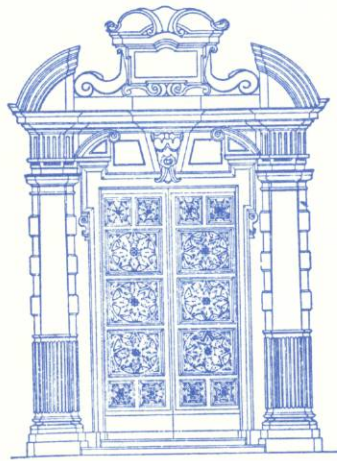


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of *Ramphocelus*, with Remarks
on Evolution in the Genus
(Aves: Thraupinae)

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ABSTRACT

Ramphocelus festae Salvadori, taken in Chiriqui, Panama, is shown to be a probable hybrid between *R. passerinii* and *R. dimidiatus*. *Ramphocelus inexpectatus* Rothschild, presumed to be from central Panama, is suggested to be a backcross between pure *R. icteronotus* and a hybrid *R. icteronotus/dimidiatus*. Evolutionary patterns between and within the three species groups of *Ramphocelus* are discussed. Diminution in the amount of red carotenoids visible in the plumage due to increasing melanization or dilution to yellow, appears to be one of the main derived plumage states within the genus.

INTRODUCTION

Many problematical names were once proposed for certain specimens of *Ramphocelus* in the 19th century. In the belief that there could not be so many species with unknown distributions in a genus whose members are so common and conspicuous, Griscom (1932) undertook to "dispose" of these "imaginary" species. Through examination of the literature, and in some cases the actual specimens, he concluded that one of these questionable names was a straightforward synonym of the Peruvian species *R. melanogaster*, whereas most of the rest had been applied to hybrids either between *R. flammigerus* and *R. icteronotus* originating in Colombia, or between *R. dimidiatus* and *R. icteronotus* that certainly or probably came from Panama. In two cases in which he did not examine specimens, he misinterpreted the original descriptions, which lead him to what we believe were erroneous conclusions. The results of our examination and analysis of these specimens appears below. We considered the possibility of intergeneric hybrids and made appropriate comparisons, but found no characters in any of the specimens discussed below to indicate relationships outside the genus *Ramphocelus*.

Ramphocelus festae

Enrico Festa (1868-1939), a pupil and protégé of the famous ornithologist Tommaso Salvadori, was one of the last naturalists of the old school of Vertebrate Systematics of Turin University. His love for natural history prompted him to carry out collecting expeditions in little-known regions, beginning the very year of his graduation from university. In 1891 he visited Tunisia; in 1893 Lower Egypt, Syria, Palestine and Lebanon. In 1895, having received an official refusal to enter Yemen from Arab authorities, he turned his attention to Central and South America, and decided to explore part of Panama and Ecuador, where he spent three years collecting zoological specimens. He eventually secured numerous scientific riches for the Turin University Museum, including 450 mammals, about 3100 birds, 170 reptiles and amphibians, 150 fishes, and several thousands of invertebrates, which were sent for study to the most distinguished experts of the time.

During his collecting expedition to Panama in 1895, which was devoted mainly to exploration of the Darién, whence he was to bring back the first significant ornithological collections from the province, Festa was introduced to "a Chiriquí collector, a certain Arcé, from whom I bought several interesting specimens of mammals and birds from that region" (translated from Festa, 1909: 50). Festa's collections of birds were studied by Tommaso Salvadori (Salvadori & Festa, 1899) who found among the specimens from Chiriquí an unusual tanager that he described as a new species, *Ramphocoelus festae* (Salvadori, 1896).

The generic name is now rendered as *Ramphocelus*, and the specific name, as it commemorates Enrico Festa, should take the masculine genitive ending ("*festai*"), and is an incorrect original spelling that is subject to emendation. Because, as we shall show, the name pertains to a probable hybrid and consequently has no nomenclatural standing, we have not made this alteration.

Subsequent authors either uncritically carried *R. festae* as a good species (e.g. Ridgway, 1902), or regarded it as one of a number problematical forms of *Ramphocoelus* whose status had not been resolved (e.g. Berlepsch, 1911). Griscom (1932:202), with reference only to Salvadori's original description, stated that: "I have no hesitation in declaring *festae* to be an abnormal erythrism of *R. passerinii*, a well known phenomenon in other groups of red tanagers". We undertook a first-hand investigation of the holotype of *R. festae* (MZUT 11494), with the interesting result that it proves to be a probable hybrid between *R. passerinii* and *R. dimidiatus*.

