



Other Contributions

Report of bilateral gynandromorphy in a Green Honeycreeper (*Chlorophanes spiza*) from Colombia

Reporte de ginandromorfía bilateral en *Chlorophanes spiza* en Colombia

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ABSTRACT. We report recent sightings, substantiated by color photographs and a short video, of a bilateral gynandromorph of the Green Honeycreeper (*Chlorophanes spiza*) from Villamaria, in the department of Caldas, Colombia. The bird exhibited typical male plumage on its right side and female plumage on the left. It was present for at least 21 months, and its behavior largely matched that of other wild Green Honeycreepers, although it often waited until they were gone before feeding on fruit that was put out daily by the property owners. We provide a comprehensive list and review of previous records of passerine bilateral gynandromorphy, noting which sex's plumage occurred on the left side. We observe that female plumage is possible on either side, supporting the double-fertilization model of bilateral gynandromorphy.

RESUMEN. Reportamos avistamientos recientes, corroborados por fotografías a color y un video corto, de una ginandromorfía bilateral de *Chlorophanes spiza* en Villamaria, departamento de Caldas, Colombia. El ave presentaba un plumaje típico de macho en el lado derecho y de hembra en el izquierdo. Estuvo presente durante al menos 21 meses, y su comportamiento coincidía en gran medida con el de otros *C. spiza* silvestres, aunque a menudo esperaba a que se fueran para alimentarse de la fruta que los propietarios de la finca ponían a diario. Proporcionamos una lista exhaustiva y una revisión de los registros anteriores de ginandromorfía bilateral de paseriformes, señalando el plumaje de qué sexo se produjo en el lado izquierdo. Observamos que el plumaje femenino es posible en ambos lados, conclusión que apoya el modelo de doble fecundación de la ginandromorfía bilateral.

Key Words: gynandromorph; plumage; sex determination; sex differences; sexual dimorphism

INTRODUCTION

Bilateral gynandromorphy is the condition in which one side of an organism exhibits male characters and the other female. The condition is known in a large number of animal groups, most often those that are sexually dimorphic (in which it is more readily detectable). A number of avian examples have previously been reported; in Table 1, we present a comprehensive list of robust, published reports of gynandromorphy in passerines, from which we have omitted several doubtful or ambiguous examples. Our list documents which phenotype was expressed on the left side of the animal.

In birds, the phenomenon is thought to arise as a result of an error during egg meiosis, with subsequent double fertilization by separate sperm (Agate et al. 2003, Zhao et al. 2010, Ma 2013). As a consequence, one side of the bird has heterogametic (ZW) female cells and the other homogametic (ZZ) male cells (DeCosta et al. 2007, Ma 2013). Examination of the internal structure of the brain and other organs of gynandromorphs has been instrumental in our understanding of sex determination and sexual behavior in birds (Agate et al. 2003, Zhao et al. 2010, Clinton et al. 2012).

Here, we report the second known observation of a bilateral gynandromorph Green Honeycreeper (*Chlorophanes spiza*), a member of the Thraupidae (tanagers), which is common and conspicuous over its range from southern Mexico to southeastern Brazil. The species feeds largely on nectar, fruit, and insects, and often frequents feeders supplying fruit. The plumage is strikingly sexually dimorphic, females being grass green, slightly paler

underneath, whereas males are aqua blue (sometimes described as “viridian green”; Zamudio and Burns, 2020) with a black hood, mask, and chin. Bill color is also sexually dimorphic: males have a bright yellow mandible and lower maxilla, with a black culmen; females have a dull yellow mandible and a black maxilla. Juveniles largely resemble females. Although males have, on average, slightly longer wings and tails than females, there is considerable variation within each sex and much overlap (Zamudio and Burns 2020). Similarly, there appears to be no significant difference in mass between males and females (Zamudio and Burns 2020). The iris of adult birds is a bright reddish brown; that of juveniles is duller (Zamudio and Burns 2020).

MATERIALS AND METHODS

Reserva Natural Demostrativa Don Miguel is a small farm with large patches of secondary forest, ca. 10 km southwest of the city of Manizales in Colombia. The proprietors have set up a feeding station for bird watching, supplying fresh fruit and sugar water. Numerous tanager species, as well as orioles, thrushes, and euphonias can often be seen in mixed flocks at these feeders.

RESULTS

Between October 2021 and June 2023, a bilaterally gynandromorphic Green Honeycreeper was observed at the feeding station by J.M. The bird was not present every day, however. Indeed, it appeared to stay in the vicinity for periods of about 4–6 wks and then vanish for another 8 wks or so. On 2 Jan 2023, it was also seen by E.C.-T., H.G.S., and Abigail Smith (Fig. 1).

