and Great Slave Lake with slight increase in size and no change in color, but from Louisiana to Massachusetts, wherever its range² meets that of Stone's Grackle, it intergrades with that form through an intermediate known as *Quiscalus quiscula ridgwayi* (No. 3). In Louisiana the zone of intergradation is about forty miles in width. In the Lower Hudson Valley, Long Island, and southern New England region it is much wider.

Turning now to Louisiana, the only state whence I have sufficient material to determine in some detail the distribution of these birds, the map and distribution table beyond, show that, broadly speaking, the southern part of the state is occupied by *stonei*, with intergrades toward the Florida Grackle, and in the southeast by occasional specimens of the last-named

¹ For preceding papers see Bull. Amer. Mus. Nat. Hist. IX, 1892, pp. 1-20; The Auk, LII, 1935, pp. 21-29; Ibid., pp. 418-420.

² Throughout this paper I am dealing only with breeding ranges and breeding birds.

form. Seventy-five miles west and about forty miles north of the range of *stonei* we enter the range of *æneus*. To the west *stonei* and *æneus* apparently do not meet. To the north they completely intergrade, sometimes within a distance of twenty miles, sometimes even at the same locality.

THE DEVELOPMENT OF STONE'S GRACKLE.

These data, in connection with those derived from a study of our Grackles elsewhere, support the belief that *aneus* has entered Louisiana from the west, *stonei*, from the east. In other words, that *stonei* has not been derived from *aneus* as, for example, the Boat-tailed Grackle (*Cassidix mexicanus major*) is said to have been derived from the Great-tailed Grackle (*Cassidix mexicanus mexicanus mexicanus*), but is a bird of different geographic origin which has been brought into contact with *aneus* by mutual range-extension. When their ranges are sufficiently separated the birds remain distinct; but when they come together they intergrade.

For example, in southern Louisiana *stonei*, and its intergrades toward the Florida Grackle, are found west to Lake Arthur. At this point, Mr. McIlhenny tells me, their further range extension westward is prevented by the occurrence of a prairie region unsuited for their occupation and in which they do not occur. Their range, therefore, is here separated from that of *aneus* by a distance of about 75 miles, beyond which, from Beaumont, Anahuac and Liberty, Texas, we have 27 specimens of typical *aneus*.

A similar instance on a larger scale is found in Tennessee where, as I have stated¹ on the authority of Mr. A. F. Ganier, *stonei* is found in the eastern, *æneus* in the western part of the State, their ranges being separated by the Cumberland Plateau where Grackles are not known to breed. These cases, in my opinion, support the theory that *stonei* is a representative of the Florida Grackle and not, as I have tentatively suggested, "in whole or part the cumulative result of prolonged hybridism [with *æneus*], which, in the course of innumerable generations, has extended its influence from the boundaries of the range of *æneus* to well within the territory now occupied by the Purple Grackle [= No. 2 of the map]."

There are, however, several facts in connection with the development of *stonei* from the Florida Grackle which do not altogether conform to our idea of how an environmental race is formed.

Although this change is gradual, the cause or causes that produce it do not seem to act uniformly on all the individuals of the same area. Note, for example, the presence at three localities in southeastern Louisiana of both the Florida and Stone's Grackle and intermediates between them. A similar phenomenon has been found elsewhere, and since we do not expect the same environment to produce different results at one place it apparently

¹ The Auk, 1935, p. 28.

Vol. LIII 1936

follows that the characters exhibited by *stonei* are not of environmental origin. Furthermore, the wide range of *stonei* and its consequent occurrence under different climatic conditions, for example, those of southern Louisiana and northern New Jersey, is additional evidence that its characters are not the product of its environment.

If we exclude the possibility of the present or past influence of *aneus*, we cannot attribute the existence of *stonei* to hybridism, for the breeding of a form with itself cannot properly be called hybridism, and in the earlier stages of its gradual separation from the Florida bird the nascent *stonei* is still essentially *quiscula*.

To what factors, then, may we attribute the development of stonei?

