RELATIONSHIPS OF THE RACES OF PHAEOPROGNE TAPERA AND THEIR PROBABLE SIGNIFICANCE.

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THE PROBLEM.

THE genus *Phaeoprogne* of Baird is confined to South America, ranging from northern Venezuela southward through the Tropical Zone and beyond to the Province of Buenos Aires, Argentina. It contains two forms, a northern and a southern one. For the former, in 1912, I proposed the name *Phaeoprogne tapera immaculata* in the belief that the name *tapera* of Linneus was applicable to the latter. But in 'The Auk' for April, 1929, Mr. W. E. Clyde Todd,[1] confirming Baird,[2] shows that the northern bird should be known as *tapera* Linneus, the southern, as *fusca* Vieillot. Dr. Hellmayr[3] has also reached the same conclusion, and in its fundamental aspects we may, therefore, consider this question of names as nearly settled as such questions ever can be.

Mr. Todd, however, calls these birds *Phaeoprogne tapera* and *Phaeoprogne fusca*, while I would call them *Phaeoprogne tapera tapera* and *Phaeoprogne tapera fusca*. This sounds very much like the difference between tweedledum and tweedledee, but I hope to show that the use here of binomials conceals certain significant biological facts to which, so far as nomenclature can, trinomials give expression.

Mr. Todd does not hesitate to state in italics that these two birds are "perfectly distinct *species*" and "that their respective ranges overlap over an extensive area." It is my belief, however, that these two forms are mutually representative, intergrading races and that their breeding ranges overlap only along the line of intergradation. The evidence on which this opinion is based seems to me to be of sufficient importance to warrant presentation.

The problem is not a new one to me. In 1917,[4] when writing on Colombian birds, I stated that I was unable to explain it, but

[1] The Auk, XLVI, 1929, pp. 186–189.
[2] Rev. Amer. Bds., 1865, pp. 285, 286.
[3] Field Mus. Pub., 255, 1929, p. 265.
[4] Bull. Amer. Mus. Nat. Hist., XXXVI, 1917, p. 503.

treated the two forms as subspecies. In referring to this paper Mr. Todd (*loc. cit.*) writes that I "admitted that they behaved as if they were two different species." While this comment doubtless relates to my discussion of the birds' relationship, it might be interpreted as applying to their habits, whereas I know nothing pertinent concerning the behavior of either race.

THE EVIDENCE.

The coloration of these two birds may be easily visualized if we liken the northern *P. t. tapera* to a Rough-winged Swallow, the southern *P. t. fusca* to a Bank Swallow with a median line of spots extending from the center of the breast-band to the belly. In size[2] and in the color of the upper parts the two birds agree, the differences between them being evident only on the lower parts. These differences consist chiefly in the possession by *fusca* of a line of spots from the center of the pectoral band usually to the center of the belly; these parts being grayish anteriorly, white posteriorly, unmarked in *tapera.* In many specimens of *fusca* the throat is whiter and more sharply demarked from the breast-band, which is more clearly defined than in *tapera.*

The plain-breasted bird, *tapera,* is known to range from Bahia, the lower Xingú, Tapajoz, Purús, upper Ucayali, and northwest Peru, north to the Guianas, Caribbean slopes of Venezuela, and vicinity of Carthagena, Colombia.

The spotted-breasted bird, *fusca,* is known to occupy the area from Santa Cruz, Bolivia, and Matto Grosso, Brazil, south to the