GEOGRAPHICAL AND HISTORICAL PROBABILITIES

The identity of Festa's "certain Arcé" is actually less than certain, as both Enrique Arcé and his son of the same name collected birds in western Panama

around the turn of the century (the following summary is taken from published and unpublished sources in files assembled by Alexander Wetmore and now housed in the Division of Birds, Smithsonian Institution). The elder Arcé came originally from Guatemala, where he was trained to prepare birds by the British ornithologist Osbert Salvin (1835-1898). Salvin sent him to Costa Rica in 1864, in which year he later went to Chepo, Panama, whence he collected his way westward in Veraguas and then in Chiriqui, where he settled for good. Both he and his son, "Enriquito", collected birds for H.J. Watson of Boquete, probably in the 1890's, and Enriquito also assisted the industrious collector W.W. Brown in the early 1900's. The elder Arcé died very approximately about 1908, and the son about 1952.

The only locality information for the specimen of *R. festae* is "Chiriqui", the modern province of which is the westernmost on the Pacific slope of Panama. In the 19th century, however, this was sometimes used more inclusively for the western portion of the isthmus west of Veraguas and could at times include localities in the Atlantic drainage that are now part of the province of Bocas del Toro. Nonetheless, Olson knows of no specimens to indicate that either Arcé collected even in the Caribbean drainage and it is highly unlikely that father or son ever extended his activity to the lowlands of Bocas del Toro.

Because the general provenance of the specimen is not in doubt, we have confined our comparisons to the four species of *Ramphocelus* that occur in western Panama: *R. dimidiatus*, *R. sanguinolentus*, *R. passerinii*, and *R. icteronotus*. The last two are vicariant forms that replace each other somewhere along the southern shore of the Laguna de Chiriqui between the Valiente Peninsula and the town of Chiriqui Grande (Olson, 1993). The reds in the plumage of *R. festae* show no indication of dilution, and therefore, because the light colored portions of the plumage of *R. icteronotus* are yellow, we have not considered that species further in the comparisons.

The geographical and historical probability of the hybrid combinations that remain are assessed as follows:

Extremely unlikely - *R. dimidiatus* X *R. sanguinolentus*. These two species may not come in contact anywhere. In western Panama the former occurs only in the Pacific lowlands and the latter only in the Caribbean lowlands. *R. sanguinolentus* has once been taken on the Pacific slope in Veraguas (Ridgely, 1976), where a low pass in the cordillera permits lowland forms to cross over. This is also the southern and easternmost occurrence of the species. In both *R. dimidiatus* and *R. sanguinolentus* the undertail coverts are entirely red, whereas they are black in *R. festae*, except near the vent. We do not give this parental combination any further consideration.

Less unlikely - *R. passerinii* X *R. sanguinolentus*. These species overlap in Panama in the lowlands of Bocas del Toro, where both approach the sou-

thern limits of their ranges and the latter is generally scarce. Although it is unlikely that either Arcé would have collected in this area of overlap, the superficial similarity of the pectoral band of *R. festae* to that of *R. sanguinolentus* makes this possible hybrid combination worth further analysis.

Most likely - *R. dimidiatus* X *R. passerinii*. These species overlap broadly in Chiriqui, where Arcé and son conducted most, if not all, of their collecting in the late 1800's.

MORPHOLOGICAL ANALYSIS

The sexes of *R. sanguinolentus* are practically identical, whereas *R. passerinii* and *R. dimidiatus* are strongly sexually dichromatic, the females being either much duller (*R. dimidiatus*) or completely different, orangish-olive rather than black with a scarlet rump (*R. passerinii*). Because *R. festae* shows such a predominance of black in the plumage, the specimen is assumed to be a male.

