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SYNTOPIC BREEDING SUGGESTS MIMICRY OF THE BLACK-AND-WHITE SEEDEATER (*SPOROPHILA LUCTUOSA*) BY THE BLACK-AND-WHITE TANAGER (*CONOTHRAUPIS SPECULIGERA*)

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Resumen. – Reproducción sintópica sugiere que la Tangara Negriblanca (*Conothraupis speculigera*) mimetiza al Espiguero Negriblanco (*Sporophila luctuosa*). – En aves, el mimetismo visual interespecífico ha sido raramente documentado, aunque se han citado varios ejemplos. La similitud excepcional en los patrones de plumaje de dos especies simpátricas, la Tangara Negriblanca (*Conothraupis speculigera*) y el Espiguero Negriblanco (*Sporophila luctuosa*), es un ejemplo potencial de mimetismo visual que no ha sido previamente reconocido. A diferencia del Espiguero Negriblanco, las características del plumaje de la Tangara Negriblanca no se encuentran en ninguna otra especie relacionada, sugiriendo que estas han convergido al patrón del Espiguero Negriblanco a través de selección natural. Además, la distribución reproductiva de la Tangara Negriblanca, aunque poco conocida, es ampliamente solapada por la del Espiguero Negriblanco, el cual es más abundante. Las observaciones presentadas aquí, que indican que la Tangara Negriblanca se reproduce entre agregaciones reproductivas del Espiguero Negriblanco, sugieren que la similitud convergente es un resultado de las interacciones interespecíficas. La diferencia en la abundancia de estas dos especies sugiere convergencia evolutiva por un nuevo mecanismo en el que el imitador puede ser más grande que el modelo.

Abstract. – Interspecific visual mimicry has rarely been well documented in birds, although numerous putative examples have been cited. The exceptional similarity in plumage pattern between the co-occurring Black-and-white Tanager (*Conothraupis speculigera*) and Black-and-white Seedeater (*Sporophila luctuosa*) is a potential example of visual mimicry that has not been previously recognized. Unlike the Black-and-white Seedeater, the plumage characteristics of the Black-and-white Tanager are found in none of its close relatives, suggesting that it may have converged on the pattern of the Black-and-white Seedeater through natural selection. Furthermore, the breeding distribution of the Black-and-white Tanager, although poorly known, is extensively overlapped by the more abundant Black-and-white Seedeater. The observations reported here that the Black-and-white Tanager breeds among breeding aggregations of Black-and-white Seedeaters suggest that the convergent similarity is a result of interspecific interactions. The difference in abundance of these two species suggests evolutionary convergence by a novel mechanism whereby the mimic can be larger than the model. *Accepted 18 April 2005.*

Key words: Black-and-white Seedeater, Black-and-white Tanager, *Conothraupis speculigera*, convergence, mimicry, Peru, *Sporophila luctuosa*.

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INTRODUCTION

Intraspecific female mimicry (Slagsvold & Saetre 1991) and mimicry of brood hosts by brood parasites (Nicolai 1974) are well documented forms of visual mimicry in birds. However, visual mimicry is also thought to occur in response to social interactions between species (Willis 1963, Moynihan 1968, Saetre *et al.* 1993). The best demonstration of the latter phenomenon involves an oriole (*Oriolus*) and a friarbird (*Philemon*), in which parallel geographic variation is driven by interspecific antagonistic behavior (Diamond 1982). Although it can provide irrefutable evidence of mimicry, parallel geographic variation is rare and should not be considered a prerequisite for the demonstration of interspecific visual mimicry, of which there are many putative examples (see Diamond 1982). Interspecific visual mimicry can be reasonably inferred if three criteria are demonstrated: 1) evolutionary convergence in non-adaptive plumage traits of one species (the mimic) on another (the model), in a phylogenetic context; 2) overlap of the distribution of the mimic by the model sufficient that the model could comprise a significant selective force; and 3) physical interaction or close proximity of the model to the mimic in nature. Species pairs that satisfy these criteria would provide ideal candidates for experimental tests that seek to identify the cause of natural selection for extreme similarity.