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Table 1. Documented cases of bilaterally gynandromorphic plumage in passerines.[†]

Family	Species	Common name	Location	Left side plumage phenotype	Reference
Pipridae	<i>Corapipo altera</i>	White-ruffed Manakin	Panama	Male	DeCosta et al. (2007)
Panuridae	<i>Panurus biarmicus</i>	Bearded Reedling	Poland	Female	Stepniewski and Surmacki (2023)
Pycnonotidae	<i>Pycnonotus nigricans</i>	Black-fronted Bulbul	Transvaal, South Africa	Female [‡]	Storey and Harrison (1969)
Hirundinidae	<i>Hirundo rustica</i>	Barn Swallow	Hungary	Female	Holyński and Szentendrey (1977)
Muscicapidae	<i>Phoenicurus phoenicurus</i>	Common Redstart	Germany	Male	Welter (1962)
	<i>P. ochruros</i>	Black Redstart	Switzerland	Male	Weggler (2005)
			Switzerland	Female	Martinez (2020)
			Germany	Female	Moritz (1976)
Passeridae	<i>Passer domesticus</i>	House Sparrow	Spain	Male (two cases)	Abella (2002)
			England	Male	McCanch (1992)
	<i>P. montanus</i>	Eurasian Tree Sparrow	Illinois, USA	Female [§]	Bohlen (2006)
Ploecidae	<i>Ploceus cucullatus</i>	Village Weaver	Cabinda, Angola	Female	Neunzig (1924)
Estrilidae	<i>Chloebia gouldiae</i>	Gouldian Finch	Australia	Female (two cases)	Crew and Munro (1938)
	<i>Taeniopygia guttata</i>	Zebra Finch	Laboratory	Female	Agate et al. (2003)
Passerellidae	<i>Pipilo erythrophthalmus</i>	Eastern Towhee	Tennessee, USA	Female	Laskey (1969)
			Pennsylvania, USA	Male	Anonymous (2001)
			Rhode Island, USA	Male	Brenner et al. (2019)
Fringillidae	<i>Fringilla coelebs</i>	Eurasian Chaffinch	Netherlands	Female	Blaauw (1890)
	<i>F. montifringilla</i>	Brambling	Germany	Female (two cases)	Kumerloeve (1987)
	<i>Coccothraustes vespertinus</i>	Evening Grosbeak	Massachusetts, USA	Female	Shaub (1960)
			New York and New England, USA	Male	Shaub (1960)
			Maine, USA	?	Packard (1962)
			Virginia, USA	Male	Laybourne (1967)
			New Jersey, USA	Male	Cadbury (1973)
			Minnesota, USA	Female	Tordoff (1983)
	<i>Loxia curvirostra</i>	Common Crossbill	?	Female	Kumerloeve (1987)
	<i>Pyrrhula pyrrhula</i>	Eurasian Bullfinch	?	Female	Cabanis (1874)
			France	Female	Kumerloeve (1987)
			?	Female (eight cases)	Kumerloeve (1987)
			?	Male (four cases)	Kumerloeve (1987)
	<i>Carpodacus rhodochrous</i>	Pink-browed Rosefinch	Kashmir	Male	Alström and Olsson (1988)
	<i>C. roseatus</i>	Common Rosefinch	Nepal	Male	Kumerloeve (1987)
	<i>Spinus spinus</i>	European Siskin	?	?	Harrison (1964)
Icteridae	<i>Icterus spurius</i>	Orchard Oriole	Pennsylvania, USA	Female	Townsend (1882)
	<i>Quiscalus mexicanus</i>	Great-tailed Grackle	Mexico	?	Patten (1993)
Parulidae	<i>Setophaga caerulescens</i>	Black-throated Blue Warbler	California, USA	Male	Patten (1993)
Cardinalidae	<i>Cardinalis cardinalis</i>	Northern Cardinal	Tennessee, USA	Female	Laskey (1969)
			Illinois, USA	Female (two cases)	Bohlen (2006)
			Illinois, USA	Male	Peer and Motz (2014)
			Virginia, USA	Female	Jones and Bartlett (2017)
			Ohio, USA	Female	Jones and Bartlett (2017)
			Arkansas, USA	Female	Tumilson et al. (2018)
			Indiana, USA	Male [¶]	Clark (2018)
			Missouri, USA	Male [¶]	Missouri Department of Conservation (2018)
			Pennsylvania, USA	Female	Anonymous (2019)
			North Carolina, USA	Female	Rodríguez-Ruiz and Castro-Gutiérrez (2022)
			Texas, USA	Male	Rodríguez-Ruiz and Castro-Gutiérrez (2022)
			Mexico	Female	Rodríguez-Ruiz and Castro-Gutiérrez (2022)
	<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	Pennsylvania, USA	Female	Mulvihill and Leppold (2005)
			Massachusetts, USA	Male	Brown (2015)
			Pennsylvania, USA	Female	Powdermill Nature Reserve (2020)
Thraupidae	<i>Chlorophanes spiza</i>	Green Honeycreeper	?	Male	Kniesche (1914)
			Colombia	Female	This report
	<i>Sporophila caerulescens</i>	Double-collared Seedeater	Rio de Janeiro, Brazil	Female	Sick (1967)
	<i>S. maximiliani</i>	Great-billed Seed Finch	Goiás, Brazil	Male	Filho and Teixeira (1982)