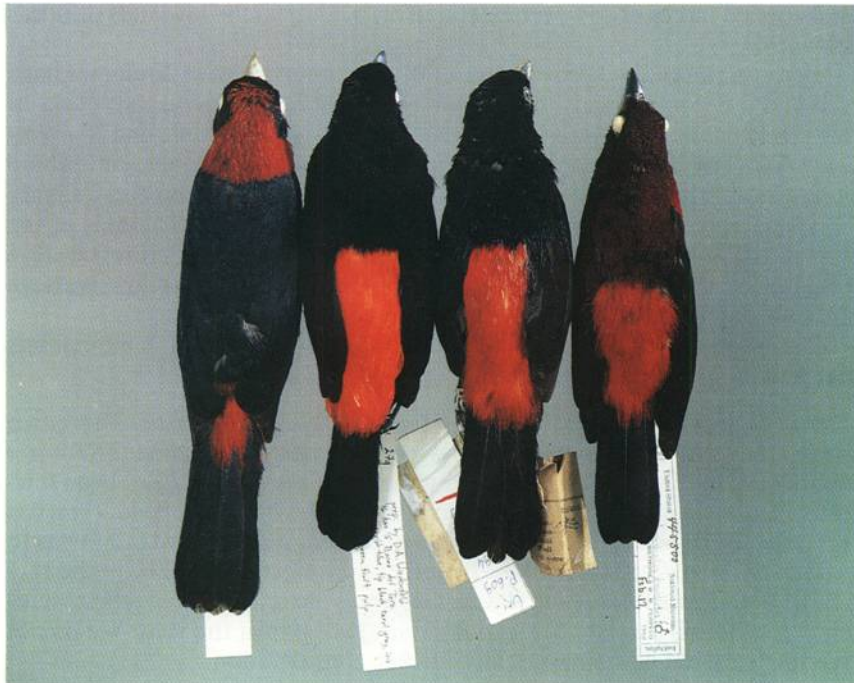


Fig. 1 - Dorsal view of study skins of male *Ramphocelus* (left to right): *R. sanguinolentus*, *R. passerinii*, *R. "festae"*, and *R. dimidiatus*.



Fig. 2 - Ventral view of study skins of male *Ramphocelus* (left to right): *R. sanguinolentus*, *R. passerinii*, *R. "festae"*, and *R. dimidiatus*, female *R. passerinii costaricensis* to show orange pectoral band.

To characterize the plumage of *R. festae* briefly (Figs. 1, 2), the specimen is all black except for a relatively narrow, dull reddish band across the upper breast, reddish feathers at the base of the under tail coverts, and a large red rump patch and upper tail coverts. There is also some red visible, with magnification, in the feathers along the flanks.

Males of *R. passerinii* are entirely glossy black except for a patch of dense scarlet (decidedly orangish-red) feathers extending about from the interscapular area to, and including, the upper tail coverts.

Because Griscom (1932) pronounced *R. festae* to be merely an aberrant *R. passerinii* we shall first detail how it differs from males of that species. The rump is fully as extensive as in *R. passerinii* with feathers of the same dense quality but 1) of a much darker, less orangish red. The posterior part of the crissum is black but 2) the feathers in the area below the vent are red, again of a darker color, whereas in *R. passerinii* the crissum is entirely black (occasionally with a few small, scattered scarlet feathers just below the vent). 3) There is a fairly large, crescentic pectoral band of orangish red suffused with black in *R. festae*, whereas in *R. passerinii* the underparts are entirely black.

This red pectoral band is reminiscent of that in *R. sanguinolentus*, in which, however, the band is larger and continuous with the red sides of the hindneck, nape and crown. We were at first inclined to believe that one of the parents of *R. festae* was *R. sanguinolentus* but further examination convinced us that this is not the case for the following reasons:

1) In *R. sanguinolentus* the bill is paler and much heavier and swollen than in either *R. passerinii* or *R. dimidiatus*. Although the bill in *R. festae* is damaged, it shows no indications of intermediacy towards the condition in *R. sanguinolentus*. It does have the bluish upper mandible similar to *R. passerinii*, in contrast to black in *R. dimidiatus*, but so far as can be discerned is not different from the former.

2) The feathers of the crown and nape in *R. sanguinolentus* are lanceolate and lack barbules at the tip, whereas in *R. passerinii* and *R. dimidiatus* they are short, dense, and velvety, giving rise to the term "plush tanager" once used for members of this genus. *R. festae* is like the last two in this respect and shows no approach to *R. sanguinolentus*.

3) The underwing coverts and axillars in *R. sanguinolentus* are a beautiful pale, vermilion red, whereas in the other taxa, including *R. festae*, they are entirely black.

4) The red in the rump of *R. sanguinolentus* is confined to the upper tail coverts, the rest of the rump feathers being black with grayish bases, whereas in *R. passerinii* and *R. dimidiatus* the red rump patch extends halfway up the back and consists of silky feathers with very dense white down at the bases. The rump in *R. festae* is just as in the last two species and shows no approach to intermediacy with *R. sanguinolentus*, either in extent or quality of feathers.

5) Microscopical examination of the rump feathers by Carla Dove (Smithsonian Institution) shows *R. sanguinolentus* to have heavily pigmented downy barbules that are longer than in *R. passerinii*, *R. dimidiatus*, or *R. festae*, in all of which the barbules are whitish.

We consider that the absence in *R. festae* of any tendency towards the distinctive traits of *R. sanguinolentus*, along with geographical and historical probability, make it extremely unlikely that the latter was involved in the parentage of *R. festae*.

CONCLUSIONS

If *R. festae* is a hybrid rather than an aberrant individual of *R. passerinii*, then *R. dimidiatus* would be the only likely other parent. Wing (75.5 mm) and tail (69.4 mm) measurements of *R. festae* are equivocal with regard to determining parentage, due to considerable overlap in measurements between the supposed parental forms. *R. festae* agrees better in size with more individuals of *R. passerinii* than *R. dimidiatus*, as the latter tends to be larger, especially in length of the tail.

