

**Article II.—THE NORTH AMERICAN SPECIES OF THE  
GENUS COLAPTES, CONSIDERED WITH SPECIAL  
REFERENCE TO THE RELATIONSHIPS OF C.  
AURATUS AND C. CAFER.**

By J. A. ALLEN.

It has been known for more than thirty years that at certain points where the habitats of *Colaptes auratus* and *C. cafer* adjoin birds occur presenting the characters of the two species combined in the most heterogeneous manner, to account for which various hypotheses have been advanced. In order to arrive at the facts of the case, and to reach if possible a solution of the problem, I solicited, some months since, the loan of material for the prosecution of the investigation here detailed. Through the kindness of my fellow-workers, I have been able to bring together 785 specimens of the genus *Colaptes*, representing all of the North American and West Indian forms of the genus. These include nearly all of the available specimens in the leading public and private museums of this country, so far as they were considered especially desirable in the present connection.<sup>1</sup>

I am especially under obligations to Mr. Robert Ridgway, Curator of Birds in the U. S. National Museum, for securing for me the use of the specimens under his charge, and to Mr. William Brewster for the loan of one of the most extensive and valuable series of these birds extant. Captain Platte M. Thorne, 22d Inf., U. S. A., sent a series of unusual interest from Colorado and Montana, which he has kindly presented to this Museum. Valuable specimens have also been presented by Mr. L. Belding, of Gridley, Cal., and Mr. R. T. Lawrence, of Olympia, Wash. To various other ornithologists I am under deep obligations for the generous loan of specimens, to each of whom I tender my sincere thanks for their kind coöperation. The subjoined schedule indicates the source and amount of the material on which the present paper is based, arranged alphabetically under the names of con-

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<sup>1</sup> The series of *C. auratus* from eastern North America might have been greatly extended had it been deemed necessary.

tributors. The number of specimens received from any single source does not necessarily justly represent the relative value of the contribution, since some of the smaller lots often contain specimens of the highest interest, either on account of the localities represented or from the peculiar character of the specimens themselves.

Charles F. Batchelder, Cambridge, Mass. 6 specimens.  
 Lyman Belding, Gridley, Cal. 5 specimens.  
 Capt. Charles E. Bendire, U. S. A., Washington, D. C. 2 specimens.  
 William Brewster, Cambridge, Mass. 206 specimens.  
 Frank M. Chapman, New York City. 9 specimens.  
 Charles B. Cory, Boston, Mass. 3 specimens (*Colaptes gundlachi*).  
 Jonathan Dwight, Jr., New York City. 12 specimens.  
 B. T. Gault, Glen Ellyn, Ill. 3 specimens.  
 E. W. Hasbrouck, Washington, D. C. 5 specimens.  
 Gustave Kohn, New Orleans, La. 8 specimens.  
 R. T. Lawrence, Olympia, Wash. 5 specimens.  
 Prof. John Macoun, Canadian Geological Survey, Ottawa, Can. 21 specimens.  
 Dr. Edgar A. Mearns, U. S. A., Fort Snelling, Minn. 15 specimens.  
 George H. Ragsdale, Gainesville, Texas. 2 specimens.  
 George B. Sennett, New York City. 22 specimens.  
 Ernest E. Thompson, Toronto, Can. 2 specimens.  
 Capt. P. M. Thorne, 22d Infantry, U. S. A., Fort Keogh, Mont. 27 specimens.  
 American Museum of Natural History, 178 specimens.  
 Princeton College, 38 specimens.  
 U. S. Department of Agriculture (through Dr. C. Hart Merriam), 10 specimens.  
 U. S. National Museum (through Robert Ridgway), 208 specimens.

The following statement indicates, in a general way, the geographical sources of the material used.

Alabama, 3 specimens.	Idaho, 1 specimen.
Alaska, 8 specimens.	Illinois, 10 specimens.
Alberta, Brit. Am., 4 specimens.	Indiana, 7 specimens.
Arctic America (British), 9 specimens.	Indian Territory, 4 specimens.
Arizona, 82 specimens.	Iowa, 10 specimens.
Arkansas, 1 specimen.	Kansas, 6 specimens.
Assinaboia, Brit. Am., 3 specimens.	Louisiana, 10 specimens.
British Columbia, 58 specimens.	Lower California, 72 specimens.
California, 71 specimens.	Maine, 4 specimens.
Canada, 5 specimens.	Maryland, 10 specimens.
Chihuahua, 23 specimens.	Massachusetts, 16 specimens.
Colorado, 45 specimens.	Mexico (southern parts), 10 specimens.
Connecticut, 2 specimens.	Michigan, 4 specimens.
Cuba, 6 specimens.	Minnesota, 15 specimens.
Dakota (both States), 12 specimens.	Mississippi, 2 specimens.
Florida, 46 specimens.	Missouri, 1 specimen.
Georgia, 1 specimen.	Montana, 44 specimens.
Grand Cayman, W. I., 3 specimens.	Nebraska, 7 specimens.
Guadalupe Isl., L. Cal., 5 specimens.	Nevada, 10 specimens.
Guatemala, 9 specimens.	New Brunswick, 3 specimens.

New Hampshire, 2 specimens.  
New Mexico, 1 specimen.  
New Jersey, 18 specimens.  
New York, 23 specimens.  
North Carolina, 12 specimens.  
Ohio, 1 specimen.  
Oregon, 7 specimens.  
Pennsylvania, 10 specimens.

Sonora, 6 specimens.  
Tennessee, 9 specimens.  
Texas, 24 specimens.  
Utah, 2 specimens.  
Virginia, 8 specimens.  
Washington, 13 specimens.  
Wyoming, 8 specimens.

In addition to the specimens examined, much information has been gathered from the literature of the subject, and some from unpublished sources, derived from correspondence, particularly in regard to Texas, California and Arizona.

