



Median-crown stripe variation in two ant-tanagers (Cardinalidae)

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Received: 8 April 2024 / Revised: 26 December 2024 / Accepted: 29 December 2024
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Abstract

We document median-crown stripe variation in two dichromatic neotropical cardinalid species, the red-crowned ant-tanager *Habia rubica* and the red-throated ant-tanager *Driophlox fuscicauda*. While definitive (adult) males always have a red median-crown stripe and juveniles lack stripes, definitive females and formative birds (those after molting the juvenile plumage) of both sexes exhibit up to three variants: no stripe, intermediate dull-yellow stripe, and full bright-yellow stripe. Among these age/sex groups, occurrence of full stripe was highest in definitive female red-crowned ant-tanagers, followed by formative males of both species. By contrast, the median-crown stripe occurs at low frequencies in definitive female and formative red-throated ant-tanagers. We propose that this phenotypic plasticity in degree of the median-crown stripe may have evolved as an adaptation to the complex social systems of these two species, likely facilitating the formation of heterogeneous territorial groups and increasing winter survival and extra-pair fertilizations.

Keywords Bayesian regression · Delayed plumage maturation · Female-mimicry hypothesis · Phenotype variation

Introduction

Bird plumage varies among individuals of the same species, often between sexes (Gray 1996; Price and Birch 1996). This variation typically manifests through overall coloration and/or pattern design and is known to have fitness consequences, resulting in part from the species' social system (Møller 1987; Amundsen et al. 1997; Galeotti et al. 2003). For example, in the great tit *Parus major*, plumage brightness associates with male parental abilities, in the Eurasian siskin *Spinus spinus*, black bib associates with dominance in males, and in the common waxbill *Estrilda astrild*, regularity of barred plumage associates with individual quality (Senar et al. 1993; Senar et al. 2002; Marques et al. 2016). Moreover, variation of plumage traits may facilitate diversification of life strategies within a species (Lank et al. 1995;

Gross 1996), and it also can vary throughout the lifetime of the individual, typically transitioning the most between early and adult life (Rohwer 1986; Londoño et al. 2022). Plumage maturation has important implications for the social life of birds (Lyon and Montgomerie 1986; Hawkins et al. 2012), and in some species it may take several years to attain the definitive plumage, even in passerines (Doucet et al. 2007).

Many passerine species exhibit head marks, such as forehead patches (Järvistö et al. 2013) or crown stripes (Rohwer and Rohwer 1978), which largely carry out signaling functions. In the Americas, crown stripes are frequently found in Tyrannidae, Regulidae, Passerellidae, and Parulidae although they are largely absent in most families. Among 51 species of the family Cardinalidae, only the ant-tanagers have crown-stripes. The red-throated ant-tanager *Driophlox fuscicauda* was traditionally classified in the genus *Habia* with the red-crowned ant-tanager *H. rubica*, but was recently split to account for the paraphyletic relationships among ant-tanagers (Scott et al. 2024).

The red-crowned and red-throated ant-tanagers are highly polytypic and have wide geographic ranges: the red-crowned has 17 subspecies occurring from Mexico to Argentina while the red-throated has six subspecies occurring from Mexico to northern Colombia. Both species have similar size and appearance, are sexually dichromatic, and present delayed plumage maturation (Howell and Webb 1995; Hilty 2020;

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Chiver et al. 2024). Their natural histories are also similar, as they maintain territories year-round, either in pairs or in groups of up to eight individuals, with frequent changes of association among individuals and individual reversions of territorial tactics (Willis 1960a, 1960b; Chiver et al. 2024). They have complex social lives, and a poorly understood mating system defined as social monogamy (Chiver et al. 2024), with the occasional presence of reproductive helpers, usually unrelated to the breeding pair in red-crowned ant-tanagers (Sandoval 2007; Chiver et al. 2024). This social flexibility is associated with broad patterns of phenotypic expression among individuals (i.e., wide variation of morphological aspect) and reversibility of social strategies within the individual (Schradin 2013).