The plumage in *R. dimidiatus* is essentially all red except for black flight feathers and a black patch on the belly. Although the head and mantle are much duller than the rump and flanks, with magnification these feathers are seen to be red, but are rendered duller because the tips of the barbules are black. Because males of *R. passerinii* and its close relatives *R. icteronotus* and *R. flammigerus*, appear superficially to be such intensely black birds, except on the rump, it is important to note that when the *undersides* of the black feathers are viewed with magnification, the barbs can be seen to be distinctly pigmented with red or orangish. Even in *R. icteronotus*, which has a bright yellow rump, the barbs of the black feathers are orangish below, not yellow. Therefore, beneath the black, these birds are in essence all red, but the carotenoid pigments have been overlain and masked by melanins.

Thus, reduction in the amount of melanin might partly explain the appearance of *R. festae*. The red band on the upper breast occurs in exactly the same position as the orange band across the breast seen in females of *R. passerinii* (Fig. 2), as also noted by Berlioz (1933). The chief distinguishing feature of the Pacific-slope subspecies *R. passerinii costaricensis*, which presumably gave rise to *R. festae*, is the more intensely orange breast band in females as compared to the nominate form. Perhaps this band is present in males as well, but is masked by melanins.

Brush (1970) established two highly relevant facts regarding coloration in species of *Ramphocelus* and other tanagers. First, the red and yellow colors in *R. dimidiatus*, *R. icteronotus*, and *R. flammigerus* are caused by a single carotenoid pigment that varies only in relative concentration to achieve the differing shades observed. Second, in melanic mutants of the Scarlet Tanager, *Piranga olivacea*, abnormally dark feathers retained the structure of typical carotenoid-bearing feathers, so that the increase in amount of melanin is under separate genetic control and is superimposed on normal pigment and structure.

For *R. festae* to be an atypical individual of *R. passerinii*, as suggested by Griscom (1932) and Berlioz (1933), would require the simultaneous appearance of two independent abnormalities. An individual with only abnormal concentrations of carotenoid would simply have a darker red rump patch, whereas if there were only an abnormal reduction in the amount of melanin expressed, the red carotenoids should be in concentrations typical of the species. On the other hand, hybridization of *R. passerinii* with the dark red species *R. dimidiatus* would presumably provide a genetic basis both for decreased suppression of carotenoids by melanins as well as for darkening the coloration of the carotenoids that are expressed. Therefore we suggest that *R. festae* is a probable hybrid between *R. dimidiatus* and *R. passerinii*. If this is the case, it is of further interest, as the result of this hybridization produced a bird so different in appearance from hybrids between *R. dimidiatus* and *R. icteronotus* (see below).

Ramphocelus inexpectatus

Ramphocelus inexpectatus Rothschild (1897) is a striking black and yellow tanager known only from two specimens. The second (AMNH 509650) was referred to *R. inexpectatus* by Hartert (1919), and differs from the holotype (AMNH 509649) in lacking an orangish tint to the yellow portions of the plumage, lacking a slight scaly yellow pattern on the crown, and having the inner under wing coverts yellow instead of black. These specimens are of unknown origin but were stated to be of "Panama make". They were from the same dealer, and have the same make, as the type and referred specimens of *R. dunstalli* Rothschild (1895), which in turn are similar in color and pattern to specimens known to have been taken in the canal area of Panama that are considered to be hybrids between *R. icteronotus* and *R. dimidiatus* (Griscom 1932).

Griscom's assessment of "*R. dunstalli*" appears to be correct. The male illustrated here (Figs. 3, 4) has the dark head and mantle of *R. icteronotus*, but the feathers of the nape and upper breast, and to a lesser extent the mantle, are



Fig. 3 - Dorsal view of study skins of male *Ramphocelus* (left to right): *R. icteronotus*, *R. "dunstalli"* = hybrid *R. icteronotus* X *R. dimidiatus*, and *R. dimidiatus*.



Fig. 4 - Ventral view of study skins of male *Ramphocelus* (left to right): *R. icteronotus*, *R. "dunstalli"* = hybrid *R. icteronotus* X *R. dimidiatus*, and *R. dimidiatus*.

noticeably suffused with red. The sides and crissum are reddish, as in *R. dimidiatus*, but the black area of the midline of the belly is much more extensive than in that species. The red parts of the plumage are an orangey-scarlet, intermediate between the crimson of *R. dimidiatus* and the yellow of *R. icteronotus*. The female (Figs. 5, 6) is likewise a nearly perfect intermediate. It has the entire head, including chin and throat, dark brownish, resembling *R. dimidiatus*. The mantle has the scaly appearance of *R. icteronotus* but the margins of the feathers are an orangey-brown rather than olive. The entire underparts and rump are orange and perfectly intermediate between the dull red of *R. dimidiatus* and the yellow of *R. icteronotus*.