In this paper, I present observations of breeding activity in the rare Black-and-white Tanager (*Conothraupis speculigera*) that document its occurrence amidst aggregations of Black-and-white Seedeaters (*Sporophila luctuosa*). While differing in size, these two species are extremely similar in plumage, and may represent an example of interspecific visual mimicry that has not been previously recognized. I argue that the Black-and-white Tanager (*Conothraupis speculigera*) may have converged on the Black-and-white Seedeater (*Sporophila luctuosa*) as a result of interspecific interactions.

EVOLUTIONARY CONVERGENCE

Black-and-white Seedeater and Black-and-white Tanager males are characterized by black upperparts, wings, tail, head, throat, and upper breast (see Fig. 1). The lower breast, belly, flanks, and crissum are white. Each species has white bases to the primary feathers that form a prominent spot (speculum) on the side of the sitting bird, and a conspicuous white flash in flight. The subtle differences in appearance between males of these two taxa are that the Black-and-white Tanager has gray on the rump and sides, a concealed white crown patch, red irides (not brown, as in the Black-and-white Seedeater), a longer but proportionally shallow bill, a darker gray culmen, and larger overall body size (Black-and-white Tanager males, mean = 26.9 g, SD = 2.5, n = 15; females, mean = 25.5 g, SD = 3.8, n = 12; Black-and-white Seedeater males, mean = 12.9 g, SD = 2.9, n = 6; females, mean = 11.1 g, SD = 1.0, n = 3). Female plumages of each species, also relatively similar, are a fairly uniform, cryptic pale olive-brown color. Black-and-white Tanager females are slightly more yellow with diffuse streaking on the underparts.

Although the genera *Sporophila* and *Conothraupis* were previously thought to be in separate families (Emberizidae and Thraupidae, respectively), it is now recognized on the basis of genetic data that both genera are part of the large Neotropical thraupine radiation (Tribe Thraupini; Bledsoe 1988, Sibley & Ahlquist 1990). No exhaustively sampled, well-resolved phylogeny exists for the Thraupini, but the most comprehensive available molecular phylogeny (Burns *et al.* 2002) indicates that 1) *Sporophila* is sister to *Oryzoborus* in clade with no other close relatives, and 2)

