



## SHORT NOTE

INDEPENDENT OBSERVATIONS OF PHAEOMELANIC MALES OF THE VARIABLE SEEDEATER (*SPOROPHILA CORVINA*) WITH COMMENTS ABOUT ITS POTENTIAL FOR EVOLUTIONARY DIVERGENCEDiego Ocampo<sup>1,2\*</sup>, Alejandro Quesada<sup>3</sup>, César Oconitrillo<sup>4</sup>, Rodney Lobo<sup>4</sup>, J. Albert C. Uy<sup>5</sup><sup>1</sup> Department of Biology, University of Miami, FL 33146, USA.<sup>2</sup> Museo de zoología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica.<sup>3</sup> Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica.<sup>4</sup> Ciencias Forestales y Vida Silvestre, Sede Atenas, Universidad Técnica Nacional. Costa Rica.<sup>5</sup> Department of Biology, University of Rochester, Rochester, NY 14627, USA.

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**Abstract** · Plumage coloration largely depends on the type and concentration of pigments present in feathers. Therefore, changes in pigment deposition may result in aberrant colorations which, in turn, will likely interfere with the plumage color's function (e.g., signaling, protection). Published records of aberrant plumage colors underestimate the type and frequency of these phenotypes, especially in the tropics. Here, we report five independent observations of phaeomelanin males of the Variable Seedeater (*Sporophila corvina*), in which typically white feathers were instead chestnut-red, likely due to the deposition of phaeomelanin. Our observations add to previous reports of aberrant melanin-based coloration in this species, suggesting that genomic region(s) influencing the expression of phaeomelanin are a biased target for mutations. Because mutations affecting the regulation of melanin deposition result in novel plumage phenotypes, we discuss aberrant phenotypes as an important source of variation fueling rapid divergence among populations of this avian clade.

**Resumen** · Observaciones repetidas e independientes de machos feomelánicos del semillero variable (*Sporophila corvina*) y notas sobre su potencial de divergencia evolutiva

El color del plumaje depende en gran medida del tipo y concentración de los pigmentos presentes en las plumas. Por lo tanto, cambios en la deposición de pigmentos pueden resultar en coloraciones aberrantes, que a su vez pueden interferir con las funciones de la coloración (e.g., señalización, protección). Los registros publicados de plumajes aberrantes subestiman el tipo y frecuencia de estos fenotipos, especialmente en los trópicos. Aquí presentamos cinco observaciones independientes de machos feomelánicos del semillero variable (*Sporophila corvina*), en el cual las plumas típicamente blancas eran de color castaño rojizo, probablemente debido a la deposición de feomelanina. Nuestras observaciones son consistentes con reportes previos de coloraciones aberrantes a base de melanina en esta especie, lo que sugiere que las regiones genómicas que influyen la expresión feomelanina son objeto constante de mutaciones. Debido a que las mutaciones que afectan la regulación de deposición de melanina dan como resultado nuevos fenotipos, discutimos los plumajes aberrantes como una fuente importante de variación capaz de promover la rápida divergencia entre poblaciones de este clado de aves.