But what then is *R. inexpectatus*? Berlepsch (1911:1139), in his review of tanagers, considered *R. inexpectatus* to be an "excellent species" ("*ausgezeichneten Art*"). In the main part of his text, Griscom (1932:199), in the absence of the specimens, which were then still in Rothschild's possession, regarded *R. inexpectatus* as an intermediate between *R. flammigerus* and *R. icteronotus* with erroneous locality information. He also remarked that one such intermediate

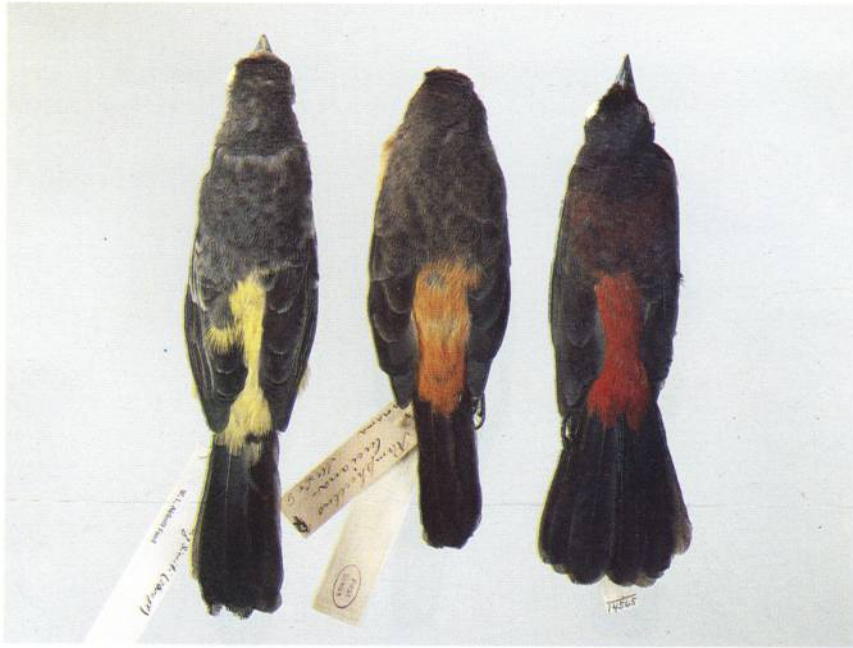


Fig. 5 - Dorsal view of study skins of female *Ramphocelus* (left to right): *R. icteronotus*, *R. "dunstalli"* = hybrid *R. icteronotus* X *R. dimidiatus*, and *R. dimidiatus*.

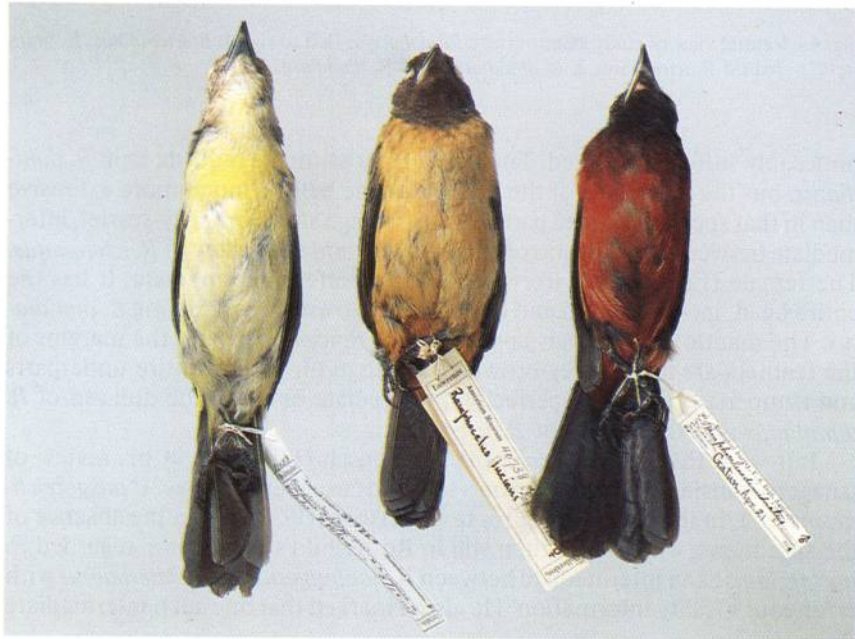


Fig. 6 - Ventral view of study skins of female *Ramphocelus* (left to right): *R. icteronotus*, *R. "dunstalli"* = hybrid *R. icteronotus* X *R. dimidiatus*, and *R. dimidiatus*.