The large amount of material thus brought together has naturally been utilized incidentally for other purposes than that of its bearing on the relationship of *C. auratus* and *C. cafer*, since it afforded exceptionally favorable opportunities for studying the characters of the several forms in their first or nestling plumages, as well as in respect to seasonal, individual and geographical variation. Consequently, a few paragraphs are devoted in the present paper to each of these subjects. Mr. Frank M. Chapman, Assistant Curator in this department, has also further utilized this material as the basis of his paper 'On the Color-Pattern of the Upper Tail-Coverts in *Colaptes auratus*,' recently published in this Bulletin.<sup>1</sup>

## I.—THE RELATIONSHIPS OF *Colaptes auratus* AND *C. cafer*.

In 1858 Professor Baird, in his Report on North American Birds,<sup>2</sup> first called attention to the unique and since then notorious case of *C. auratus* and *C. cafer* (or *C. mexicanus*, as then designated), as presented by a large series of specimens from the region of the Upper Missouri and Yellowstone Rivers, in which the characters of the two birds were combined in a constantly varying and often asymmetrical manner. His material enabled him to present very fully the leading facts of the case, and led him to conclude that the state of affairs thus revealed pointed clearly to hybridization on a grand scale between the two species

<sup>1</sup> Vol. III, No. 2, Art. XXI, pp. 311-314, Aug., 1891.

<sup>2</sup> P. R. R. Expl. and Surv., Vol. IX, pp. 122-124.

in question, notwithstanding the startling nature of such an assumption. While he named the variously intermediate birds *Colaptes hybridus*, he distinctly stated that the name was not given in a specific sense, but merely for the convenient designation of the intermediate birds. Under this name they were currently known in literature for the next quarter of a century. For a time Professor Baird's explanation of the case was very generally accepted as probably correct, but later other hypotheses were suggested. Thus, in 1872, when the distribution of the so-called 'hybrids' was supposed to cover a much smaller area than the examination of the present available material shows to be the case, it was argued that the peculiar intergradation between these two forms might be due to the action of environment,<sup>1</sup> in accordance with certain well-established laws of geographic variation affecting many other species having a somewhat similar distribution. This suggestion met with sufficient favor to render for a time the question at least an open one.<sup>2</sup>

In 1877 it was suggested that these intermediate birds might be "remnants of a generalized form from which two 'incipient species' have become differentiated," and that "this 'hybrid' series is gradually losing its neutral character through the nearer approach, generation by generation, of its members to the characters of one or the other of the two specialized forms."<sup>3</sup> In 1884 it was suggested that the so-called hybrids, or birds of mixed character, may constitute "perhaps . . . a hybrid, and perhaps . . . a transitional form."<sup>4</sup>

The most recent writer on the subject treats the intermediate birds as a "race," with the nomenclatural status of a species, under the name *Colaptes ayresi*,<sup>5</sup> which is only an earlier name for Baird's *C. hybridus*. While admitting that this 'race' was "produced originally by the union of *C. auratus* and *C. mexicanus*" (= *cafer*), the suggestion is made that these intermediate birds may be, in some cases, "a sign of reversion to a remote ancestral plumage."<sup>6</sup>

<sup>1</sup> Cf. Allen, Bull. Mus. Comp. Zool., III, No. 6, 1872, pp. 118, 119.

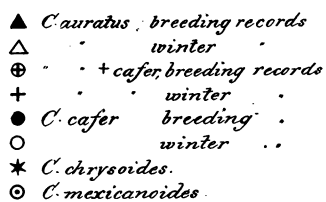
<sup>2</sup> Cf. Coues, Birds of the Northwest, 1874, p. 293.

<sup>3</sup> Ridgway, Orn. 40th Parallel, 1877, p. 556.

<sup>4</sup> Coues, Key to N. Am. Bds., revised ed., 1884, p. 492.

<sup>5</sup> A name given by Audubon in 1843 to mixed birds from the Upper Missouri country.

<sup>6</sup> Hargitt, Cat. Bds. Brit. Mus., XVIII, 1890, p. 8.



MAP SHOWING THE DISTRIBUTION OF THE NORTH AMERICAN FORMS OF *Colaptes* AND AREAS OF INTERGRADATION BETWEEN *C. auratus* AND *C. cafer*.



Before proceeding further, it may be well to consider briefly the distinctive characters and the geographical distribution of each of the several North American forms of the genus *Colaptes*. Beginning at the southward, we have first *C. mexicanoides*, restricted, so far as now known, to Guatemala,<sup>1</sup> but possibly ranging northward to the southern border of Mexico. This is essentially *C. cafer* with the coloration intensified, the black cross-bars of the whole dorsal plumage being broadened, the white rump more or less spotted with black, the entire top of the head and nape rufous instead of cinnamon, and the quills and malar stripe a deeper, darker red. Whether the habitats of *C. mexicanoides* and *C. cafer* actually meet, and whether or not the two forms intergrade, lack of material leaves us in doubt, the region where this should occur, if actually taking place, being unrepresented in the material at hand. The most southern specimens of *C. cafer*, however, tend decidedly toward *C. mexicanoides*, and one example, from Mirador (U. S. Nat. Mus., No. 42,065), may be regarded as a good intermediate, being nearly as much like the one as the other. Allowing the sum of the characters of *C. mexicanoides* to be represented by 100, 80 per cent. of them may be considered as common also to *C. cafer*, as this form is represented in Mexico, with a probability of complete intergradation, since the differences separating them are wholly differences of degree.

The habitat of *C. cafer*, in considering the relation of this form to its northern congeners, is of special interest. *C. cafer* is found from the southern border of Mexico northward throughout Mexico, excepting western Sonora and Lower California, and thence northward over the western part of the United States and British America, from about the eastern base of the Rocky Mountains to the Pacific Coast.

*C. rufipileus*, from Guadalupe Island, off Lower California, is an insular form of *cafer*, differing from *cafer* mainly in smaller size, much longer bill, and rather deeper colors, in this latter respect rather more resembling *C. cafer saturator* of the Northwest Coast. It was evidently derived from Californian rather than Mexican stock.

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<sup>1</sup> See the accompanying map.

*C. cafer saturator*, from the coast region of Washington and British Columbia, is the inevitable, naturally-to-be-expected Northwest Coast form of *C. cafer*, differing from the latter in slightly larger size and much deeper colors, and passing by insensible gradations into the paler bird of the adjoining interior. Both of these forms are evidently offshoots from the pure *cafer* stock, modified by environment under the ordinary laws of geographic variation prevailing over the regions in question.