[2] My material does not confirm Mr. Todd's statement that "the distance between the tips of the longest secondaries and the tips of the longest primaries in the closed wing . . . is constantly longer in *fusca* than in *tapera* by 10 mm. or more . . ." For example: in four females of *fusca* from Matto Grosso, Brazil, this measurement is 54, 54, 55 and 58 mm., while in five females of *tapera* from the junction of the Napo and Marañon it is 60, 60, 62, 65, 66 mm. Again, in two males from La Plata, Argentina, it is 60 and 70 respectively, while in two from Maripa on the lower Orinoco, it is 60 and 68 respectively. Measurements of 51 additional specimens confirm those just given. The truth is that the extent of this measurement is affected by the make-up of the skin. If, as usual when skinning, the secondaries are stripped from at least the proximal half of the ulna, their subsequent position in the closed wing of the dried skin depends upon the extent to which the wing is closed and the degree of accuracy with which they are restored to their original point of attachment. Both these factors are variable, with consequent variability in "the distance between the tips of the longest secondaries and the tips of the longest primaries," which prevents this measurement from being diagnostic.

Area 1. *Phaeoprogne tapera tapera.*

Area 2. *Phaeoprogne tapera fusca.* Black dots represent localities within the range of the former at which *P. t. fusca* has been taken.

Province of Buenos Aires, Argentina. From this area *tapera* is unknown; *but scattered individuals of typical fusca have been found throughout the range of tapera.* This is the crux of the problem.

Mr. Todd records six such specimens from two localities in northern Venezuela among his 61 specimens of *tapera.* The American Museum has eleven such specimens from five localities in the range of *tapera tapera.*

It is on the occurrence of these specimens of *fusca* in the range of *tapera* that Mr. Todd doubtless bases his belief in the specific distinctness of the two birds as well as his statement that "their respective ranges overlap over an extensive area." But in my opinion, these northern specimens of *fusca* are winter visitants probably from the southern part of its range. If this be true, it has an obvious bearing on the relationships of the two birds, and is also an important addition to our scanty knowledge of the winter range of birds that migrate northward after nesting in Argentina and adjoining areas. The evidence on which this belief is based is as follows:

1. In at least the southern part of its range *fusca* is a migrant. Wetmore[1] writes that at Kilometer 80, west of Puerto Pinasco, Paraguay, it was not seen until September 17, 1920, and that on October 21 it was already present at Dolores, Buenos Aires. Daguerre[2] states that in Rosas, F. C. S., Argentina, this Martin arrives at the end of October and departs at the end of April. On the other hand, Young,[3] writing from the coastland of British Guiana, records "*Progne tapera*" as present from May to September and writes "I have not seen any at other times of the year, which might suggest that these were non-breeding birds." This statement, in connection with Hellmayr's record of *fusca* from Georgetown, suggests that true *tapera* does not breed on the Guiana coast.

2. With exceptions which appear to be explainable, the available records of *fusca* from the range of *tapera* were made during its non-breeding season. They are as follows: Brazil: San Bento, Maranh˜o, ♀ ad., Aug. 28, 1923.[4] Peru: Orosa, south bank Marañon below Iquitos, 3 ♂, Sept. 11, 1926. Venezuela: Es-

[1] Bull. U. S. Nat. Mus., No. 133, 1926, p. 345.
[2] El Hornero, II, 1922, p. 269.
[3] Ibis, 1929, p. 237.
[4] Pub. 255, Field Mus., 1929, p. 265. Hellmayr mentions also specimens with spotted breasts from Maribitañas on the Rio Negro and Georgetown, British Guiana.

meralda, upper Orinoco, 1 ♂, 1 ♀, Oct. 2, 1 ♀, Oct. 29, 1 ♀, Nov. 1, 1 ♀? Nov. 6; Suapure, lower Orinoco, 1 ♀, Apr. 27, 1899; El Trompillo, Carababo,[1] 1 ♂, May 11, 1914, 1 ♂, May 14, 1914, 1 ♂, May 18, 1914, 1 ♀, May 19, 1914; Guachi, Zulia,[1] 2 ♂, Aug. 23, 1922. Colombia: Turbaco, near Cartagena, 1 ♂, Aug. 3, 1911; Rio Sinu, 1 ♀, Nov. 21, 1911.

The November dates above recorded are sufficiently near the breeding season of *fusca* to call for comment.