in the collection of the AMNH “agrees exactly with the description of *R. inexpectatus* Rothschild”. This can only have come from misreading Rothschild’s description, as there is no specimen in the AMNH collections then available to Griscom that is at all similar to *R. inexpectatus*. In his summary, however, Griscom (1932:202) enigmatically listed *R. inexpectatus* as a cross between *R. chrysonotus* and *R. icteronotus*. But *R. chrysonotus* he regarded as a synonym of *R. chrysopterus*, and *R. chrysopterus* he considered to be a hybrid between *R. flammigerus* and *R. icteronotus*. So, if one charitably allows that Griscom actually intended to say what he wrote, however circuitously it may have been presented, then he would presumably have regarded *R. inexpectatus* as a backcross between a hybrid *R. icteronotus/flammigerus* parent and pure *R. icteronotus*.

A backcross is probably the best interpretation of the origin of *R. inexpectatus*, but not involving *R. flammigerus*. Intergrades between *R. flammigerus* and *R. icteronotus* occur frequently in the wild (Sibley, 1958; Hilty & Brown, 1986) and are not uncommon in collections. But the males are simply black birds with ochraceous-orange rumps and do not look at all like the specimens of *R. inexpectatus*, in which the entire underparts are bright yellow except for a black belly patch and black chin and upper throat.

This gives these birds a striking overall resemblance to the pattern of coloration seen in the red-and-black Amazonian species *R. nigrogularis* (Figs. 7, 8). That species differs in having the sides of the head, crown, and nape red, whereas these areas are black in *R. inexpectatus*. The similarities in general plumage pattern between *R. inexpectatus* and *R. nigrogularis* are only superficial and not indicative of relationship. The black feathers in *R. inexpectatus* are underlain by carotenoids as in all other members of the *R. flammigerus/R. passerinii* group, whereas in *R. nigrogularis* the black feathers are truly black and show no reddish coloration in the ventral surface of the barbs.

Because the light-colored areas of *R. inexpectatus* are yellow, it has been sometimes been regarded as an aberrant *R. icteronotus* (e.g. Hellmayr, 1936), the only species in the genus in which the carotenoid pigment is in such low concentration as to appear yellow. But the pattern of yellow is very different from that in *R. icteronotus*, although it is very similar to that seen in hybrids between *R. icteronotus* and *R. dimidiatus*. The resulting offspring of any combination of *R. icteronotus* and pure parental types of any other species of *Ramphocelus* would be expected to be orange or reddish, however. The best explanation we can offer for the origin of the specimens of *R. inexpectatus* is that they represent backcrosses between a hybrid *R. icteronotus/dimidiatus* and pure *R. icteronotus*. If they were homozygous for yellow plumage, then perhaps the reds of the *R. dimidiatus* grandparent would not be expressed, whereas the basic plumage pattern of the hybrid parent would be retained.

All of the known hybrids between *R. icteronotus* and *R. dimidiatus* and their presumed backcrosses evidently came from the central part of the Pana-



Fig. 7 - Ventral view of study skins of male *Ramphocelus* (left to right): *R. nigrogularis*, *R. "inexpectatus"*, and *R. icteronotus*.

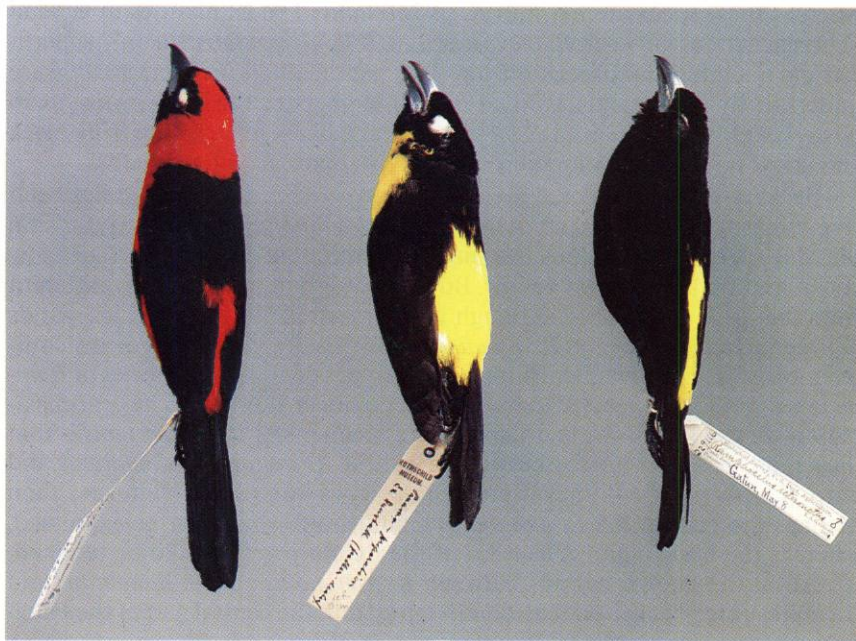


Fig. 8 - Lateral view of study skins of male *Ramphocelus* (left to right): *R. nigrogularis*, *R. "inexpectatus"*, and *R. icteronotus*.

manian isthmus where the canal now exists. What was responsible for the seeming rash of hybridization in the last half of the 19th century that has not been reported since? The two parental types co-exist elsewhere, including the eastern Caribbean slope of Panama, apparently without producing hybrids. In the area of the canal, however, *R. icteronotus* is rare or perhaps only seasonal on the Pacific slope (Ridgely, 1976; Wetmore *et al.*, 1984), where it might also be a relatively recent arrival.