*C. chrysoides* is found in the peninsula of Lower California, where it is the sole representative of the genus; it also ranges into Sonora, and thence northward into southern Arizona and south-eastern California. To the northward and eastward its habitat thus reaches, and at some points (at least in winter) overlaps that of *C. cafer*, with which, however, it appears never to blend. At least a large series of Arizona specimens of both species presents no intermediates. While it would be rash to assert that the two forms will not be found to interbreed in Sonora, where for a long distance their ranges must adjoin, and whence as yet material is lacking, I believe that the few intermediates hitherto doubtfully supposed to exist will prove to be *cafer* + *auratus*, wrongly identified as *cafer* + *chrysoides*. In *C. chrysoides* we have, as regards general characters, a small, pale form presenting the general appearance of *mexicanoides*, it being rather nearer this species in the aggregate of its characters than it is to *cafer*; it differs from either, however, in one very radical feature of coloration, namely, in the quills being golden, as in *auratus*, instead of red, as in the *cafer-mexicanoides* group. Yet the golden quills are the only color feature which in any way recalls *auratus*, and hence does not necessarily imply any close genetic relationship between *chrysoides* and *auratus*. Besides, in the large series of *chrysoides* examined there is no trace of any of the distinctive features of *auratus*, such as the red nuchal crescent, the black malar stripes, or the peculiar coloration of the head. If we let the sum of the characters of any form of *Colaptes* be represented by six, five of the characters of *C. chrysoides* would be shared in common with the *cafer-mexicanoides* group and one only by *auratus*.

*C. auratus*, while ranging over the northern and eastern three-fourths of the continent of North America, has also two outlying



insular forms, *C. chrysocaulosus* of Cuba, and *C. gundlachi* of Grand Cayman, both evidently offshoots from the *auratus* stock, modified by environment, and differing from *auratus* somewhat as *mexicanoides* differs from *cafer*.

The species of *Colaptes* found north of the Isthmus of Panama thus fall into three groups, two of which are much more closely related to each other than either of these two is to the third. These are (1) the *cafer-mexicanoides* group, (2) the *chrysoides* group, (3) the *auratus* group. The first and the last, so far as features of coloration are concerned, are the most unlike, having no special characters in common, and yet it is these two, *cafer* and *auratus*, which, as shown by the material now in hand, thoroughly intergrade wherever their habitats meet, that is, over a belt of country from 300 to 400 miles wide, and some 1200 to 1500 miles long. They are also more or less mixed from the eastern border of the Great Plains westward to the Pacific Coast, from about the latitude of 38° northward to about latitude 55°.

The leading distinctive characters of *C. auratus*, as compared with *C. cafer*, are :

<i>Auratus.</i>	<i>Cafer.</i>
1. Quills <i>yellow</i> .	Quills <i>red</i> .
2. Male with a <i>black</i> malar stripe.	Male with a <i>red</i> malar stripe.
3. Adult female with <i>no</i> malar stripe.	Adult female with (usually) a distinct <i>brown</i> malar stripe.
4. A <i>scarlet nuchal crescent</i> in both sexes.	<i>No nuchal crescent</i> in either sex.
5. Throat and fore neck <i>brown</i> .	Throat and fore neck <i>gray</i> .
6. Whole top of head and hind neck <i>gray</i> .	Whole top of head and hind neck <i>brown</i> .
7. General plumage with an <i>olivaceous</i> cast.	General plumage with a <i>rufescent</i> cast.

Characters shared in common by both are :

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|-----------------------------------|------------|
| 1. General size.                  | 4. Habits. |
| 2. Proportion of parts.           | 5. Notes.  |
| 3. General pattern of coloration. |            |

In size, in the general pattern of the coloration, in habits and notes, the two species are indistinguishable.

The presence of a nuchal crescent in both sexes in the one and its absence in the other, the striking contrast in the color of the malar stripes, and of the quills of the wings and tail, and the transposition of the colors of the crown and throat, are, however,

not simply differences of degree, but of a radical nature. In fact, no two congeneric species could well present more striking differences as regards coloration.

The manner of the interblending of the characters of the two species in the mixed birds has an important bearing upon the problem of the relationship of the two birds, as regards (1) the way in which the characters of the two species are combined, and (2) the geographical area over which the mixed birds are distributed.

HOW THE CHARACTERS OF THE TWO SPECIES ARE COMBINED.—As has been long known—indeed, as shown by Baird in 1858—the ‘intermediates’ or ‘hybrids’ present ever-varying combinations of the characters of the two birds, from individuals of *C. auratus* presenting only the slightest traces of the characters of *C. cafer*, or, conversely—individuals of *C. cafer* presenting only the slightest traces of the characters of *C. auratus*—to birds in which the characters of the two are about equally blended. Thus we may have *C. auratus* with merely a few red feathers in the black malar stripe, or with the quills merely slightly flushed with orange, or *C. cafer* with either merely a few black feathers in the red malar stripe, or a few red feathers at the sides of the nape, or an incipient, barely traceable scarlet nuchal crescent. Where the blending of the characters is more strongly marked, the quills may be orange yellow or orange red, or of any shade between yellow and red, with the other features of the two birds about equally blended. But such examples are exceptional, an unsymmetrical blending being the rule, the two sides of the same bird being often unlike. The quills of the tail, for example, may be part red and part yellow, the number of yellow or red feathers varying in different individuals, and very often in the opposite sides of the tail in the same bird. The same irregularity occurs also, but apparently less frequently, in the quills of the wings. In such cases the quills may be mostly yellow with a few red or orange quills intermixed, or red with a similar mixture of yellow. A bird may have the general coloration of true *cafer* combined with a well-developed nuchal crescent, or nearly pure *auratus* with the red malar stripes of *cafer*. Sometimes the body plumage

is: that of *C. auratus* with the head nearly as in pure *cafer*, or exactly the reverse may occur. Or we may have the general plumage as in *cafer* with the throat and crown as in *auratus*, and the malar stripe either red or black, or mixed red and black, and so on in almost endless variations, it being rare to find, even in birds from the same nest, two individuals alike in all their features of coloration. Usually the first trace of *cafer* seen in *auratus* manifests itself as a mixture of red in the black malar stripe, either as a few red feathers, or as a tipping of the black feathers with red, or with merely the basal portion of the feathers red. Sometimes, however, there is a mixture of orange or reddish quills, while the malar stripe remains normal. In *C. cafer* the traces of *auratus* are usually shown by a tendency to an incipient nuchal crescent, represented often by merely a few red-tipped feathers on the sides of the nape; at other times by a slight mixture of black in the red malar stripe.