The Florida Grackle is not a variable form. In the color of its head it shows less variation than any other form of the group; but individuals rarely occur which show a pronounced approach to *stonei*. In my first paper on this subject I find that I actually referred four specimens in a series of seventy-two to "Phase No. 2," the phase I subsequently described as *stonei*. Among the fifty-seven specimens now available there are three of this nature. Two are from Jupiter, the other from Gainesville, and it seems probable that their variations from the typical bird, found in numbers at both these localities, is mutational in character and hence inherent. I suggest, therefore, that the changed population conditions incident to extension of range have permitted these mutational characters to find expression in *stonei*, which we may provisionally consider as neither the product of its environment nor of hybridism, but of heritable, individual variation, or mutation.

Further evidence of the origin of *stonei* from the Florida bird is supplied by the not infrequent occurrence in its range, and even in the area of its intergradation with *aneus*, of specimens with a violet-purple head. A violet-purple head is the distinctive character of *Quisc Alus quiscula*. All Florida birds possess it, but I have yet to see a specimen from well within the range of *aneus* in which it is typically developed. Its presence, therefore, may be attributed to the influence of the Florida, rather than that of the Bronzed Grackle, and it thus supplies additional evidence of the origin of *stonei* from *quiscula*.

THE INTERGRADATION OF stonei AND æneus IN LOUISIANA.

Returning now to Louisiana we find that at some point, as yet unknown, but evidently not more than seventy-five miles north of Beaumont, Texas, whence we have ten specimens of *æneus*, that form enters Louisiana on the first steps of its eastward range-extension. The first locality on this route represented in our collection is Boyce, Louisiana, some fifty miles east of the Texas line and eighty miles north of Lake Arthur (whence we have one stonei and one intermediate toward quiscula). Twenty specimens from Boyce (May 20–22, 1935; ten males and ten females) are referable to *aneus* but two males have some blue-tipped feathers on the nape, indicating the proximity of *ridqwayi*. One of seven male specimens of *aneus*, collected May 11 in a small colony of building birds two miles south of Meeker, and three in five collected at Bunkie, forty miles southeast of Boyce, May 23, 1935, are similarly marked. Of seven specimens collected May 12 and 13, eight miles south of Bunkie, four are *æneus*, three have the blue-tipped post-nuchal marks mentioned above, and one is halfway between *æneus* and *ridgwayi*, indicating that we are approaching the center of the area of intergradation. It is evident, therefore, that at Boyce we are on or very near the line that marks the southern limit of the range of true *æneus* in this part of Louisiana. This line evidently extends southeastward to Bordelonville (May 9) and Moreauville (May 7), and thence eastward to Centreville, Mississippi (April 29). Ten specimens from the first-named station are all æneus, but one in a series of ten from Moreauville and Centreville has a few blue spots on the nape and a second from Centreville is halfway toward ridgwayi. The remaining eight are true æneus.

Ten specimens from Natchez (April 30), thirty-five miles north of Centreville, are, as might be expected, true *æneus*, but two in a series of ten from six miles south of Vidalia (May 2), which is across the Mississippi from Natchez, show in a slight degree the blue nape markings I have before mentioned. Similar markings, however, are sometimes found on specimens well within the range of *æneus*, for example, Hamilton, Kansas, and Erie, Pennsylvania, where they are evidently attributable to individual variation.

Having thus determined, with doubtless a fair degree of accuracy, the southern limit of the range of true *æneus* in Louisiana and the adjoining part of Mississippi, I attempt now to draw a line marking the northern limit of the range of stonei in that state. Here my material is not quite so adequate. It appears to show, however, that in the central part of the state this line runs between Coule Croche and Opelousas in St. Landry Parish. From the former we have the three specimens taken June 3, 1895, by Mr. McIlhenny. I refer them to stonei, but all three have the head of the Florida bird and a slight greenish tinge above and below which also indicates their relation to quiscula; and two have a bronzy tinge on the rump and, to a lesser degree, on the flanks which suggests the influence of *œneus.* I am at a loss to know how to interpret this latter character. South Florida birds not infrequently have the rump unmarked, purple bronze, but in these Coule Croche specimens, and some other examples of stonei from throughout its range, the rump is more bronzy and it is an open question whether this change is to be attributed to individual variation or an indirect connection with *œneus*. This increase in bronze on the rump is

Vol. LIII 1936

shown in a specimen from Newport News, Virginia, which is very near *quiscula*, and also in the type of *stonei*.

The five specimens from Opelousas were taken June 2, 1895, also by Mr. McIlhenny. They have the head less violet than in the Coule Croche specimens, but in two of them the bronze is somewhat more pronounced and there is a suggestion of ridgwayi in the greenish markings of the back and underparts, which induces me to list them as intermediates between *stonei* and *ridgwayi*. If I am correct, the influence of *æneus* is thus shown at Opelousas.