Conceivably, then, populations of *R. dimidiatus* on the Pacific slope of the central part of the isthmus would not have had a history of contact with *R. icteronotus*. These "naïve" birds may first have contacted *R. icteronotus* as a result of clearing along the line of the Panama railroad, producing a temporary spate of hybridization, and even backcrossing, that has since evidently ceased.

DISCUSSION

Three groups of species have been recognized within *Ramphocelus* (Isler & Isler, 1987). The first of these consists of *R. sanguinolentus* and *R. nigrogularis*, which share the following characters not found in the other members of the genus: 1) lack of strong sexual dichromatism; 2) plumage pattern of red head and chest with a black face; 3) pale vermilion rather than black axillars and underwing coverts; 4) lack of red pigments in the black portions of the body plumage. The two are nevertheless rather different from one another: in *R. nigrogularis* the lower chest and flanks are red and the crissum black, whereas the opposite obtains in *R. sanguinolentus*; the rump patch is larger and the reds brighter in *R. nigrogularis*; the sexes differ more in *R. nigrogularis* than in *R. sanguinolentus*; and the bill is heavier and of a different color in *R. sanguinolentus*.

Furthermore, there is a great gap in the ranges of the two species, with *R. sanguinolentus* occurring in Caribbean Central America, and *R. nigrogularis* in Amazonia. If their similarities truly indicate them to be each other's closest relative, they would have shared a common ancestor much less recently than taxa within the other species groups of *Ramphocelus* and the generic name *Phlogothraupis*, long used for *sanguinolentus* alone, might be appropriately used as a subgeneric category to include both these species.

The second group of species includes *R. bresilius*, *R. dimidiatus*, *R. melanogaster*, and *R. carbo*. These are almost completely allopatric, except that *R. bresilius* and *R. carbo* are said to come together and hybridize in the upper Rio Doce in Minas Gerais, Brazil (Sick, 1984:685). The females of all of these species are reasonably similar to one another and the differences among males result mainly from increasing melanization of the reds in the plumage. The much abused and misapplied term "superspecies" is actually suitable and useful in connection with this group of species.

Because evolution in *Ramphocelus* (less "*Phlogothraupis*") appears to have proceeded towards increasing melanization, we would identify *R. bresilius*, an all red bird with black wings, tail, and belly, as representing the primitive state in this species group. The addition of melanin to the tips of the barbules on the head, chest, and dorsum, leaving the rump and flanks pure red, would produce a bird looking like *R. dimidiatus* and *R. melanogaster*, the males of which are practically identical. An increase in melanin in the dorsum and its addition to the flank feathers would in turn give rise to a bird like *R. carbo*.

We interpret the pattern of distribution of this superspecies as follows. An original stock similar to *R. bresilius* was divided into eastern and western populations, the latter giving rise to a population similar to *R. dimidiatus*/*R. melanogaster*. This population in turn was divided into eastern and western vicariants, with the eastern one evolving into *R. carbo*. The last has become geographically dominant, expanding westward and replacing the redder western populations, leaving *R. dimidiatus* isolated in Colombia and Panama and the essentially identical *R. melanogaster* as a relict in the Huallaga Valley of Peru. Again taking increasing melanization as a derived state, the species group consisting of *R. passerinii*, *R. icteronotus*, and *R. flammigerus*, would be the most advanced assemblage in the genus. That two of these species have hybridized with *R. dimidiatus* indicates a fairly close degree of relationship between the two species groups.

The males of *R. passerinii*, which is found from western Panama to Mexico, are identical to those of *R. flammigerus*, of the slopes of the Cauca Valley in Colombia. The females, while distinct, are more similar to one another than either is to *R. icteronotus*. Both retain reds in the plumage, which, by using the rest of the genus as the outgroup, would be the primitive state. As in the case where *R. carbo* apparently made disjunct relicts of *R. dimidiatus* and *R. melanogaster*, it is possible to visualize *R. icteronotus* as being a more derived form that has occupied the intervening portions of the range between *R. passerinii* and *R. flammigerus*. In this species, rather than having the reds diminished through melanization, they are diluted so as to appear yellow, although the pigment is chemically identical and only the concentration has changed (Brush, 1970).