THE GEOGRAPHICAL AREA OVER WHICH THE MIXED BIRDS ARE DISTRIBUTED.—In 1858, when Baird described his *Colaptes hybridus*, and for many years after, mixed birds were known only from the upper Missouri and Yellowstone region. Later they were noted from California, and more recently from various points along the western border of the Great Plains, from Texas northward to the British boundary.

Occasional specimens of *C. auratus* from the Atlantic States, showing a few red feathers in the malar stripe, have also been for some time known, but the occurrence of a large proportion of mixed birds in California has only lately been recorded. Yet the distribution of mixed birds, as shown by the material now brought together,<sup>1</sup> proves to be far more extended and general than till now has been supposed. Instead of the mixed birds being comparatively limited in distribution, they are found to have a wide dispersion, occurring, as already stated, with considerable frequency from the eastern border of the Great Plains westward to the Pacific Coast, and from near the Mexican boundary northward to some distance north of the United States, with, however, the area of greatest abundance much more local-

<sup>1</sup> See the accompanying map.

ized. No mixed birds, however, have been seen from any part of Mexico, nor from any part of Arctic America, where in the one case only pure *cafer* is found, and in the other only pure *auratus*.

East of the Mississippi River, from Florida northward and westward to Alaska, *C. auratus* rarely shows any outcropping of the characters of *C. cafer*. Perhaps one male in a thousand (or more probably a still smaller proportion) shows a few red feathers in the malar stripe, varying in different individuals from the faintest perceptible trace to a mixture of one-fourth to one-third red. A single bird from Louisiana (Coll. Gustave Kohn) has the malar stripe wholly red and the whole head nearly as in *cafer*, and a single specimen from Toronto, Canada (Coll. E. E. Thompson, No. 206<sup>1</sup>) has the tail about half orange red, with other traces of *cafer* characters; and I have heard of what purports to be the capture of a nearly pure *cafer* specimen in Pennsylvania, but this latter case is not well authenticated. Specimens with a slight amount of red in the malar stripe are represented in the material I have examined from Massachusetts, Long Island, New Jersey (five specimens), Pennsylvania, Virginia, Florida (several), Louisiana (several), Tennessee, Ohio, Indiana, Illinois (several), Michigan (two), and Minnesota. They seem to be quite as frequent along the Atlantic seaboard as at any point east of the Mississippi River. Material from the States immediately west of this line, from Iowa southward, is scanty, but the few specimens seen do not indicate a larger proportion of birds with red in the malar stripe than occur in Florida or New Jersey. It is hence probable that nearly pure *auratus* prevails westward to the eastern border of Texas, the Indian Territory, Kansas, and Nebraska, and over the greater part of both Dakotas and Manitoba. Birds from eastern Texas, eastern Kansas, and eastern Montana, taken in the breeding season, generally, or at least frequently, show some traces of the characters of *cafer*, the malar stripe frequently being more or less mixed with red. In southeastern Texas, and thence northward through middle Texas, and over the Plains to, and doubtless much beyond, the northern boundary of Montana, mixed birds are the rule, the characters of the two species being blended in every conceivable combination, pure *cafer* or pure

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<sup>1</sup> See Auk, Vol. II, 1885, p. 335.

*auratus* being rarely met with, except in winter, when, in consequence of migration, pure *auratus* is more or less frequent in Kansas, the Indian Territory, and Texas, considerably to the westward of its normal limit in the breeding season.<sup>1</sup> At the same time there is an influx into the same region of nearly pure *cafer* from the westward, resulting in a commingling of birds presenting mixed characters with those of normal character.

In western Texas, New Mexico, Arizona, and southern California, the prevailing form in the breeding season is probably nearly pure *cafer*, but in winter the proportion of perfectly pure birds is much smaller, owing to the southward migration of slightly-mixed birds from further north. In a series of over 30 males from Arizona, taken between October 1 and March 30, more than one-third show either traces of black in the malar stripe, or traces of a scarlet nuchal crescent, or both. One female has all the quills orange yellow, but generally the equally large series of females shows no recognizable characters of *auratus*.

In central and western Colorado, Utah, and Nevada, the characters of *cafer* evidently prevail, at least in the breeding season; in eastern Colorado in winter and during migrations mixed birds are the more common, and have been taken in the breeding season at Fort Garland in the same State. Similar specimens have been taken in Utah and Nevada, every one of my series of seven males from Nevada showing traces of the red nuchal crescent, and some of them other characters of *auratus*.

Of Idaho almost nothing is known. The single specimen I have seen is a mixed bird. In Wyoming mixed birds appear to be the rule, with *auratus* characters prevailing in the eastern part of the State and *cafer* characters in the western. The same is apparently true of Montana. Birds from eastern Oregon, eastern Washington, and eastern British Columbia, or from the area east of the Cascades, also present a strong infusion of *auratus* characters; some specimens being two-thirds to three-fourths *auratus* and others nearly pure *cafer*, with rarely a normal bird of either species. The bird of the coast region, from the mouth of the

<sup>1</sup> Mr. H. P. Attwater writes me that at San Antonio "Typical *auratus* is common in winter; the bulk migrate earlier than *C. cafer*. Typical *cafer* is rare; hybrid Flickers of several shades are common. All the forms have been observed migrating together."

Columbia River northward, is *C. cafer saturator*, but a large proportion of the specimens, even from Puget Sound and Vancouver Island, show traces of *auratus* characters, in some instances very prominent traces, even to yellow quills interspersed with red ones. Indeed, Mr. Fannin states that true *C. auratus* occurs as a rare visitor on Vancouver Island and the adjoining mainland.<sup>1</sup>

In central and northern California the two forms are as thoroughly mixed as at any point east of the Rocky Mountains, both *auratus* and *cafer* occurring in a nearly pure state, with birds presenting every possible combination of the characters of both species. Of 40 specimens from central California, chiefly from Marin and adjoining counties, three are nearly pure *auratus*, the only feature of *cafer* being a very slight mixture of red in the malar stripe—not more than occasionally occurs in birds from the Atlantic States; six (of which four are females, and hence have less significance) are apparently pure *cafer*; of the remaining 31 *auratus* characters prevail in eight, and *cafer* characters in twenty, with three in which the *cafer* and *auratus* characters are about evenly divided. In San Bernardino, San Diego, and adjoining counties in southern California (I have one specimen of pure *auratus* from Warm Springs) traces of *auratus* characters are rare, while in Oregon, so far as material shows, about the same conditions of mixture occur as are found in central California. Indeed, as most of the California specimens before me were taken either in the autumn or winter, it is fair to conclude that many of them were migrants from further north, probably from Oregon or eastern Washington, since more or less mixed birds occur as far north as Sitka, and even Chilkat. Beyond this point, to the northward and eastward, *cafer* appears to be replaced by pure *auratus*, from which region, through migrants, is doubtless derived the strong infusion of *auratus* characters in the birds of California.