The median-crown stripe of both species is reported to be absent in juveniles and present in the definitive (adult) plumage, which is red in males and yellowish brown in females (Hilty 2020; Chiver et al. 2024). During examination of museum specimens and images among the Macaulay Library to study the molt of Cardinalidae species (Guallar et al. 2018, 2020), we verified that a median-crown stripe occurs in definitive males of all subspecies of these two ant-tanagers but that the definitive and formative (plumage resulting from the molt of the juvenile plumage; Howell et al. 2003) plumages of females and the formative plumage of males (which is yellowish brown) exhibited a great deal of median-crown stripe variation in both species, from lack of stripe to full bright yellow stripe. Our goal was to

estimate the frequency of occurrence of the median-crown stripe per sex and age in definitive females and formative birds of both sexes and investigate how sex and age correlate to median-crown development. Since variation in the occurrence and development of the median-crown stripe may be relevant to understanding the complex social life, behavior, and natural history of these two neotropical passerine species, we discuss its potential role using theories of delayed plumage maturation.

Methods

We gathered data from 172 specimens (82 of red-crowned and 103 of red-throated ant-tanagers) from Mexico, 12 from Central America, and two from Peru (see Supplementary Material Table S1). Since median-crown stripe development only varies in the formative plumage of both sexes and the definitive females (thus, in three age/sex groups), we discarded data from juveniles and definitive males from analyses. We eventually analyzed 39 red-crowned and 67 red-throated ant-tanagers.

Median-crown stripe showed ample variation, which we categorized as three obvious variants based on its development (Fig. 1): 0 = no stripe, 1 = intermediate stripe (ill-defined patch with only a mustard wash at base of crown feathers), and 2 = full stripe (well-defined patch with bright yellow crown feathers forming a wide central stripe). We

Fig. 1 Development of median-crown stripe in the red-crowned ant-tanager (specimens from Colección Nacional de Aves, Mexico DF). Top to bottom: P0024439 (intermediate; formative female) P009781 (full stripe; definitive female) P0024437 (no stripe; formative female) 29270 (definitive male). Also, notice differences in overall coloration



determined the age of every specimen using molt limits (Guallar et al. 2018) and sex based on that of the specimen labels (when available).

We estimated the effect of sex and age on the frequency of median-crown stripe variants fitting the following multinomial regression model for each species, which applies a Bayesian framework using WinBUGS (Supplementary Material; Imperial College and Medical Research Council 1996–2007; Ntzoufras 2009):

$$y_i \sim \text{Multinomial}(p_i, 1)$$

$$\varepsilon_i \sim \alpha + \beta_1 * \text{age}_i + \beta_2 * \text{sex}_i$$

$$p_i \sim \frac{\exp(\varepsilon_i)}{\text{sum}(\exp(\varepsilon_i))}$$

The multinomial distribution is an adequate approach to model random categorical variables with more than two possible outcomes, such as the three median-crown stripe variants defined. We specified low informative priors for β to account for the lack of previous knowledge (Rubin et al. 2013), ran 40,000 updates for three Markov chains, discarded the first 5,000 ones as burn-in, and thinned the outcome to 1 of each 10 updates to reduce autocorrelation (Meyn and Tweedie 2009). We monitored the Gelman-Rubin statistic to check model convergence (Gelman and Rubin 1992). Finally, we computed the mean occurrence, lower and upper credible intervals (2.5% and 97.5%) from the 3,500 final predicted values $\left(\frac{\text{updates} - \text{burn in}}{\text{thinning}}\right)$ for each median-crown stripe variant per age/sex group.

Given the large geographic ranges of these two ant-tanagers and the large subspecies variation they have, we regressed latitude on median-crown stripe to check whether there is any latitudinal trend per age/sex group within each species.

Results

Although quantification of the overall plumage coloration among formative birds is beyond the scope of this article, it varied in both sexes from yellowish brown (dominant) to reddish (infrequent), with no obvious pattern of association with the median-crown stripe variant (Fig. 1).