We are now left with an area approximately forty miles wide, and in some places even narrower, in which to complete the intergradation of *stonei* and *æneus*. In fact actual intergradation of these extremes is shown by our specimens to occur at single localities and even in one colony.

Thus at a point on Highway No. 1, two miles south of Livonia and about thirty miles east of Opelousas, Mr. Nolan found grackles "nesting in oaks" and on May 16, 1936, collected 10 males. This series contains four specimens of *stonei*, one of *ridgwayi*, three intermediates between *ridgwayi* and *aneus*, nearer the latter, and two of *aneus*. Doubtless additional specimens would bridge the gap between *stonei* and *ridgwayi*. These birds, Mr. Nolan writes, were taken from one colony, and they offer, therefore, the most satisfactory evidence of the interbreeding of *stonei* and *aneus* that collecting has thus far revealed. In view of the prolonged period that these birds have doubtless been in contact it is indeed surprising that there should still exist conditions which so nearly resemble those we may imagine prevailed during the early stages of their association.

Essentially similar conditions were found by the collector at a station three miles south of Melville, about fifteen miles northwest of Livonia and twenty miles northeast of Opelousas. At this point a "colony of grackles were found nesting in cypress and pecan trees near the levee of the Atchafalaya River on Highway 816" and ten males were collected on May 14. Of these one is *stonei*, with a bronze rump and flanks, three are intermediates between *ridgwayi* and *æneus*, of which two are nearer the former and one nearer the latter, and six are typical *æneus*, except for an unusual amount of violet-purple in the head. Thus, again, we have both parental forms and intermediates between them breeding in one colony.

Our specimens indicate that a similar association is found in West Baton Rouge Parish (exact locality not stated) about fifteen miles southeast of Livonia, whence A. A. Allison sends us eight males, as follows: one *stonei*, March 5, 1903, "probably about to breed"; two between *stonei* and *ridgwayi*, April 18 and May 20, "breeding;" three *ridgwayi*, March 5, 1903 "perhaps about to breed," April 15 and May 21, "breeding;" one between *ridgwayi* and *æneus*, nearer the latter, May 12, "breeding;" one *æneus* with head of quiscula, May 9, "breeding." While not so conclusive as that supplied by specimens taken on the same day in one colony, here is further evidence of the breeding at one station of *stonei* and *aneus* and connecting intermediates.

From Baton Rouge on the east side of the Mississippi I have already recorded six male Grackles taken by Nolan May 24, 1935. Four are *stonei* and two *ridgwayi*. Possibly additional collecting would have resulted in the discovery of *æneus*, which, as we have just seen, is found on the west side of the river, while six miles south of Olive Branch, fifteen miles northeast, Nolan took ten specimens on April 27 of which six are *æneus* and four very near it. These birds were not breeding but they doubtless represent the nesting form.

Of eight specimens collected May 4 in a plowed field four miles north of Lindsay, and about twenty from the Olive Branch Station, four are between *aneus* and *ridgwayi*, three being nearer the former, one nearer the latter.

Of nine specimens collected May 6 in a plowed field on Highway 139 at the north end of the False River between New Roads and Port Allen, seven are *aneus*, two are halfway between *aneus* and *ridgwayi*.

Five specimens collected May 15 on Highway 384 at Woodside were nesting in cypress trees. Four are *æneus*, one is intermediate between *æneus* and *ridgwayi*, nearer the former.

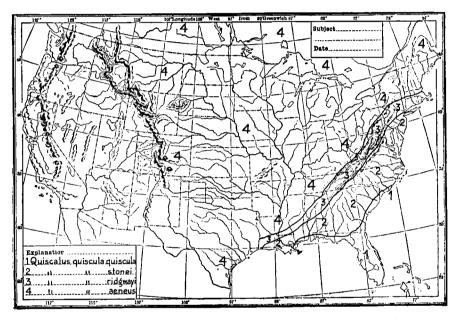
This review of specimens from the area in Louisiana lying between the ranges of *stonei* and *æneus* demonstrates the complete intergradation of these birds, at times in the same locality or colony, and also indicates that *ridgwayi* is the product of their union. But as the pure strain of the primary parental forms became separated by their ever increasing progeny, *æneus* at the northern, and *stonei* at the southern border of the area of intergradation would breed only with the intergrade *ridgwayi* which thus on one side would merge with *æneus* and on the other with *stonei*. These, indeed, are the conditions revealed by our collections. Doubtless they would be shown more conclusively by further collecting at an increased number of selected stations, particularly in the southern part of the zone of intergradation.