The fact that *R. flammigerus* and *R. icteronotus* now hybridize frequently as a result of human-caused habitat disruption (Sibley, 1958; Hilty & Brown, 1986) is not necessarily an indication that these are more closely related to each other than either is to *R. passerinii*. We do not know what happens at the contact between *R. passerinii* and *R. icteronotus*, although if they hybridize it would be in an extremely restricted area, as they replace each other very abruptly in Bocas del Toro, Panama (Olson, 1993). When each hybridizes with *R. dimidiatus*, the resulting offspring are very different from one another, suggesting there may be greater genetic differentiation between *R. passerinii* and *R. icteronotus* than the external appearances of the males would indicate.

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RIASSUNTO

Alcuni insoliti ibridi di Ramphocelus, con osservazioni sull'evoluzione del genere (Aves: Thraupinae).

Ramphocelus festae Salvadori, raccolto nel Chiriqui, Panama, è un probabile ibrido tra *R. passerinii* e *R. dimidiatus*. *Ramphocelus inexpectatus* Rothschild, la cui provenienza presunta è Panama centrale, può essere un "backcross" (reincrocio) tra un *R. icteronotus* puro e un ibrido di *R. icteronotus/R. dimidiatus*. Nel presente lavoro vengono discussi i moduli evolutivi tra e all'interno dei 3 gruppi di specie appartenenti al genere *Ramphocelus*. La diminuzione quantitativa di carotenoidi rossi visibile nel piumaggio, dovuta ad un'aumentata melanizzazione o ad una diluizione verso il giallo, sembra essere uno dei principali stadi di derivazione del piumaggio nell'ambito di questo genere.

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REFERENCES

- BERLEPSCH H., 1911. Revision der Tanagriden. Verhandlungen des V. Internationalen Ornithologen-Kongresses in Berlin 30 Mai bis 4 Juni 1910:1001-1148.
- BERLIOZ J., 1933. Étude critique des tangaras du genre *Rhamphocelus*. L'Oiseau et la Revue Française d'Ornithologie. (n.s.)3: 581-602.
- BRUSH A.H., 1970. Pigments in hybrid, variant and melanic tanagers (birds). Comparative Biochemistry and Physiology, 36: 785-793.
- FESTA E., 1909. Nel Darien e nell'Ecuador. Torino, Unione Tip. Editrice Torinese.
- GRISCOM L., 1932. Notes on imaginary species of *Ramphocelus*. Auk, 49: 199-203.
- HARTERT E., 1919. Types of birds in the Tring Museum. Novitates Zoologicae, 26: 123-178.
- HELLMAYR C.E., 1936. Catalogue of Birds of the Americas. Part IX Tersinidae-Thraupidae. Field Museum of Natural History Zoological Series, 13.
- HILTY S.L. & BROWN W.L., 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey.

- ISLER M. & ISLER P., 1987. The Tanagers. Smithsonian Institution Press. Washington, D.C.
- OLSON S.L., 1993. Contributions to avian biogeography from the archipelago and lowlands of Bocas del Toro, Panama. *Auk*, 110(1): 100-108.
- RIDGELY R., 1976. Guide to the birds of Panama. Princeton University Press, Princeton, New Jersey.
- RIDGWAY R., 1902. The birds of North and Middle America. Part 2. Bulletin of the United States National Museum, 50.
- ROTHSCHILD W., 1895. A new species of tanager. *Novitates Zoologicae*, 2: 481.
- ROTHSCHILD W., 1897. [Original description of *Rhamphocoelus inexpectatus*]. Bulletin of the British Ornithologists' Club, 7(42): 32.
- SALVADORI T., 1896. Descrizione di una nuova specie del genere *Rhamphocoelus* di Chiriqui. Bollettino dei Musei di Zoologia ed Anatomia Comparata Univ. Torino, 11(249): 1-2.
- SALVADORI T. & FESTA E., 1899. Viaggio del Dott. E. Festa nel Darien e regioni vicine: Uccelli. Bollettino dei Musei di Zoologia ed Anatomia Comparata Univ. Torino, 14(339): 1-13.
- SIBLEY C.G., 1958. Hybridization in some Colombian tanagers, avian genus *Ramphocelus*. Proceedings of the American Philosophical Society, 102(5): 448-453.
- SICK H., 1984. Ornitologia Brasileira. 2 vols. Editora Universidade de Brasilia.
- WETMORE A., PASQUIER R. & OLSON S.L., 1984. Birds of the Republic of Panama. Part 4: Order Passeriformes, Suborder Passeres, Hirundinidae (Swallows) to Fringillidae (Finches). Smithsonian Miscellaneous Collections, 150(4): vi + 670 pp.