Although *fusca* reaches the Province of Buenos Aires in September, Hudson[2] states that it does not nest until November or December, and Gibson[3] writes that "eggs are most generally taken in December." This late date has been attributed to the bird's habit of using the homes of the Ovenbird (*Furnarius*) and the necessity of waiting until the young of that species had flown; but Friedmann[4] records finding at Santa Elena, Entre Rios, "a nest in a hole about thirty feet up in a tall tree" on January 13, containing "one young bird nearly ready to leave." Whatever, therefore, may be the cause for the delay of *fusca* in nesting, it is evident that even birds taken in Colombia in late November could readily reach their nesting grounds near the beginning of the breeding season of their species.

Swallows are rapid flyers, and in this connection it is desirable to recall that in the spring our Barn Swallow is found in South America for at least six weeks after it reaches the latitude of Washington. We have specimens taken at Corumbá in southern Brazil, March 23, on the coast of Peru, April 10, and the Bogotá Savanna, May 13, while Todd and Carriker[5] state that it was present in large numbers around Rio Hacha (Santa Marta) during the first week of May, 1914.

So far, therefore, as their dates of occurrence are concerned, there is no reason to doubt that the specimens of *fusca* here recorded from the range of *tapera* are winter visitants.

3. The plumage of specimens of *fusca* from the range of *tapera* indicate that they were migrants.

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[1] Coll. Carnegie Mus.
[2] Proc. Zool. Soc., 1872, p. 608.
[3] Ibis, 1880, p. 23.
[4] Bull. Mus. Comp. Zool LXVIII, 1927, p. 210.
[5] Ann. Carn. Mus., XIV, 1922, p. 435.

It is well known that as a rule the "fall" molt (postnuptial or postjuvenal) in Swallows is deferred until the birds reach their winter quarters. With this fact in mind let us examine our specimens of *fusca* from the range of *tapera.* I follow the order in which they are listed above. The three males from Orosa (Sept. 11) are in fresh, wholly unworn plumage and have evidently just finished the molt. The sexual organs were not enlarged. On the contrary, two males of *tapera tapera* taken at the same place on the same day are in somewhat worn plumage and had large testes. Apparently, therefore, the specimens of *fusca* were migrants, those of *tapera* breeding birds. All the Esmeralda (Oct. 2–Nov. 6) birds are nearing the end of a complete molt. Since the primaries are still involved the cause for their late stay seems apparent. The Suapure (April 27) bird is in much worn plumage but has new first and second (from within) primaries in each wing. Presumably it had but recently arrived from the south and was beginning its postnuptial molt. Two specimens of *tapera tapera* taken at the same locality April 8 and 30 are just completing a full molt.

Three of the four May specimens of *fusca* from El Trompillo are essentially like the April 27 specimen from Suapure, that is, in worn plumage and beginning to molt. In the fourth (May 18) the molt has apparently not yet started. The August specimens from El Guachi, Venezuela, and Turbaco, Colombia, and the November bird from the Rio Sinu, are just concluding a full molt.

It appears, therefore, that, excepting the three freshly plumaged September specimens from Orosa and one worn May specimen from El Trompillo, all my "winter" specimens of *fusca* are in molt. On the other hand, not one of my 30 specimens of *fusca* taken in their breeding range between September 3 (Chapada, Matto Grosso) and April 1 (Corumbá, Matto Grosso) show signs of molt.

4. The American Museum has an ultra-typical specimen (wing, 104 mm.) of *Pygochelidon patagonica,* taken at Cumaná, northeastern Venezuela, May 23, 1925, by G. H. H. Tate. It is in worn, faded plumage, while a male of *P. cyanoleuca* (wing, 89 mm.) taken at San Antonio, northeastern Venezuela, April 27, is in fresh plumage. We have also six specimens of this South Temper-

ate Zone species taken by Watkins at Perico, Rio Chinchipe, North Peru, July 20, and one from San Ignacio, July 2. There are both adult and immature birds in this series and all are in molt. This species is not known to nest north of Argentina and is migratory from at least Buenos Aires southward.[1]

There is no reason to doubt that all these Martins and Swallows were 'winter' visitants at the localities in which they were taken; nor indeed should we be surprised that these highly mobile creatures should extend their migrations from Argentina to the Caribbean when we recall that our own Barn Swallow winters as far south as Argentina.