Under these circumstances the abundance and degree of development of *ridgwayi* should depend on the extent of territory it occupies and hence the distance of its removal from the influence of the original parents.

As one critically examines the accompanying distribution table he is impressed by the comparative absence of specimens showing the full development of the characters that distinguish ridgwayi. This circumstance is in part due to the fact that most of our stations in the area of intergradation are nearer to the range of *æneus* than to that of *stonei* but also, I feel, to the proximity and relative abundance of the parents concerned.

While specimens of *ridgwayi* from Louisiana can be duplicated from

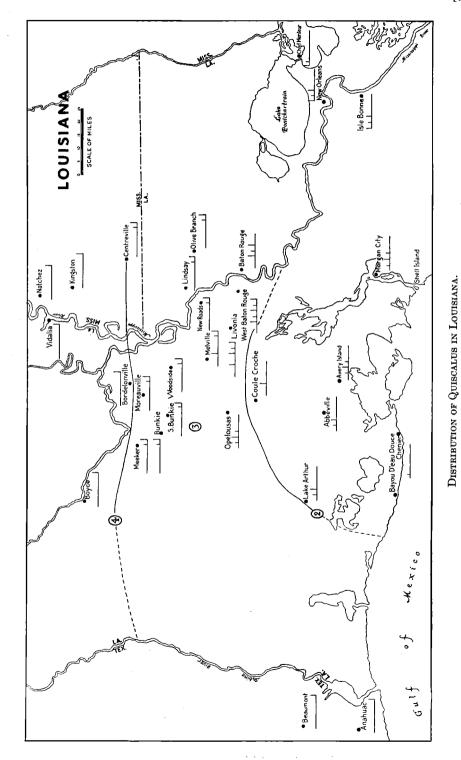
wherever *aneus* and *stonei* come together when breeding; in eastern Long Island, for example, *ridgwayi* is the prevailing form, and although the intergradation with *aneus* is complete, true *aneus* is almost unknown. Without evidence from other parts of the birds' range it would, in truth, be difficult to account for the origin of these east Long Island birds. One asks, therefore, how hybrids may occur in a locality where actual contact of the presumed parents must rarely if ever take place. In reply I suggest that Long Island, or at least the eastern part of it, was formerly inhabited by *aneus* which has been nearly absorbed by the intrusion of *stonei* from the

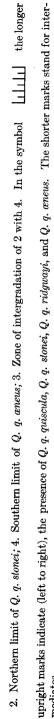


SEMI-DIAGRAMMATIC MAP SHOWING BREEDING RANGES OF THE FOUR FORMS OF QUISCALUS.

west, leaving only the results of their union to develop their distinctive characters by interbreeding.

Moreover, it should be noted that *stonei* and *ridgwayi* and their intergrades winter only within the range of *stonei* whence, in returning to their breeding areas on the Atlantic side of the zone of intergradation, they are not unlikely to nest in new stations and thereby extend their influence. Thus in the New York City region the ranges of *stonei* and *æneus* are separated by approximately two hundred miles while in Louisiana they are within 40 miles, or less, of one another and there is consequently a much smaller area for the development of the distinctive characters of the intergrades.





mediates.

CHAPMAN, Remarks on Quiscalus.

Southern Louisiana West To Texas	Florida Grackle No. 1	Intermediates	Stone's Grackle No. 2	Intermediates	Ridgway's Grackle No. 3	Intermediates	Bronzed Grackle No. 4
Chef Menteur, La. New Orleans, La. Isle Bonne, La. Grand Isle, La. Bayou La Fourche, La. Shell Island, La. Morgan City, La. Avery Island, La. Avery Island, La. Bayou D'eau Douce, La. Chenier, La. Lake Arthur, La. Beaumont, Texas. Liberty, Texas. Sourh CENTRAL LOUISIANA To SourhwEst MISSISSIPPI	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	2 1 4 2 1 1 7 1 2 1 1	4 2 5 1 4 10 3 1	1 1			10 7 10
Coule Croche, La. Opelousas, La. Livonia, La. Baton Rouge, La. Baton Rouge, La. G mi. so. of Olive Branch, La. Lindsay, La. New Roads, La. Melville, La. Woodside, La. 8 mi. so. Bunkie, La. Bunkie, La. Bordelonville, La. Bordelonville, La. Bordelonville, La. Bordelonville, La. Kingston, Miss. Natchez, Miss. Vidalia, La.		1	3 2 4 1 3 2	2 2 1	1 3 2	3 1 3 4 2 3 4 4 3 1 1 2 2 ?	2 1 7 4 7 6 4 4 2 9 10 6 10 8 110 8 110 8