[†] Several cases discussed by Kumerloeve (1987) that he considered doubtful or dubious (e.g., those of a Goldcrest, *Regulus regulus*, and a Eurasian Magpie, *Pica pica*) are omitted. Similarly, other records included in previous lists that do not show bilateral symmetry (e.g., an Italian Sparrow, *Passer italiae*, recorded by Iapichino and Massa [1989]) or that do not show male/female differences (e.g., a Hooded Crow, *Corvus cornix*, reported by Rensch [1926]) are omitted.

[‡] Plumage is not sexually dimorphic in this species. An ovary was present on the left side, a testis on the right. The left wing was ca. 3% smaller, matching the usual sexual difference.

[§] Plumage is not sexually dimorphic in this species. An ovary was present on the left side, a testis on the right.

^{||} The case reported by Harvey (1926) and Seth-Smith (1928) does not seem to be a case of bilateral gynandromorphism. Rather, the female bird concerned had different plumages on each side of the head, but the different colors are those of different morphs, not sexes.

[¶] Reported as leucistic, rather than gynandromorphic. Demarcation is not perfectly bilateral.

Fig. 1. Bilaterally gynandromorphic Green Honeycreeper near Manizales, Colombia, 20 May 2022. (Photos J.M.)



The bird was photographed on several occasions (Fig. 1) and a short video was also made (see Supporting Information; https://figshare.com/articles/media/DSCN2268_MOV/23739894). It had typically male plumage on its right side and typically female plumage on its left, although this pattern had a few feathers out of place especially on the head. The bill appeared to be consistent with male coloration, although the lower left of the mandible was possibly a duller yellow. The iris was bright reddish brown.

The bird did not behave in any way that was unusual for a Green Honeycreeper, and it vocalized on several occasions. It was not differentially harassed by other Green Honeycreepers or other birds observed at the feeders. Nevertheless, at some point, the individual was territorial, not letting other individuals of its species approach the feeders. We do not know if this behavior was related to the breeding season (May to July), however. The gynandromorph usually waited for the other honeycreepers to leave the feeders before landing to feed itself. In general, it avoided others of its species, and the others also avoided it; it seems unlikely, therefore, that this individual would have had any opportunity to reproduce.

DISCUSSION

Our report appears to be the second record of bilateral gynandromorphy in the Green Honeycreeper, and the first of a living bird. Although the head pattern might be considered a little reminiscent of that of a juvenile male (see van Dort 2015), the iris color of our bird clearly indicates it was adult. Moreover, juvenile male plumage does not molt in a bilateral pattern, and our bird was observed for a period greater than the length of the juvenile stage. Most cases of bilateral gynandromorphy have several feathers out of place (e.g., Cadbury 1973, Agate et al. 2003, Brenner et al. 2019).

Interestingly, the previous report (Kniesche 1914) noted the reverse pattern to our observation, with the left side of the bird male, rather than, as in our case, female. Many authors (e.g., Kumerloeve 1954, Filho and Teixeira 1982, Graves et al. 1996,

Abella 2002, and DaCosta et al. 2007) have held that, in most cases of bilateral gynandromorphs, the plumage on the left side was female, in keeping with the observation that in most avian species (and notably all passerines) females normally have only their left ovary functional (Jacob and Bakst 2006). The examples in Table 1 suggest, however, that there is no general pattern. Indeed, most species for which multiple reports are available seem to show that either pattern is possible, which we note is consistent with double fertilization.

Whether the internal organs of our bird were also bilaterally gynandromorphic is impossible to tell. Nevertheless, given that avian gonad development is cell autonomous, dependent on the chromosomal makeup of the cells rather than hormones diffusing across the whole body (Clinton et al. 2012), that would be expected. Several observations of gynandromorphic passerines also support our expectations. The Eurasian Chaffinch reported by Blaauw (1890), the Evening Grosbeak described by Tordoff (1983), and the Northern Cardinal dissected by Jones and Bartlett (2017) all had an ovary on the left and a testis on the right, corresponding to the plumage. Similarly, Agate et al (2003) reported that gonadal type agreed with plumage in their gynandromorphic Zebra Finch, whose left-side plumage was female and which had a histologically normal ovary on the left, but a mature testis on the right. This bird was behaviorally male, successfully courting and mating with a female, although the eggs were infertile. The two Gouldian Finches reported by Crew and Munro (1938) had female plumage on their left sides, as for the Zebra Finch, but they were behaviorally female, mating with males and laying eggs. The single bird examined by dissection had an ovary on the left, but no testis on the right (Crew and Munro 1938). We note, however, that all these examples had female plumage on the left side. We are aware of at least three exceptions. A Common Rosefinch with right-sided female plumage (and then, apparently only in some feathers) had testes on both sides, but also a small ovary on the right (Kumerloeve 1987). Laybourne (1967) reported an Evening Grosbeak with an ovary on the left and a testis on the right, even though the plumage was male on the left and female on the right, and the same result obtained in the only suboscine case known, a White-ruffed Manakin (DaCosta et al. 2007).