Median-crown stripe occurrence was highly probable in red-crowned ant-tanagers: it occurred in all definitive females, 93% formative males, and 32% formative females. Contrastingly, median-crown stripe had a low probability of occurrence in red-throated ant-tanagers: only occurred in 7% of definitive females and 15% formative males presented any, whereas it was absent in formative females

(Fig. 2). Median-crown stripe development increased with age and was reduced for formative females as compared with males (Fig. 2; Table 1). Formative males showed higher mean development than formative females in both species although differences were only significant for red-crowned ant-tanagers (Wilcoxon test: $W = 10$, $P = 0.009$). Conversely, definitive females had higher mean development than formative males in the red-crowned ant-tanager (Wilcoxon test: $W = 135$, $P = 0.025$), whereas definitive females had lower mean development than formative males in the red-throated ant-tanager (Wilcoxon test: $W = 205$, $P = 0.491$).

There were also significant differences in the frequency of median-crown stripe variants among the three subspecies of the red-throated ant-tanager although only for formative males (Chi-square test: $\chi^2_4 = 12$, $P = 0.017$; Table 2). A Bonferroni posthoc test indicated that differences were driven by the frequency of no-stripe among subspecies for this plumage ($P = 0.005$; Beasley and Schumacker 1995). This is consistent with the latitudinal trend we found among formative male red-throated ant-tanagers ($\beta = -5.21 \pm 1.02$, $P < 0.001$; Fig. 3), since only the southern subspecies *fuscauda* has median-crown stripe (at least among the three subspecies in our dataset; Table 2). However, these results should be taken with caution due to the small sample sizes.

Discussion

Our results are consistent with the classical age/sex bias of hierarchical dominance in temperate passerines, with males showing more striking plumage than females and the definitive plumage brighter than the formative plumages within each sex (Piper 1997). Variation of the median-crowned stripe in ant-tanagers may be mediated by environmental drivers, geographic distribution, diet, and even social environment (Laucht and Dale 2012; Ramírez-Barrera et al. 2019; Robles-Bello et al. 2022; Delhey et al. 2023). In fact, the latitudinal bias found among subspecies of the red-throated ant-tanager suggests that the occurrence and function of the median-crown stripe may differ between its subspecies. This is a limitation of this study implying that our results may not be generalizable to the subspecies of which we do not have information (10 of the red-crowned ant-tanager and three of the red-throated ant-tanager; Table 2).

Red-crowned ant-tanagers exhibit a remarkable variability within age/sex group (except juveniles and definitive males), suggesting that median-crown stripe likely plays a more complex role in this species than in the red-throated ant-tanager. Plasticity of definitive female and formative plumages in ant-tanagers may have evolved in parallel to their heterogeneous social environments (Tuttle 2003). The median-crown stripe could act as a signal amplifier of the overall coloration or be a stand-alone badge (Hasson

Fig. 2 Probability of occurrence of three median-crown stripe variants for three plumages of red-crowned (nDF = 34 nFF = 20 nFM = 13) and red-throated ant-tanagers (nDF = 22 nFF = 8 nFM = 9). Wide credible intervals associated with low sample sizes