RELATIONSHIPS.

If, as I believe, the evidence above presented shows that the specimens of *fusca* occurring in the range of *tapera* are 'winter' visitants and not residents, and that hence the ranges of the two forms do not "overlap over an extensive area" and consequently that they are not unquestionably specifically distinct from each other, what then are their relationships?

Unfortunately, my material does not afford a conclusive answer to this question. Between the southern known breeding limits of *tapera* and the northern known breeding limits of *fusca* there is a wide area from which we have no specimens. However, the specimens available warrant the advance of some suggestions. They are: (1) the breast-spots of *fusca* are a mutational character; (2) the whiter throat and better defined breast-band of some specimens of *fusca* are geographic characters; (3) the two forms intergrade.

Now let us see to what extent these theories are supported by facts and their interpretation.

Sixteen of our fifty-six specimens of *tapera tapera* show a tendency toward the development of spots on the breast. In some they are barely evident, in others so well marked that, so far as this character is concerned, these specimens are fairly intermediate between *tapera* and *fusca*. These birds are from the upper Ucayali, Orosa, and Puerto Indiana at the mouth of the Napo, Peru; Rio Curaray, and Duran, opposite Guayaquil, Ecuador; Manaos, Brazil; and

[1] Chapman, Amer. Mus. Novit., 30, 1922, p. 4.

Maripa, lower Orinoco, Venezuela. There is thus exhibited by specimens from throughout a large part of the range of *tapera* a tendency to develop, by individual variation, that is, mutation, black spots on the breast. In some specimens these spots are so well developed that they approach certain specimens of *fusca,* which have a minimum number of spots. It is within the range of demonstrated possibilities that given favorable environmental condition this inherent tendency to vary in a definite direction might become a dominant characteristic. Such conditions appear to have arisen as *tapera* has extended its range southward into Argentina.

Further evidence that these breast spots are mutational in character is supplied by the sporadic occurrence of the same type of marking in other Swallows. It is more frequently present than absent in *Riparia riparia riparia,* in some specimens of which these central breast spots are so well developed that they look like miniatures of *Phaeoprogne t. fusca.* Such specimens suggest that fundamentally and germinally these two species are more closely related than our classification indicates. We have also a specimen of *Riparia cincta suahelica* from Elmenteita, Kenya Colony, which has more spots on the median breast line than most specimens of *fusca.* In specimens of the three forms of *Pygochelidon* median breast-spots are not infrequent and the occurrence of this unusual marking in these, and possibly other Swallows, is an evidence of their common origin.

It has been said that some specimens of *fusca* have the throat whiter and more clearly defined from the sharply marked brownish gray breast-band than others. Specimens from the southern part of the range of this race are thus marked.[1] It is also significant that all the specimens herein recorded from the range of *tapera* are of this character; and, as migrants, it is not impossible, though wholly theoretical, that these northern birds may have come from the southern part of the range of the race.

In Matto Grosso these throat and breast characters are by no means so well marked; the throat averages grayer and the pectoral band, as a rule, is no better defined than it is in *tapera.* Were it

[1] Fort Wheeler, Paraguay; Embarcacion and La Plata, Argentina; Palmares, Rio Grande do Sul, Brazil.

not for their breast-spots it would not, indeed, be possible to separate most Matto Grosso specimens from average examples of *tapera*. Even in the last-named character a specimen from Descalvaldos, Matto Grosso, so closely approaches one from Manaos and another from the Curaray, eastern Ecuador, and a third from the upper Ucayali, Peru, that no one seeing these four examples would question the propriety of applying the same name to them all; while of the intergradation of the two forms they represent not the slightest doubt can be entertained.