To summarize the foregoing, we find that *cafer* unmixed with *auratus* occupies Mexico, but that very soon, after crossing the United States boundary we begin to meet with specimens showing slight traces of the characters of *auratus*, and that as we proceed northward these traces become more frequent and more

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<sup>1</sup> Check List of British Columbia Birds, 1891, p. 29.

pronounced, across the whole breadth of the habitat of *cafer*, till north of the United States we pass into the habitat of pure *auratus*. There is also the same blending in passing eastward from the eastern base of the main chain of the Rocky Mountains. Thus the blending is complete along the line of junction of the habitat of the two species, or from southeastern Texas northward along the western edge of the Plains into British America and thence westward in British America to the Pacific Coast in southern Alaska. From this line we may trace the mixed birds westward and southward over nearly the whole range of *cafer* north of Mexico, due apparently from not only the mixing of the two species wherever their habitats adjoin, but through the intrusion, mainly from the northward, of *auratus* into the habitat of *cafer* through the southward migration of *auratus* in winter, some of the latter apparently remaining as summer stragglers to breed.

The conditions here outlined are shown graphically on the accompanying map, compiled primarily from specimens actually examined by the writer, but supplemented to a considerable extent by an examination of the available literature bearing on the subject. An attempt is made to distinguish by the use of different symbols, in the case of not only *C. auratus* and *C. cafer*, but of the intergrades as well, the nature of the record as regards season, as explained on the map itself. The boundary lines are of course to some extent hypothetical.<sup>1</sup>

CONCLUSIONS.—The facts elicited in the present investigation tend strongly to confirm Baird's startling hypotheses of hybridization on a grand scale between *Colaptes auratus* and *C. cafer* to account for the occurrence of birds presenting ever-varying combinations of the characters of the two species over the Plateau and Great Basin regions of the continent. None of the other hypotheses thus far advanced so fully, or in fact to any great extent, meet the requirements of the case. In no instance do we meet with stages or methods of geographical variation at all comparable with what is seen in the case of *C. auratus* and *C. cafer*.

<sup>1</sup> The habitats of *C. chrysoides* and *C. cafer* overlap; the lighter line is intended to indicate the northern and eastern boundary of that of the former, the heavy line the southwestern boundary of that of *cafer*.

[March, 1892.]

The transition between geographic forms, however diverse, is gradual and symmetrical, affecting all parts of the plumage equally and simultaneously, and is obviously correlated with changes in the physical surroundings; also the differences between the most extreme forms are merely differences of degree. In the case of *Colaptes* the essential differences between *auratus* and *cafer* are radical; they are, in fact, contrasting characters; and the intergradation is irregular, with all sorts of asymmetrical combinations of the characters of the two forms, and no correlation between their intergradation and the conditions of environment.

In California, British Columbia, Montana, Wyoming, Kansas, and southern Texas, we get the same irregular and multifarious combinations of the characters of the two species. On the other hand, the phenomena of intergradation, as regards both the nature of the intergrades and their geographical distribution, are just what we should expect them to be on the theory of interbreeding. Furthermore, it is a matter of observation that very unlike birds pair together, and that individuals of the same brood are often very diverse in appearance. While I know of no record of pure *cafer* birds being found mated with pure *auratus* birds, that such mating has many times occurred seems beyond question, since this might happen at any point along a line more than a thousand miles in extent where the habitats of the two species adjoin. On either side of this boundary the influence of one species upon the other fades out gradually as the distance from the line increases, till in Mexico, in the United States east of the Mississippi River, and in Alaska and eastern British America, it becomes practically *nil*. The outcropping of *auratus* characters in *cafer* in British Columbia and in the United States west of the Rocky Mountains, and the gradual fading out of this infusion to the southward, can readily be accounted for by the migration of *auratus* from the north into the northern border of the habitat of *cafer*, and the gradual wide dispersion southward of the intermediates resulting from the interbreeding of the two species. The very slight traces of *cafer* characters occurring in rare instances in *auratus* in the East may be readily supposed to be due to the sporadic dispersion eastward of waifs from the habitat of *cafer*,



since it is known that nearly all western birds occasionally stray eastward even to the Atlantic seaboard. The capture near New Orleans and Toronto of strongly marked 'hybrids' shows that at least 'intermediates,' if not representatives of pure *cafer*, stray far to the eastward of their proper habitat.

It is thus unnecessary to suppose that the appearance of a few red feathers in the malar stripe of specimens of *auratus* taken in the Atlantic States indicates a tendency to a reversion to some hypothetical 'ancestral type' which had the malar stripe red, or that the presence of black feathers in the malar stripe, or an incipient scarlet nuchal crescent, in birds from Arizona, Nevada, and southern California, indicates a similar tendency to a hypothetical ancestor which had black malar stripes and a red nuchal crescent; since the slight infusion of *cafer* blood in the one case, and of *auratus* blood in the other, of which we have almost indubitable proof, affords an adequate and satisfactory explanation of these odd phenomena.

The large infusion of *auratus* blood shown in the *Colaptes* stock in Oregon and northern California is easily explained by the fact that *C. auratus*, like many other eastern birds, can find easy access to the northwest coast either by way of the low divide in Wyoming, or from the northward, the habitat of *auratus* reaching the Pacific Coast in northern British Columbia and Alaska.