DISTRIBUTION OF Quiscalus quiscula IN LOUISIANA.

HYBRIDISM.

Accepting as proven the intergradation of *æneus* and *stonei* it remains now to determine how it is achieved.

In my first paper on this subject I advanced the theory that their union was accomplished by hybridism. Further study has convinced me of the correctness of this view and I fail to see how anyone thoroughly familiar with the facts can refuse to accept it. Robert Ridgway wrote:¹ "My own opinion in the matter exactly coincides with Mr. Chapman's," but subsequent writers have either rejected the theory of hybridization or considered it not proven. For this reason, and because increased data permit me to write with greater definiteness, I restate here the argument for the union of the Bronzed and 'Purple' Grackles by hybridism.

Hybridism in birds may be (1) sporadic or occasional, as among certain individuals; it may be (2) more or less frequent but not regular, as with *Vermivora pinus* and *Vermivora chrysoptera*; or it may be (3) regular and result in the intergradation of the parental forms along the line of junction of their respective ranges, as with *Colaptes auratus* and *Colaptes cafer*.²

Hybridism between species or races, as compared with hybridism between individuals, calls for a meeting of the ranges of the forms concerned. It is not, therefore, the interbreeding of individuals of a developing race which in a connected, even if changing, series have a continuous distribution.

According to this view, intergrades between Sturnella magna magna and Sturnella neglecta are hybrids, while those between Sturnella magna magna and Sturnella magna argutula are not. Again, in the gradual development of Quiscalus quiscula stonei from Q. q. quiscula the intermediates between them are not considered hybrids but in the comparatively abrupt intergradation of stonei with æneus, they are.

The case of *Quiscalus* belongs in the third group of hybridizing conditions which I have here briefly defined. In a recent paper (The Auk, 1935, p. 21) I have attributed the "coming together" of their ranges to the influences of post-glacial dispersal. In the present paper additional reasons are presented in support of the belief that stonei is a representative of the Florida Grackle and has, therefore, entered Louisiana from the East. It may also be suggested that the complete intergradation of *stonei* and *aneus*, wherever their ranges meet, is further evidence of their common origin in a preglacial period, as postulated in the paper just referred to.³ It may, however, be asked that if they are now representatives of a common preglacial ancestor why *aneus* should be so stable, *stonei* so variable? While therefore it is admitted that the factors which have led to the development of stonei are not definitely known, there is, I feel, no reason to doubt its descent from quiscula. With this theory accepted, and I can think of no other to replace it, I proceed to restate the evidence for the hybridization of stonei and æneus.

It is unfortunate that, from the nature of the case, this evidence should be

¹ Bull. 50, U. S. Nat. Mus., p. 215.

² Cf. Allen, Bull. Amer. Mus. Nat. Hist., IV, 1892, p. 33.

³ Quiscalus quiscula is recorded from the Pleistocene near St. Petersburg, Florida by Wetmore. (Smiths. Misc. Coll. 85, no. 2, 1931, p. 41.)

based wholly on specimens whose parentage is unknown, nor have I one observation reporting the actual breeding together of Purple and Bronzed Grackles. And unless such observation were accompanied by the specimens concerned it would have little value. Typical males of the different forms may be distinguished in life by an experienced observer under proper light conditions. But the females too nearly resemble one another to make possible the fine discrimination required in studies of this kind. Skins of typical females of the Bronzed and Purple Grackles are easily distinguished but I am unable satisfactorily to determine the status of intermediates between them.

Furthermore, in view of the fact that the nestling plumage of all the members of the genus *Quiscalus* is essentially alike, the characters of a Grackle family can not be determined without collecting the parents and rearing the young until they have acquired their first winter plumage. This is not impossible, but, so far as I know, it has not been done.