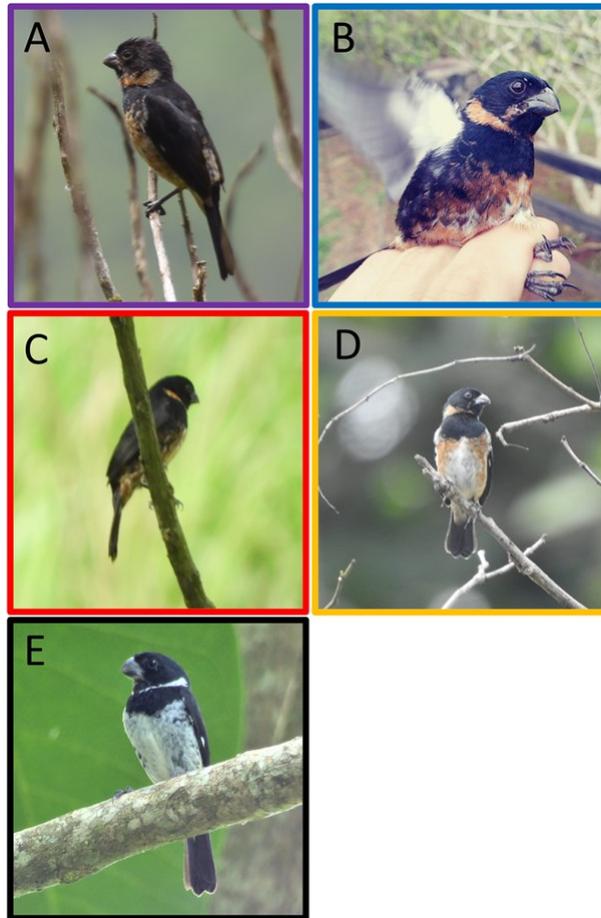
**Key words:** Costa Rica · Erythromelanism · Feathers · Panama · Plumage aberration

Plumage coloration plays an important role in signaling, concealment, protection, and thermoregulation (Hill & McGraw 2006, Protas & Patel 2008). Therefore, novel plumage color that deviates from the regular or common pattern may disrupt its function, resulting in significant disadvantages to individuals (Buckley 1982, Truax & Siegel 1982, Withgott & McMahon 1993, van den Hout et al. 2013). Published records of plumage aberrations most likely underrepresent the type and frequency of such phenotypes in wild populations (Gonçalves Jr. et al. 2008) and the incidence of aberrant colorations in tropical regions is even less understood, since most comprehensive studies come from the temperate zones (e.g., Sage 1963, Mikula et al. 2017, Zbyryt et al. 2021). Nevertheless, reports on plumage aberrations in Neotropical populations have increased in the last few decades (e.g., Aráoz et al. 2012, Ayala-Pérez et al. 2013, Cadena-Ortiz et al. 2015, Smith & Rios 2017). Compiling observations of such aberrant coloration in Neotropical birds can provide more insights into the type and frequency of these abnormal phenotypes in the tropics, as well as their possible effects and evolutionary implications in wild populations.

Feather coloration depends on the identity and relative abundance of the deposited pigments, as well as the scattering of light mediated by feather structure (Shawkey & Hill 2006, D'Alba et al. 2012). In birds, melanin is one of the most common pigment types. The two variants of the pigment, eumelanin and phaeomelanin, are responsible for black/grey and dark brown coloration, and lighter buff and rufous colors, respectively. In the mid-20th century, a third melanin variant was hypothesized, erythromelanin, which was thought to be responsible for rufous and chestnut-red colorations. Erythromelanin was considered

Submitted 8 March 2021 · First decision 25 June 2021 · Acceptance 28 October 2021 · Online publication 23 May 2022

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**Figure 1.** Phaeomelanic males of the Variable Seedeater (*Sporophila corvina*) seen in: A) Veraguas, Panama 2019; B) Gamboa, Panama 2019; C) San Ramon, Costa Rica 2020; and D) Atenas, Costa Rica 2020. E) Typical plumage coloration of *S. corvina* in the south Pacific coast of Costa Rica.

to be a third independent melanin variant on the basis that some birds retained the chestnut-red coloration even in the absence of eumelanin, phaeomelanin, or both (Harrison 1965). However, this putative variant has not been chemically characterized (Huddon 2005, Galván & Solano 2016). Additionally, eumelanin and phaeomelanin alone can explain the occurrence of chestnut-red coloration (McGraw et al. 2005). As such, the presence of a third type of melanin pigment in feathers is currently considered very unlikely.