CONCLUSIONS.

From the study of this material and its associated data I venture to present the following conclusions: (1) That the specimens of *fusca* taken in the range of *tapera* are not residents but "winter" visitants. (2) That migrants from the South Temperate Zone winter as far north as the Caribbean. (3) That the breast-spots of *fusca* are mutational in nature and in *Phaeoprogne* have their origin in *tapera* from which *fusca* was derived. (4) That the white throat and well defined pectoral band are most fully developed in the more southern specimens of *fusca*. (5) That in these respects specimens from Matto Grosso are intermediate. (6) That *tapera* and *fusca* intergrade in part by individual variation in the development of the breast-spots, in part by geographic variation in the color of the throat and pectoral band.

SPECIMENS EXAMINED.

I am deeply indebted to Mr. W. E. Clyde Todd for the loan of the four specimens from El Trompillo, and two from Venezuela. The remaining specimens are in the collection of the American Museum.

Phaeoprogne tapera tapera.—Brazil: Bahia, 1; Santa Rita, Bahia, 1 (Aug. 11); Victoria, Rio Xingú, 1 (Feb.); Manaos, 2 (July 25). Peru: mouth Urubamba, 1 (Oct. 12); Lagarto, upper Ucayali, 2 (Feb. 22, 26); Sta. Rosa, upper Ucayali, 4 (Nov. 18–21); Orosa, Marañon, 3 (Sept. 5–11); Pto. Indiana, Napo and Marañon, 6 (June 16–28); Pilares, Piuva, 4 (June 16–18); Lamor, Piuva, 1 (June 13). Ecuador: Curaray and Napo, 1 (Jan. 20), 1 (Feb. 1), 2 (May 5, 7), 4 (Dec. 11); Duran, opp. Guayaquil, 3 (May 21), 2 (July 3, 4). Venezuela: Maripa, lower Orinoco, 2 (Mar. 1, 2), 1 (May 15), 3 (Dec. 11–23); Suapure, lower Orinoco, 2 (Apr. 8, 30);

Tucacas, Falcon, 1 (Oct. 18); Campos de Merida, 1 (Nov. 8). Colombia: Chicoral, upper Magdalena, 3 (Oct. 6, 10); Algodonal, lower Magdalena, 2 (Jan. 23); Bogota, 1.

Phaeoprogne tapera fusca.—Argentina: La Plata, Buenos Aires, 2 (Sept., Jan.); Embarcacion, Salta, 1 (Jan. 28); Paraguay: Fort Wheeler, Chaco, 1 (Oct. 12). Brazil: Palmares, sea-level, Rio Grande do Sul, 5 (Oct. 7–15); Corumbá, 1 (Apr. 1), 1 (Nov. 9); Urucum, near Corumbá, 4 (Dec. 1–15); Rio Taquary, Matto Grosso, 2 (Dec. 19); San Lorenzo River, Matto Grosso, 1 (Jan. 2); Descalvados, Matto Grosso, 2 (Nov. 20); Chapada, Matto Grosso, 1 (Jan. 29), 2 (Feb. 6), 2 (Sept. 3, 7), 1 (Oct. 30), 3 (Nov. 15, 30), 1 (Dec. 1). Peru: Orosa, Marañon, 3 (Sept. 11). Venezuela: Esmeralda, upper Orinoco, 5 (Oct. 2–Nov. 6); Suapure, lower Orinoco, 1 (Apr. 27); El Trompillo, Carababo,[1] 4 (May 11–18); Guachi, Zulia,[1] 2 (Aug. 23). Colombia: Turbaco, near Cartagena, 1 (Aug. 3) Rio Sinu, 1 (Nov. 21).

[1] Coll. Carnegie Museum.

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