Not unexpectedly, given that our bird was never captured, we did not perceive any bilateral size difference. By contrast, in addition to an example in the domestic chicken (Morris et al. 2018), Lowther (1977) showed that such asymmetry was present in two House Sparrow skeletons he considered gynandromorphic. The right-hand, male sides of the two Gouldian Finches reported by Crew and Munro (1938) were ca. 2% larger than the left, female sides, and the male-sided right wing of a Black-fronted Bulbul was ca. 3% larger than the left female-sided wing (Storey and Harrison 1969). Similarly concordant, albeit small, size differences were also present in an Evening Grosbeak (Laybourne 1967) and a Common Redstart (Moritz 1976).

The Eastern Towhee described by Brenner et al. (2019) was observed feeding fledglings, although it was not possible to confirm that it was the genetic parent. We cannot, of course, say whether or not our bird was fertile. We did not observe any courtship behavior or pairing in our bird, and strongly suspect it did not reproduce. That we did not see any unusual feeding

behavior of our bird or any unexpected interactions with other birds is consistent with observations of other gynandromorphs (e.g., Evening Grosbeak. Cadbury 1973; Common Redstart, Welter 1962), although, like the House Sparrow described by McCanch (1992), it was inclined to be a loner. Nevertheless, gynandromorphs do not always stay single: a gynandromorphic Northern Cardinal apparently paired with a female (Bohlen 2006), and a gynandromorphic Black Redstart was observed to form a stable pair with a typical male (Martinez 2020). Moreover, a Black Redstart with left male plumage showed typical male behavior and successfully fathered five chicks (Weggler 2005). We note that our observations over a 21-mo period extended over a much longer period than any other reported case of bilateral gynandromorphy, showing that our bird was well able to survive day-to-day events.

There are numerous reports of bilateral gynandromorphy in various other passerines (Table 1), but there do not appear to be many involving members of the Thraupidae. This paucity of cases is rather surprising, given the large number of thraupid species, many of which exhibit obvious sexually dimorphic plumage, rendering any examples highly visible. Apart from the previous Green Honeycreeper record from over a 100 yrs ago, the remaining thraupid records are from two species of *Sporophila* seedeaters, the Double-collared Seedeater (*S. caerulescens*) and the Great-billed Seed-Finch (*S. maximiliani*) (Sick 1967, Filho and Teixeira 1982). *Sporophila* had long been considered an emberizid or a fringillid, and is not phylogenetically close to *Chlorophanes* within the Thraupidae (Burns et al. 2016). As in the Green Honeycreeper, juveniles of many species resemble females. Interestingly, instances of sexually mature males with female-like plumage are known in several species of *Sporophila* (but not, to date, either of the two mentioned above) (Sick 1967, Areta 2009). Several hypotheses for the cause of such plumage anomalies are possible (e.g., paedomorphosis, and unseasonal retention of non-breeding plumage; Areta 2009). We note also that the dorsal boundary between the two plumage types in the specimen of *S. maximiliani* was not clearly demarked (Filho and Teixeira 1982). Whatever the case, these observations suggest that it is at least plausible that these apparently gynandromorphic *Sporophila* could have been males with aberrant plumage.

In summary, we document only the second record of bilateral gynandromorphy in the Green Honeycreeper (*Chlorophanes spiza*), and only the fourth record for any species of thraupid tanager. Our observations extended over an unusually long period (21 mos) and are the first of a gynandromorph of this species alive in the wild. Moreover, the bird we observed exhibited female plumage on the left and male on the right, the opposite of the previous case from over 100 yrs ago.

Author Contributions:

John Murillo: Investigation (lead), Edwin Campbell-Thompson: Investigation (supporting); Writing (supporting). Thomas F. Bishop: Conceptualization (supporting); Writing (supporting). Caroline W. Beck: Conceptualization (supporting); Writing (supporting). Hamish G. Spencer: Conceptualization (lead), Observation (supporting), Writing (lead); Project administration.

Acknowledgments:

We thank A. M. Smith for contributions to our observations, and D. Shutler, M. A. Patten, and an anonymous reviewer for comments on the manuscript.

Data Availability:

All the data are presented directly in the paper and/or supplementary material. The data consist solely of photographs and a video.

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