Abnormal colorations may result from environmental or genetic factors (Bensch et al. 2000, Møller & Mousseau 2001, Guay et al. 2012). Several studies have reviewed the nomenclature, definitions, characteristics, and causes of plumage aberrations (Guay et al. 2012, van Grouw 2013, Rodríguez-Ruíz et al. 2017). In particular, melanism is characterized as an abnormal deposition or distribution of melanin (van Grouw 2021). More specifically, erythromelanism is a particular category of melanism that involves an abnormal chestnut-red coloration that arises when erythromelanin is deposited in feathers that usually lack pigments or when it replaces eumelanin in pigmented feathers (Hosner & Lebbin 2006). However, it is currently considered that erythromelanism is most likely the product of enhanced deposition of phaeomelanin (van Grouw 2021). Consequently, erythromelanism should be properly referred to as phaeomelanism.

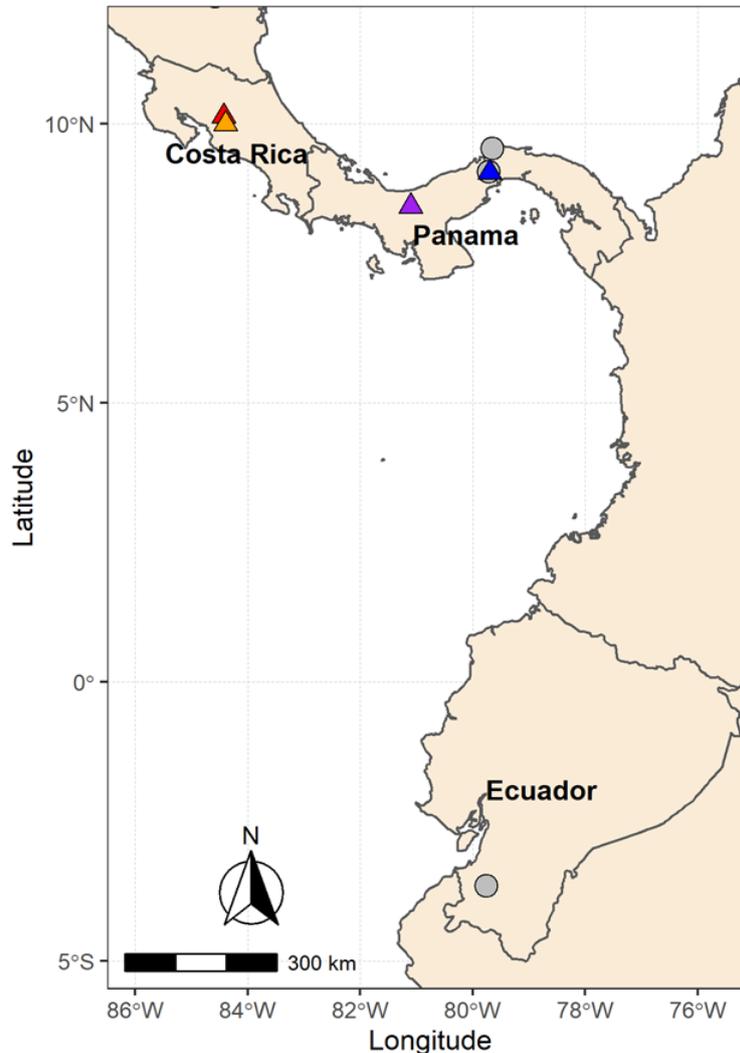
The genus *Sporophila* is restricted to the Neotropical region and comprises around 41 species of small tanagers that differ little in their morphology, but show striking variation in secondary sexual traits (del Hoyo et al. 2011, Winkler et al.

2020), including plumage coloration based on melanin pigments. The Variable Seedeater (*Sporophila corvina*) inhabits secondary growth and open areas in the lowlands from Mexico to Peru, with four subspecies currently recognized on the basis of male plumage coloration and pattern (Olson 1981, Stiles 1996). Three subspecies have a pied (black and white) coloration, while the fourth subspecies is almost completely black, except for the white underwing coverts. Here, we compiled recent observations from Costa Rica and Panama of pied *S. corvina* males showing abnormal phaeomelanistic plumage color. Based on a literature review, we discuss the possible implications of plumage aberration on the evolutionary diversification of the group.