It is of interest in this connection to note that in the earlier collections from California 'hybrid' Flickers were practically unknown, there being none in the material handled by Baird in 1858. In 1870 Dr. J. G. Cooper considered the capture of two examples of *Colaptes*, taken at Oakland, presenting characters of *auratus*, worthy of special record.<sup>1</sup> But Mr. W. E. Bryant, in Belding's 'Land Birds of the Pacific District,' published in 1890, says that specimens referable to '*hybridus*' "are now taken almost as often as *C. cafer*; in fact, it is unusual to get really good examples of *C. cafer* in some localities" (l. c., p. 72). My own series from central and northern California, as already noted, fully bears out this statement. In our standard works on North American birds, even in the latest, the habitat of the so-called '*hybridus*' is given as the region of the upper Missouri and

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<sup>1</sup> Orn. Cal., I, p. 412.

Yellowstone and the Black Hills. Now, however, we have evidence of the occurrence of mongrel birds in abundance over a belt of country, hundreds of miles wide, extending from the Rio Grande in Texas northward and westward to southern Alaska. Hence one may almost ask whether this does not favor the assumption that *C. auratus* is gradually extending its range into the habitat of *C. cafer*, particularly in California, and along the whole border of the habitat of *cafer*. Unfortunately the evidence favoring this assumption is mainly negative, owing to the deficiency of material from the habitat of *cafer* collected prior to a comparatively recent period.

Finally, it may be added, the intergradation between *Colaptes auratus* and *C. cafer* is not only unique as regards the character and geographical distribution of the intergrades, but is something superimposed upon ordinary geographic variation due to environment, since the ordinary phases of geographic variation, as seen in other birds having the same distribution, is well illustrated in the various North American forms of *Colaptes*, as has already been indicated, and as will be presently shown more in detail.

## II.—GEOGRAPHICAL VARIATION.

(1) IN SIZE.—In both *Colaptes auratus* and *C. cafer* there is a marked decrease in size from the north southward.

The average length of the wing in specimens of *C. auratus* from Arctic America is 6.35 in.; in specimens from South Florida, 5.75 in., giving an average difference of .60 of an inch between birds from the extreme north and the extreme south—equal to rather more than 10 per cent. of the average length of the wing in the southern birds. Specimens from near the northern boundary of the United States, from New England and New York westward to Minnesota, are just intermediate in size between the specimens from Arctic America and South Florida, the average length of the wing being 6.12.

The Cuban *Colaptes chrysocaulosus* is still smaller than the Florida birds (wing about 5.55), while *C. gundlachi* from Grand Cayman, is slightly smaller than the Cuban form.

In *C. cafer* geographical variation in size is less uniform, in passing from the north southward, specimens from Chihuahua and Arizona being nearly as large as specimens from Montana and British Columbia, the difference in latitude perhaps being partly offset by the greater elevation of the more southern region. Specimens from southern Mexico, however, are much smaller than those from Chihuahua and Arizona, the wing in eight males averaging 6.07.

*C. cafer saturator*, from the Northwest Coast, has the average length of the wing about 6.55, while in *C. rufipileus*, from Guadalupe Island, it is about 5.93, or about the same as in specimens from southern Mexico—a difference nearly parallel with that between *C. auratus* from Arctic America and Florida.

*C. mexicanoides* averages only a little smaller than examples of *C. cafer* from southern Mexico, the former having the wing 6.10, the latter about 6.50.

*C. chrysoides* presents great constancy in size, there being no very appreciable difference in this respect between specimens from Arizona and the southern part of the peninsular of Lower California. The length of the wing averages about 5.75—the same as in South Florida examples of *C. auratus*, and hence less than in any of the forms of the *C. cafer-mexicanoides* group.

The accompanying table of measurements (see p. 38) shows<sup>1</sup> more in detail the variation in size with locality here summarized.

(2) IN COLORATION.—The geographical variation in coloration in the various forms of *Colaptes* is quite parallel to that in other species of similar distribution, and hence presents nothing especially noteworthy. In *C. auratus* there is a lightening of the colors as we approach the Plains. This is very noticeable even in Minnesota specimens, and still more so in specimens from the Dakotas, Nebraska and Kansas.

It has been suggested that the resident form of South Florida would prove separable as a subspecies from the bird found at large further north, on the basis of its smaller size and darker colors. The average difference, however, as shown by a large

<sup>1</sup> These measurements have been made with great care by Mr. C. B. Isham, an assistant in this department of the Museum, and are hence all strictly comparable with each other.

TABLE SHOWING GEOGRAPHICAL AND INDIVIDUAL VARIATION IN SIZE IN THE NORTH AMERICAN SPECIES OF *Colaptes*.

SPECIES.	LOCALITY.	Specimens. No. of	Sex.	WING.			TAIL.			CULMEN.		
				Aver- age.	Max- imum.	Min- imum.	Aver- age.	Max- imum.	Min- imum.	Aver- age.	Max- imum.	Min- imum.
<i>C. auratus</i> .....	Arctic America.....	8	♂	6.37	6.62	6.20	4.26	4.56	4.06	1.44	1.58	1.36
"	"		♀	6.32	6.50	6.18	4.25	4.34	4.14	1.36	1.52	1.31
"	Northern United States.....	6	♀	6.16	6.40	5.94	4.09	4.52	3.90	1.40	1.54	1.26
"	"	19	♀	6.08	6.30	5.80	4.01	4.40	3.70	1.32	1.52	1.16
"	Florida.....	18	♀	5.77	5.92	5.66	3.89	4.10	3.70	1.33	1.38	1.24
"	"	10	♂	5.72	6.08	5.42	3.81	4.24	3.76	1.29	1.40	1.12
<i>C. chrysicaulus</i> .....	Cuba.....	10	♀	5.67	5.68	5.67	4.19	4.20	4.18	1.35	1.36	1.34
"	"	2	♂	5.47	5.66	5.32	4.15	4.34	4.00	1.32	1.38	1.26
<i>C. cafer</i> .....	Arizona.....	3	♀	6.53	6.70	6.36	4.45	4.78	4.20	1.43	1.48	1.40
"	"	10	♂	6.41	6.72	6.20	4.23	4.42	4.04	1.40	1.46	1.32
"	Chihuahua.....	10	♀	6.52	6.70	6.30	4.22	4.52	3.96	1.50	1.62	1.38
"	"	10	♀	6.46	6.72	6.18	4.34	4.62	3.96	1.49	1.62	1.36
"	Southern Mexico.....	7	♂	6.07	6.52	5.92	4.71	4.86	4.45	1.40	1.45	1.30
<i>C. cafer saturator</i> .....	Brit. Col. and Washington.....	10	♂	6.55	6.64	6.46	4.56	4.86	4.10	1.56	1.66	1.48
"	"	10	♀	6.51	6.82	6.36	4.53	4.84	4.16	1.47	1.56	1.40
<i>C. rufipileus</i> .....	Guadalupe Island.....	1	♂	5.94	.....	.....	4.16	.....	.....	1.58	.....	.....
"	"	4	♀	5.92	6.20	5.76	4.40	4.50	4.34	1.49	1.60	1.40
<i>C. mexicanoides</i> .....	Guatemala.....	6	♂	6.11	6.24	6.00	4.40	4.50	4.34	1.49	1.60	1.40
"	"	4	♀	5.96	6.00	5.92	4.27	4.38	4.18	1.39	1.40	1.36
<i>C. chrysoides</i> .....	Arizona.....	8	♂	5.78	5.84	5.70	3.72	4.00	3.52	1.46	1.58	1.38
"	"	4	♀	5.68	5.80	5.60	3.44	3.60	3.32	1.48	1.68	1.36
"	Triunfo, L. Cal.....	12	♂	5.74	6.92	5.54	3.72	3.94	3.40	1.36	1.40	1.26
"	"	12	♀	5.64	5.80	5.42	3.65	3.82	3.34	1.34	1.46	1.26