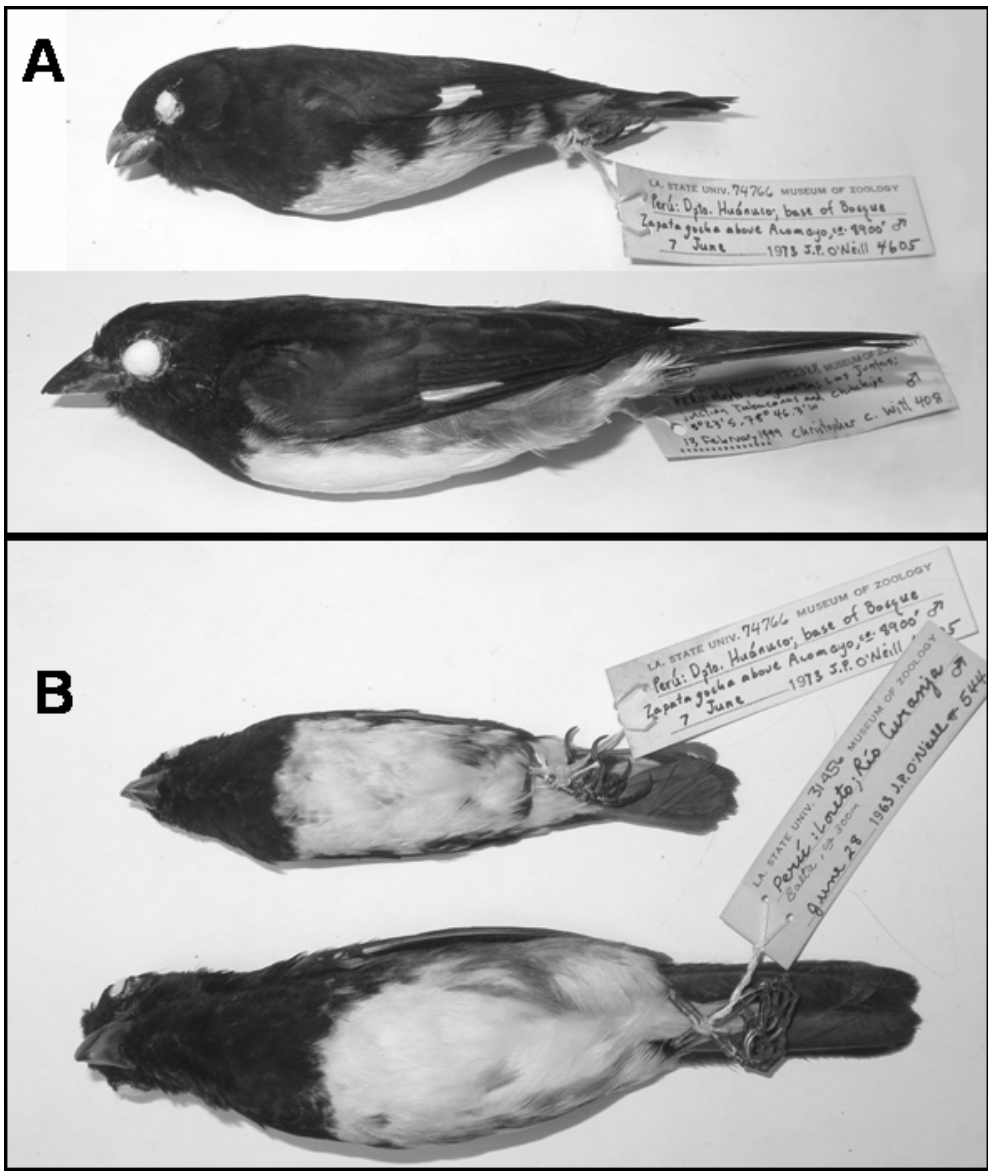

FIG. 1. Comparison of the plumage pattern of the male Black-and-white Seedeater (top specimen in each panel) and the male Black-and-white Tanager. (A) Side view; (B) ventral view.

Conothraupis is sister to *Chlorophanes*, and nested in a clade containing 30 other genera. Black and white male plumage is common among *Sporophila* (7 out of 32 species possess entirely black and white male plumage), and white wing specula are found in most *Sporophila* species (28 out of 32) as well as in the sister genus, *Oryzoborus*. Thus, the plumage

pattern of the Black-and-white Seedeater is not aberrant among members of its clade, and is likely a result of its phylogenetic history. On the other hand, the apparent sister genus to *Conothraupis* is entirely green plumaged and lacks a wing speculum. Among the 30 other genera in the *Conothraupis* clade, only 3 include species that possess black and white plumage, and only 5 include species that possess wing specula. The distinctive black and white plumage pattern and white wing speculum of *Conothraupis* appear to be synapamorphic, and not attributable to phylogenetic history alone. From a phylogenetic perspective, the extreme similarity in plumage between these two species seems to be a result of the Black-and-white Tanager converging on the 'typical *Sporophila*' plumage pattern of the Black-and-white Seedeater.

Due to the overall uncertain resolution and incomplete sampling of the current Thraupini phylogeny (Burns *et al.* 2002), more precise statistical tests of convergence that depend on inference of ancestral character states could be misleading (Cunningham *et al.* 1998). It cannot be completely ruled out that *Conothraupis* is basal to the clade containing *Sporophila* and *Oryzoborus*. However, even if this scenario were true, it remains improbable that the precise resemblance of the Black-and-white Tanager to the co-occurring Black-and-white Seedeater would result from retention of ancestral character states. An additional caveat is provided by the mysterious sister-species to the Black-and-white Tanager, the Cone-billed Tanager (*C. mesoleuca*), which shares the same basic plumage pattern. The Cone-billed Tanager is known from a only single specimen collected in 1938 in Mato Grosso, Brazil, and it is thought to be extremely closely related to the Black-and-white Tanager (Zimmer 1947). It is possible that the divergence between these two species post-dated the convergence of the Black-and-white Tanager on the Black-and-white Seedeater.

An alternative explanation for the similarity in plumage between the Black-and-white Seedeater and the Black-and-white Tanager is that they are subjected to similar selection pressures in common environments. Black and white plumage has evolved independently many times in birds, and it is thought to conceal birds from predators through disruptive coloration or countershading (Thayer 1909). It has also been suggested that black and white plumage is associated with forest-edge habitats (Willis 1976). Contrasting wing markings are thought to be important in social signaling (Butcher & Rohwer 1990), but have no known adaptive function. It is difficult to imagine that independent adaptive evolution can account for the similarity in the precise distribution of the black and white markings between the Black-and-white Seedeater and the Black-and-white Tanager. No other species in the New World shares the combination of black back, wings, tail, head, and breast, and entirely white belly, vent, and speculum. Furthermore, only two of 76 species that were found to co-occur with the Black-and-white Seedeater and the Black-and-white Tanager in a Peruvian tropical dry forest possess entirely black and white plumage, and those species are heavily barred [Lined Antshrike (*Thamnophilus tenuepunctatus*) and Fasciated Wren (*Campylorhynchus fasciatus*); unpublished data].