Observations were made in Panama (May 2019) and in Costa Rica (April and June 2020). All observations occurred by chance and at different times of the day. Most records were photographed, and the observed phaeomelanic males of the pied subspecies had abnormal chestnut-red coloration where white contour feathers typically occur (Figure 1).

From 2–4 May 2019, Diego Ocampo (DO) observed a single phaeomelanic male (Figure 1A) in Calle Santa Fe, nearby Alto de Piedra, Veraguas, Panama (8°30'56.1" N, 81°06'07.9" W; Figure 2). The bird was seen several times in a cattle pasture with isolated trees, surrounded by early secondary growth forest. The bird showed typical territorial behavior by singing from a high perch. No other males were observed in this territory and other males in the area had the black plumage typical of the Caribbean subspecies (*S. corvina corvina*).

On 23 May 2019, DO observed two phaeomelanic males



**Figure 2.** Localities of known reports of phaeomelanistic males. Grey dots in the map indicate locations reported in the literature (Olson 1966, Hosner & Lebbin 2006, Xenornis 2014). Color triangles that match the outline of boxes A to D in Figure 1 correspond to locations of phaeomelanistic males detailed in this paper.

(Figure 1B) in Gamboa, Panama ( $9^{\circ}07'06.3''$  N,  $79^{\circ}41'57.6''$  W; Figure 2). The two individuals were in a group of around 40 individuals (including males, females, and juveniles). The group stayed together in an open area, with some individuals flying to a backyard approximately 20 meters away, where a feeder with birdseeds was located. There were no antagonistic interactions towards the phaeomelanistic individuals. Moreover, the two phaeomelanistic males did not associate with each other, they behaved like any other individual in the group.

On 26 April 2020, Alejandro Quesada observed another phaeomelanistic male (Figure 1C) in Concepción, San Ramón, in the riverbanks of the Cañuela river in Alajuela, Costa Rica ( $10^{\circ}07'32.4''$  N,  $84^{\circ}25'52.1''$  W; Figure 2). The individual was moving in the river canyon through secondary growth habitat and in the edge of the riparian forest.

On 19 June 2020, César Oconitrillo and Rodney Lobo observed one phaeomelanistic male (Figure 1D) in Barrio Mercedes in Atenas, Alajuela, Costa Rica ( $9^{\circ}59'09''$  N,  $84^{\circ}23'59''$  W; Fig. 2). The male was observed in a semi-rural landscape dominated by annual crops, pastures, and fragmented riparian forest. The male was perched on a *Cassia fistula* (Fabaceae) tree approximately 15 m away.

The aberrant coloration observed in Variable Seedeater males is consistent with previously reported erythrome-

lanism, an abnormal phenotype wherein individuals express chestnut-red coloration on normally white feathers. However, as explained above, this chestnut-red coloration likely results from phaeomelanin pigments. This aberrant phenotype in the Variable Seedeater was previously reported in Panama in 1963 (Olson 1966; Figure 2) and in 2014 (Matias Diaz in Xenornis 2014; Figure 2). Another individual of this phenotype was observed in Ecuador in 2005 (Hosner & Lebbin 2006; Figure 2).

Color aberrations tend to be more common in small, isolated populations where inbreeding is presumably high (Bensch et al. 2000, Ferrer-Sánchez & Rodríguez-Estrella 2014). Nevertheless, the geographic and temporal span of these reports suggest that these observations were independent from each other (i.e., individuals were not related), which in turn suggests that this type of color aberration, in particular, might be relatively common in this species. Our observations are also consistent with previous reports indicating that phaeomelanistic individuals had normal white coloration on the wing undercoverts (Hosner & Lebbin 2006). This observation is important because it suggests that phaeomelanism in the Variable Seedeater results from mutation in regulatory elements that fine-tune the expression of melanin in different color patches, rather than mutations in coding regions, which could have larger phenotypic effects (Abolins-

abols et al. 2018).