We may return, therefore, to our specimens and summarize the evidence they present in support of the belief that *æneus* and *stonei* intergrade by hybridism. The essential data having been presented in this and preceding papers, my summary may be brief:

First.—The exceptional stability of *æneus* throughout a breeding range reaching from Texas to Newfoundland and Great Slave Lake indicates that its abrupt intergradation with *stonei*, wherever their ranges meet, is not achieved by "geographic" variation.

Second.—The intergradation is confined to a narrow zone, extending from Louisiana to Massachusetts, in which both *aneus* and *stonei*, with intergrades between them, are sometimes found breeding at the same locality or even in the same colony.

Third.—Quiscalus quiscula ridgwayi is found only and always in this zone and is considered the primary product of the union of æneus and stonei. It differs markedly from both parents but possesses characters we should expect to find in a hybrid between them. The lower back and rump are rich bronze without the iridescent tips of stonei; the general color of the wings is that of stonei but the coverts lack the iridescent marks usually present in that form; the underparts, posterior to the breast, are rich bronze with but few iridescent marks on the sides; the foreback is brassy green. Since the apparent colors of the Grackles are structural one cannot readily predict the color to be expected in a hybrid between them but when in these dorsal feathers we discover a bronze band at the base of the iridescent tip, it is evident that in each feather we have combined the characters of both parents.

In addition to the evidence derived from a study of specimens and their distribution we should also take into consideration:

Fourth.—That the colonial nesting habit of Grackles with the consequent lack of individual territorialism lends itself to close association while nesting and consequently offers opportunities for hybridism, which is further promoted by their resemblance in habits and in the appearance of the females.

I present this paper as a report of progress and emphasize anew the importance of a continued study of Grackles in field and study. Their characters are so well-marked that these birds supply us with exceptionally definite data concerning their relationships, their progeny, and the factors governing their distribution.

Amer. Mus. Nat. Hist. New York City.

POSTSCRIPT.

In response to my request Mr. McIlhenny has prepared the appended notes on the distribution of *Quiscalus* in Louisiana. They were received some time after my paper was finished.

F. M. C.

The breeding range of Quisculus quiscula aneus and Q. q. stonei in Louisiana is pretty well defined by the character of the country. Aeneus is not a colony nester but nests in scattering companies in the high, dry sections away from the swamps or wet sections. Stonei occupies the southern or swamp section of the state on both sides of the Mississippi River, west to the high prairie section, which begins at the Mermentau River and extends west to the Texas line. Stonei prefers as nesting sites trees actually growing in water, or near to water, which are heavily hung with Spanish moss. In the festoons of this moss is their favorite nesting site. Stonei nests in decided colonies, sometimes only a few nests in one tree, but often the colony will contain more than one hundred nests in a group of a few trees growing near together. A few scattering colonies are to be found a few miles west of the Mermentau River, but, generally speaking, this river is their western breeding limit in Louisiana. This river is the dividing line in the southern part of the state between the wet, wooded sections, and the dry, open prairie section. From the Mermentau River west to Texas is an almost unbroken stretch of high, dry prairie. In this prairie section neither *æneus* nor *stonei* nest.

Going north from the coastal swamps, which are timbered with cypress and tupelo gum, little or no natural high, dry land is encountered until a line running east and west from the Mississippi River to approximately a little south of Alexandria, thence south through Eunice, Crowley, Lake Arthur, to the coast. South of this line embraces practically all of the Vol. LIII 1936

breeding range of *stonei*. North of this line, generally speaking, the land is dry and hilly, and the timber is pine, red oak, and other highland trees. It is approximately along this line, or a little south of it, that *æneus* and *stonei* meet during the breeding season. This fact has been definitely determined from specimens taken at many localities and identified by Dr. Frank M. Chapman. Both of these birds are resident in the southern half of Louisiana during the winter, and flock together commonly. As the nesting season approaches the two species gather in flocks to themselves, and *æneus* moves north during the month of March. Both birds are rather late maters, and do not normally begin to nest until the middle of April. *Stonei* apparently rears two broods in a season, establishing different colonies for each brood. The first brood is usually complete and on the wing by the 20th of May. The second brood is not out of the nest until after the first of July.—E. A. MCLHENNY, *Avery Island*, *La*.