Although the similarities of the Black-and-white Tanager to the Black-and-white Seedeater can be explained by convergence, the differences in bill shape and eye color can be attributed to phylogenetic history. *Chlorophanes*, the apparent sister genus to *Conothraupis*, possesses a red eye, as do species in several other genera in the *Conothraupis* clade (LSUMZ specimen data). In addition, all taxa in the *Conothraupis* clade possess bills that are proportionately longer and shallower than

TABLE 1. Specimen data for Black-and-white Tanager specimens at LSUMNS. Localities as follows: (1) Peru: Loreto, Pucallpa, Yarinacocha, collected in 1962; (2) Peru: Loreto, Rio Curanja, Balta, 300 m a.s.l., collected in 1963 or 1967; (3) Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy., 11 km by road north of Olmos, 150 m a.s.l., collected in 1983; (4) Peru: Ucayali, western bank Rio Shesha, c. 65 km east-northeast of Pucallpa, collected in 1987; (5) Peru: Cajamarca, junction of Rio Tabaconas and Rio Chinchipe, 5°23'S, 78°46'W, 450 m a.s.l., collected in 1999.

Cat. number	Locality	Date	Sex	Mass (g)	Fat	% skull ossification	Gonad condition	Iris color	Plumage	Body molt
28636	1	31 Jul	F	-	-	-	Ovary 4 mm	-	-	-
28637	1	3 Aug	F	-	-	-	-	-	-	-
28638	1	1 Aug	M	-	-	-	Testes 1 mm	-	Imm.	-
28639	1	28 Jul	M	-	-	-	Testes < 1 mm diameter	-	Imm.	-
31456	2	28 Jun	M	-	-	-	Testes 1.5 mm	-	Adult	-
62602	2	25 Jul	F	-	-	-	-	-	-	-
113916	3	30 Aug	M	26.0	Moderate	100	Left testis 2 x 1 mm	Red	Adult	Moderate
113917	3	31 Aug	F	26.0	Light	10	Ovary 5 x 2 mm, smooth, oviduct minute	Brown	-	Heavy
113918	3	2 Sep	M	24.0	None	50	Testes 1 x 0.5 mm	Brown	Imm.	Light
113919	3	3 Sep	M	29.5	Heavy	50	Testes 1 x 0.5 mm	Brown	Imm.	None
113920	3	3 Sep	F	23.5	Trace	10	Ovary 5 x 2.5 mm, smooth, oviduct 1 mm	Brown	-	Moderate
113921	3	3 Sep	M	24.0	Moderate	10	Testes 1 x 0.5 mm	Brown	Imm.	Light
113922	3	3 Sep	F	22.5	Moderate	0	Ovary 4 x 2 mm, smooth, oviduct minute	Brown	-	None
113923	3	3 Sep	F	24.0	Heavy	0	Ovary 4 x 3 mm, smooth, oviduct minute	Brown	-	Trace
113925	3	3 Sep	M	22.0	Moderate	0	Testes 1 x 1 mm	Brown	Imm.	Heavy
113926	3	5 Sep	M	30.5	Very heavy	15	Testes 1 x 1 mm	Brown	Intermediate	None
113927	3	10 Sep	M	25.5	Moderate	50	Testes 1.5 x 1 mm	Brown	Imm.	None
113928	3	10 Sep	M	26.0	Light	0	Testes 1.5 x 1 mm	Brown	Imm.	Light
113929	3	10 Sep	M	29.5	Heavy	100	Testes 2 x 1 mm	Red	Adult	Trace
113930	3	10 Sep	F	33.0	Very heavy	100	Ovary 5 x 3 mm, ova minute, oviduct 2 mm	Red	-	Trace
113931	3	10 Sep	F	27.0	Heavy	80	Ovary 5 x 3 mm, smooth, oviduct minute	Brown	-	None
113932	3	14 Sep	M	29.0	Very heavy	10	Testes 1 x 0.5 mm	Brown	Imm.	None
113933	3	15 Sep	M	30.0	Very heavy	10	Testes 1 x 0.5 mm	Brown	Imm.	None
113934	3	15 Sep	M	27.0	Light	10	Testes 0.5 x 0.5 mm	Brown	Imm.	Heavy
113935	3	15 Sep	F	29.0	Very heavy	20	Ovary 2.5 x 2 mm, smooth, oviduct minute	Brown	-	None
113936	3	15 Sep	F	23.0	None	20	Ovary 4 x 3 mm, smooth, oviduct minute	Brown	-	None