amount of material, proves too slight and too inconstant, in either size or color, to make a separation practicable, as is readily shown by comparison of a considerable series of breeding birds from South Florida with a corresponding series from the Middle States or New England. Some of the South Florida birds are not only small, but also exceptionally dark, but the dark color proves to be due in large part to the worn condition of the plumage, consequent upon the breeding season, and in some measure to soiling of the plumage, due apparently to contact with burnt trees. Specimens nearly as dark occur, however, in New Jersey and Massachusetts, so that the average difference in color between Florida and northern birds is not readily appreciable.

*C. cafer* presents four geographical phases, correlated with very different climatic conditions. First, the pale form, found throughout the arid interior, from Central Mexico northward. Second, the darker, much deeper-colored Northwest Coast form, known as *C. cafer saturator*. Third, a quite similar phase, as regards coloration, but much smaller, from southern Mexico. Fourth, the insular *C. rufipileus* from Guadalupe Island, off the coast of southern California. This closely resembles *saturator* in color, but is much smaller and has a relatively much longer bill.

Attention has previously been called<sup>1</sup> to the small size of the birds from southern Mexico, and also to their resemblance in color to birds from Vancouver.<sup>2</sup> The specimens before me show that the birds from southern Mexico are not only much smaller than specimens from Chihuahua and Arizona, but they closely resemble in color subspecies *saturator* from the Northwest Coast, a condition of things quite in accord with the well-known lines of geographic variation in other groups, and perhaps justifying Mr. Ridgway's suggestion (l. c.) that it may prove expedient to recognize these small, dark-colored southern birds as a geographic race.

*C. mexicanoides* may perhaps be almost considered as an extreme southern differentiation of *C. cafer*, in which all the

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<sup>1</sup> Ridgway, Man. N. Am. Birds, 1887, p. 296, foot-note.

<sup>2</sup> Hargitt, Cat. Bds. Brit. Mus., XVIII, 1890, p. 19.

colors and markings are much stronger than in any form of the *C. cafer* group. So far as now known, however, it must take rank as a species instead of a subspecies.

### III.—INDIVIDUAL VARIATION, AND VARIATION DUE TO AGE AND SEASON.

(1) INDIVIDUAL VARIATION.—The range of individual variation in the various North American forms of *Colaptes* is rather greater than the average range in other species, especially in respect to color. The variation in size is perhaps sufficiently shown in the table of measurements given on page 38 (compare under each species the columns headed respectively 'maximum' and 'minimum'). The bill varies in length, in the different forms, from 15 to 25 per cent. of the mean; the length of the wing, from 8 to 12 per cent.; the length of the tail, from 12 to 18 per cent. The female, judging from the measurements of about 200 specimens, is rather more variable than the male. While the female averages smaller than the male, the largest bird of a series of specimens, taken at the same locality and at the same season, proves sometimes to be a female, while some of the smallest birds of the series may be males. The tail varies more than the wing, and the bill much more even than the tail.

Individual variation in color affects (1) the size and shape of the circular black spots on the lower plumage, (2) the width and number of the dusky crossbars of the upper plumage, (3) the size and form of the malar stripe, (4) the presence or absence of black spots on the white rump, (5) the tone of color suffusing the general plumage. The last, however, is more or less complicated with seasonal variation.

The pattern of coloration being the same in all the forms, and the extent and character of the variation similar in each, the remarks here following may be understood as applying to the group collectively, unless otherwise stated.

Each feather of the ventral surface, from the pectoral crescent posteriorly, is marked near the tip with a circular spot of black; they are smaller and more nearly circular anteriorly, larger and transversely broader posteriorly. Those of the breast vary

greatly in size and shape in different birds, being sometimes round, sometimes pear-shaped, sometimes transversely oval, and sometimes longitudinally oval. In some birds they are twice as large as in others, varying in different birds from an average diameter of 2 or 3 mm. to an average diameter of 4 or 5 mm., comparing in each case corresponding feathers.

The interscapulars, scapulars, wing-coverts and quills are barred transversely with black. These bars, usually three in number, vary enormously in width in different specimens strictly comparable as regards age, season and locality. The apical bar, for example, has usually a width of about  $2\frac{1}{2}$  mm.; the extremes vary from 1 to 4 mm., resulting of course in a very different general effect. Generally speaking, birds with small spots on the ventral surface have narrow bars on the dorsal surface, and conversely; but this is by no means an invariable rule, since birds occur with very large spots on the lower plumage and very narrow bars on the upper plumage, or the reverse. Extreme variations in the size of the spots and bars are especially common in both *C. chrysoides* and *C. cafer*; in *C. auratus* the range of variation is narrower and extreme departures from the normal are less frequent.