Hosner & Lebbin (2006) hypothesized that these types of color aberrations might be an important source of variation in *Sporophila*, fueling the diversification of plumage coloration and taxa in this rapidly evolving genus. This hypothesis is especially appealing because closely related taxa, such as pairs of sister species or subspecies, tend to share similar plumage phenotypes that vary in color (i.e., black, chestnut-red and white) or melanin concentration (Areta et al. 2011, del Hoyo et al. 2011, Burns et al. 2014). For instance, ecological and behavioral studies have demonstrated that some previously recognized *Sporophila* species actually represent different color morphs (Areta 2008, Repenning et al. 2010, Areta et al. 2011). This pattern of subtle plumage variation, together with the geographical variation in song, is expected under the recent and ongoing diversification of this group (Areta et al. 2011, Campagna et al. 2012). Genetic divergence in the expression of melanin-based coloration, as the one reported here, may be responsible for differences in plumage phenotypes. In fact, the regulatory elements of the melanogenesis pathway are repeated targets of divergent selection in this genus (Campagna et al. 2017). Significantly, populations with multiple color morphs speciate faster than monomorphic populations (Hugall & Stuart-Fox 2012). Therefore, such dynamic plumage variation observed, paired with its role in species recognition in *Sporophila* (Lijtmaer et al. 2004), may contribute to explain the particularly high speciation rate observed in this genus (Burns et al. 2014, Price-Waldman et al. 2020).

The synthesis of melanin is well understood (see Galván & Solano 2016), and any of the networks of interacting genes involved in the production and deposition of melanin are potential targets of mutations that may affect the expression of color. In pigeons, for example, mutations in more than 50 genes are known to cause diverse aberrations in color (van Grouw 2013). However, unique mutations in different genes involved in melanogenesis may have the same phenotypic effect. For example, two unique point mutations in different genes switch the synthesis of phaeomelanin to eumelanin in two isolated populations of the chestnut-bellied flycatcher (*Monarcha castaneiventris*), resulting in completely black individuals (Uy et al. 2016).

A similar switch-like mutation mediating the synthesis of eumelanin or phaeomelanin might be responsible for the abnormal coloration observed in “erythromelanic” individuals of *Podiceps nigricollis* in Europe and North America (Konter 2013). This author suggested that the extinct grebe’s species *P. andinus* was an isolated population of *P. nigricollis*, in which mutation(s) that resulted in chestnut-red neck coloration became fixed. As in *Sporophila*, coloration in grebes is melanin-based, varying in number of patches and shades of black, chestnut-red, and white. Aberrant colorations in grebes are well known and are thought to have played a key role in the divergence and radiation of this family (Konter 2015). However, our observations in *S. corvina* are not consistent with a switch-like mutation between melanin types, but rather in the deposition of melanin in feathers that typically lack pigments.

Our observations add to early reports of this aberrant phenotype, suggesting that mutation(s) targeting the synthesis and regulation of phaeomelanin may be relatively common in this clade. If this initially rare phenotype spreads

through the population, then the origin of an aberrant phenotype may represent the earliest stages of the formation of morphs, subspecies and, ultimately, species (van Grouw 2017).

## ACKNOWLEDGMENTS

We thank C Bosque, H van Grouw, WA Searcy, the Uy lab, and an anonymous reviewer for comments on early version of the manuscript. DO thanks the American Ornithological Society, the Smithsonian Tropical Research Institute, and the University of Miami (Aresty Endowment, Kushland and savage funds) for supporting the 2019 field season in Panama. DO also thanks O McMillan, S Amador, and O Lopez from STRI for helping with the logistics in Panama.

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