TABLE 1. Continuation.

Cat. number	Locality	Date	Sex	Mass (g)	Fat	% skull ossification	Gonad condition	Iris color	Plumage	Body molt
113937	3	15 Sep	F	27.5	Moderate	20	Ovary 4 x 3 mm, smooth, oviduct minute	Brown	-	None
113938	3	15 Sep	F	25.0	Light	10	Ovary 2.5 x 2 mm, smooth, oviduct minute	Brown	-	Trace
113940	3	18 Sep	M	26.0	Moderate	50	Testes 1 x 0.5 mm	Brown	Imm.	None
113941	3	19 Sep	M	27.0	Heavy	10	Testes 1.5 x 1 mm	Brown	Imm.	None
113943	3	21 Sep	M	28.0	Light	10	Testes 1 x 1 mm	Brown	Imm.	Trace
156823	4	8 Jul	F	20.0	-	25	Ovary 2 x 3 mm, smooth	Brown	-	Moderate
156824	4	1 Aug	F	20.0	Light	90	Ovary 6 x 4 mm, ova and oviduct minute	Red	-	None
CCW408	5	15 Feb	M	24.5	Moderate	100	Left testis 5 x 3 mm	Red	Adult	None

that of the Black-and-white Seedeater (and all *Sporophila* and *Oryzoborus* species).

DISTRIBUTIONAL OVERLAP

The distribution of the Black-and-white Tanager has long been an enigma (O'Neill 1966). The scant existing data indicates that it breeds during the middle to latter part of the rainy season (which lasts approximately December to May) in seasonally arid areas on the west slope of the Andes and in inter-Andean valleys in southern Ecuador and northern Peru. During the dry season (approximately June to November), the Black-and-white Tanager is not present at breeding sites (Ridgely & Greenfield 2001, pers. observ.), and the scattered records indicate that it disperses into humid lowland Amazonia in southern Ecuador, eastern Peru, northwestern Bolivia, and western Brazil (O'Neill 1966, Isler & Isler 1987, Stotz 1990). However, during August and September 1983, when El Niño-related precipitation caused normally arid areas on the west slope of the Andes to become covered with verdant vegetation, the Black-and-white Tanager was found in large numbers at localities where normally rare or absent (S. W. Cardiff & D. L. Dittmann, *in* Isler & Isler 1987). Thus, existing data suggest that non-breeding Black-and-white Tanagers are somewhat nomadic and exploit seasonal or sporadic resources. Among a series of 33 specimens collected between June and September, from both east and west of the Andes, none appear to be in breeding condition on the basis of specimen label data (Table 1).

The distribution of the Black-and-white Seedeater encompasses most of the known breeding distribution of the Black-and-white Tanager, but also extends from Venezuela to Bolivia. Like the Black-and-white Tanager, it breeds during the rainy season on both slopes of the Andes and in seasonally dry Inter-Andean valleys (Ridgely & Greenfield 2001, pers. observ.). During the non-breeding season, it disperses from breeding sites, often in large flocks, and becomes somewhat nomadic.