The malar stripe varies in form and extent in the male in all the forms, but more in *C. auratus* perhaps than in the others. It is sometimes very broad and at the same time very long, thus greatly exceeding the normal or average extent; sometimes it is very much reduced, occasionally to one-half, and in extreme cases to one-third the normal size. Thus the area may be two to three times greater in some specimens than in others.

There are occasionally indications of a malar stripe in the female. This, however, is very rare in *C. auratus* and *C. chrysoides*, but common in the *C. cafer* group, and the rule in *C. mexicanoides*, where the exceptions are rare. When present in the female it differs greatly in color from the corresponding mark in the male. In *C. auratus* a very small percentage of the females have the area occupied by the malar stripe in the male faintly tinged with grayish, the basal portions of the feathers being dusky and showing slightly at the surface. In one specimen (No. 8308, ♀ ad., Coll. Wm. Brewster), from Ann Arbor, Michigan, the feathers of

the malar area are distinctly black beneath the surface, the black extending quite to the tips of some of the feathers, forming a well-marked incipient malar stripe. This is, however, an extreme case, and almost unique. In another specimen, also from Michigan (Ypsilanti, No. 8306, ♀ ad., Coll. Wm. Brewster), a few of the feathers of the malar region are tipped with black and many others with *red*, giving rise to a very narrow *red* malar stripe slightly mixed with black. Otherwise the bird is a normal example of *C. auratus*.

In a very large series of *C. chrysoides* two females show a faint wash of cinnamon at the posterior border of the area colored red in the male. This, however, may be due merely to immaturity, the birds being apparently young of the year, in which a slight trace of the brownish malar stripe is usually present in the female prior to the first molt.

In all the forms of *C. cafer* the adult female has generally an incipient brownish cinnamon malar stripe, sometimes as well defined as is the red malar stripe in the male. In perhaps ten to twenty per cent. of the birds examined it is entirely wanting; in a large proportion it is clearly outlined, but the brownish tint is superficial and more or less mixed with gray; in fully one-third, however, it is as distinct as in the female of *C. mexicanoides*, and nearly as bright in color, being of the same rich cinnamon rufous as the forehead and the superciliary stripe. These variations have evidently no geographical significance, since the whole range of variation here indicated occurs in birds from Montana, British Columbia, Washington, California, Arizona, and Mexico, with the several phases similarly represented at each of these localities.

As regards the tone of color suffusing the general plumage, fall birds from the same locality show a wide range, whatever the species may be, and the same is true of breeding birds. In *C. auratus*, for example, the ground color of the back varies, in fall birds, from hair brown through olive to bistre (*cf.* Ridgway, Nomen. Colors), while the lower surface varies from a strong tinge of yellow to tawny vinaceous. In spring birds the lower surface varies from nearly white to dull vinaceous cinnamon, with a corresponding range of variation in the dorsal plumage.



A male example of *C. cafer saturator* (No. 1160, Coll. Prof. J. Macoun, Burrard Inlet, B. C., April 29, 1887,) is noteworthy on account of having a distinct but narrow supraloral line of *bright red* on each side, meeting in front across the base of the forehead.

(2) SEASONAL VARIATION.—The purely seasonal variation in color results as usual from (1) fading and (2) abrasion. In fall birds the plumage is more heavily suffused with coloring matter, both above and below, and the tints are thus deeper and stronger. During winter there is a gradual loss of color, which proceeds more rapidly during the spring and early summer, simply through fading from exposure, resulting in a marked change in tone. At the same time the edges of the feathers become gradually worn away, till, towards the end of the breeding season, the light-colored apical border has disappeared. This gives greater distinctness and prominence to the black spots below and the dark bars above, which in fresh plumage are partially veiled by the overlapping lighter edges of the feathers. This, with the change in the tone of the ground color, results in a very different general effect, the breeding bird appearing blacker and more heavily spotted and barred than when in fresh autumnal or winter plumage.

Seasonal change of color, due to fading and abrasion, is in general much greater than is commonly recognized, and is a factor to be constantly borne in mind in the comparison of birds from different localities. It is not perhaps greater in *Colaptes* than in many other groups.

(3) VARIATION DUE TO AGE.—Under this head will be given simply a few notes on the first or nestling plumage. In all of the forms the young birds have the whole top of the head more or less red, as in young Woodpeckers generally, through the feathers being narrowly tipped with this color. The amount of red, or the extent of this tipping, varies greatly in different individuals of even the same brood, as does likewise the shade of red, which varies from dull reddish brown to bright brick red. As regards general coloration, the markings are coarser and heavier than in the adults, and the general effect darker.

A feature of special interest in respect to the young in nestling plumage is the variable status of the malar stripe, considered as a secondary sexual character. In *C. auratus* both sexes have the black malar stripe, which in adult birds is confined to the male. In 30 specimens, varying in age from half-grown nestlings to full-fledged birds, *not one lacks the black malar stripe*, while five of them are sexed as females by their respective collectors from anatomical examination of the specimens, and attention is called on the label, to the presence of the malar stripe. While most of the other specimens are marked as males, it is quite certain that they were thus marked on the presumption that a black malar stripe denoted a male, in the young as well as in the adult.

Of four young *C. chrysoides* in first plumage two have the malar stripe red as in the adult male, while the other two have a well-defined *rufous* malar stripe, and are sexed as females by the collector. In young *C. cafer* and *C. cafer saturatus* the sexes are similarly distinguished, the malar stripe in the males being bright red and in the females *rufous*—in other words, the same as in the adults.

In *C. auratus* and *C. chrysoides* of North America, and in *C. campestris* and *C. agricola* of South America, the adult female lacks the red or black malar stripe (as the case may be) present in the male, while in two other South American species (*C. pitius* and *C. cinereicapillus*) this mark is not only wanting in the female but is only imperfectly developed in the male. Consequently it would seem that, on the theory that secondary sexual characters are first acquired by the male and later transmitted, more or less modified, to the female, the presence or absence of a malar stripe in the female would prove a clue to the genetic relationship of the North American types of the genus. When, however, we find the malar stripe present in both sexes in the young and absent in the adult female, as in the case of *C. auratus*, and present as a rule in the adults of both sexes and absent in the female in first plumage, as in the *C. cafer-mexicanoides* group, this character evidently fails to be of much service as an index to the ancestral relationships of the several forms.