PHYSICAL PROXIMITY AT BREEDING SITES

In February 1999, while conducting an inventory of birds in a tropical deciduous forest in Depto. Cajamarca, Peru, I found Black-and-white Tanagers and Black-and-white Seedeaters occurring together in hillside forest clearings with grass and dense scrub. All observations were made within 3 km of the junction of the Tabaconas and Chinchipe Rivers, which lies on the east slope of the Andes, but in the rain shadow of the southernmost extent of the Cordillera del Condor (5°23'S, 78°46'W; 400-600 m a.s.l.). The Black-and-white Seedeater was abundant, whereas only five individuals of the Black-and-white Tanager were observed during a 6-day period. I found Black-and-white Seedeaters to be concentrated in loose colonies, or breeding aggregations, where appropriate habitat (patches or clearings with grass and dense scrub) was present. Black-and-white Seedeater males sang from elevated perches in these habitat patches, creating a cacophony of blackbird-like, high-pitched song. In two such patches, I found single Black-and-white Tanager males within aggregations of Black-and-white Seedeaters, singing from elevated perches. In another Black-and-white Seedeater aggregation, two singing Black-and-white Tanager males were present on opposite sides of a grassy clearing. In all cases, the Black-and-white Seedeater far outnumbered the Black-and-white Tanager. The song of the Black-and-white Tanager was similar in tone to that of the Black-and-white Seedeater, but easy to detect among the din of song because each phrase concluded with a clear, lower-pitched, whistled note (song described in Isler & Isler

1987). Antagonistic encounters were observed among Black-and-white Seedeater males, but no interspecific antagonism was observed. The Black-and-white Tanager males were observed on multiple occasions dropping from their singing perches to forage on or near the ground in close proximity to foraging Black-and-white Seedeaters. One individual was observed carrying out an extended preening bout on an exposed dead branch. A female Black-and-white Tanager was observed foraging in dense scrub, at the edge of a clearing with an aggregation of Black-and-white Seedeaters. Voucher specimens of both the Black-and-white Tanager (CCW408) and the Black-and-white Seedeater (CCW417) were collected. The pattern of territorial advertisement song and the enlarged testes on the single collected specimen suggest that Black-and-white Tanagers were breeding at these sites (left testis 5 x 3 mm; testes of three adult male Black-and-white Tanager specimens collected between June and September range from 1.5 mm diameter to 2 x 1 mm; Table 1).

DISCUSSION

In most described cases of animal visual mimicry (Batesian or Müllerian mimicry), the mimic converges on the appearance of the model in order to affect the response of a potential predator, the intended signal receiver (Wickler 1968). If the Black-and-white Seedeater, the model, is toxic or distasteful to predators, convergence by the Black-and-white Tanager could be the result of Batesian or Müllerian mimicry (Dumbacher & Fleischer 2001). However, no evidence (such as aposematic coloration) suggests that either species is toxic. In the case of the orioles and friarbirds, the smaller mimic (oriole) converges on the larger model (friarbird) to deceive the model itself. Diamond (1982) suggested that visual resemblance of orioles to friarbirds reduced the frequency or severity of interspecific antagonistic encounters. As a result, orioles that closely resemble friarbirds are expected to experience increased survival or reproduction. I suggest that a similar mechanism is occurring in the Black-and-white Tanager and the Black-and-white Seedeater, whereby Black-and-white Tanager individuals that closely resemble Black-and-white Seedeater incur a selective advantage.

Diamond (1982) posited that social mimicry should only evolve when the mimic is smaller than the model and thus benefits differentially from the reduction in antagonism. Therefore, it seems paradoxical that the Black-and-white Tanager is larger than the Black-and-white Seedeater. I argue that, given that antagonistic encounters have an energetic cost to both winner and loser, selection for reduction of interspecific antagonism could be stronger in the less abundant species, regardless of relative size. The Black-and-white Tanager, which is generally considered rare, is less abundant than the Black-and-white Seedeater by at least an order of magnitude at the observed sites of co-occurrence in the Chinchipe River Valley. The two species occupy the same habitat patches and foraging stratum, suggesting that they are in competition for resources such as food and nest sites. The extreme similarity and larger size of the Black-and-white Tanager may allow it to be more readily recognized by the Black-and-white Seedeater as a dominant competitor, reducing the need for interspecific aggression. This would allow Black-and-white Tanagers to defend resource patches or establish interspecific territories (*sensu* Cody 1969) without expending energy chasing naïve Black-and-white Seedeater individuals.

Convergent plumage patterns, overlapping distributions, and physical proximity on breeding sites suggest that the Black-and-white Tanager is a visual mimic of the Black-

and-white Seedeater, and that the similarity in plumage has a function relating to interspecific behavior. Additional fieldwork is needed to test this hypothesis using behavioral observations, experimental tests, and more data on the breeding distribution and life history of the rare and enigmatic Black-and-white Tanager.

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