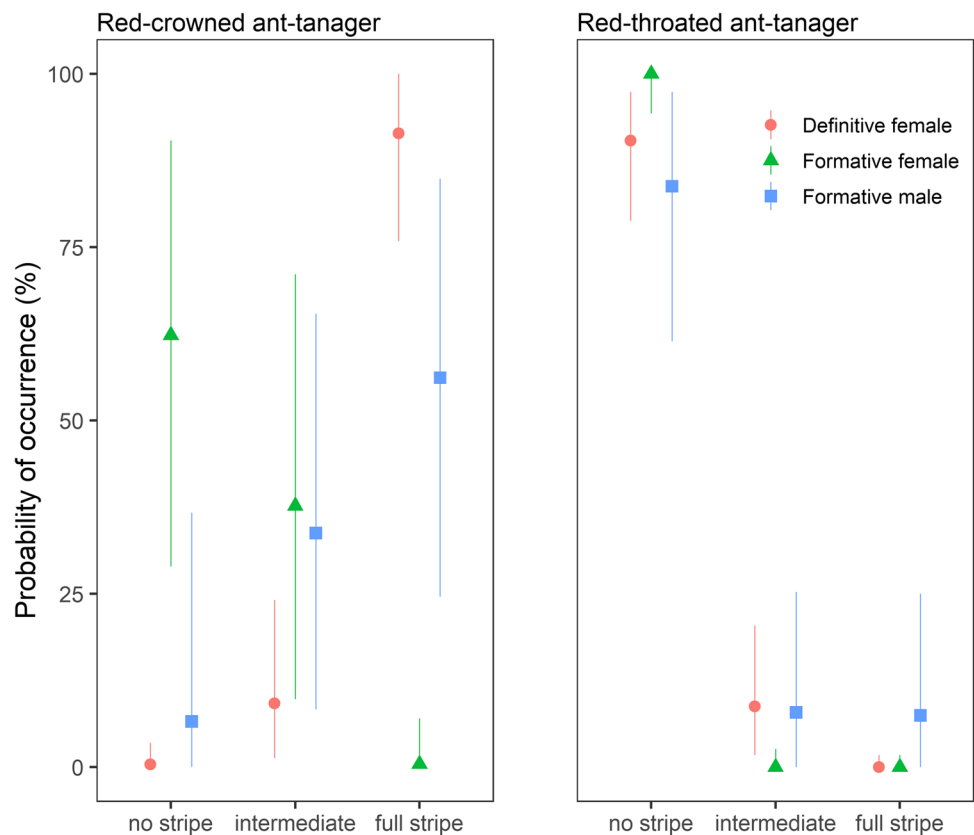


Table 1 Summary of the estimates (mean \pm sd [2.5%, 97.5% confidence intervals]) obtained from the multinomial bayesian analysis using definitive females and formative birds (juveniles and definitive males were excluded). Coefficients for the ‘no-stripe’ category were used as baseline

	Red-crowned ant-tanagers ($n = 42$)	Red-throated ant-tanagers ($n = 67$)
intercept _{full-stripe}	19.97 \pm 10.95 [3.84, 42.77]	-2.05 \pm 1.88 [-5.66, 1.15]
intercept _{intermediate}	15.44 \pm 11.02 [-1.32, 38.26]	-30.03 \pm 18.29 [-72.68, -4.7]
sex _{full-stripe}	-27.88 \pm 12.64 [-57.16, -9.60]	-19.19 \pm 15.86 [-59.65, -1.00]
sex _{intermediate}	-9.05 \pm 5.49 [-20.45, -0.72]	-5.66 \pm 16.52 [-43.10, 22.81]
age _{full-stripe}	18.94 \pm 12.03 [3.79, 50.06]	18.74 \pm 15.87 [0.25, 59.07]
age _{intermediate}	2.09 \pm 1.59 [-0.73, 5.56]	19.16 \pm 14.07 [0.61, 53.67]

1991; Senar et al. 1993), with the potential of behaviorally adjusting its conspicuousness (i.e., displaying or hiding it by raising or lowering crown feathers, respectively) and of shifting roles with time (Laczi et al. 2023). Interaction with overall coloration is particularly interesting due to the occurrence of delayed plumage maturation in these ant-tanagers (a trait likely found in dichromatic and cooperative breeding species; Beauchamp 2003). Three main hypotheses have been proposed to explain its occurrence: crypsis to reduce predation (Rohwer 1986; Rohwer and Butcher 1988), female mimicry to access resources inside other adult male territories (which can be considered a form of dishonest signaling; Brown and Brown 1988), and status signaling to reduce aggression from dominant

individuals (Lyon and Montgomerie 1986; Montgomerie and Lyon 1986).

Transition from the juvenile to the formative plumage in both sexes is highly consistent with the crypsis hypothesis in red-throated ant-tanagers because it largely remains unchanged. It is also consistent in both species with the female-mimicry hypothesis because the plumage becomes more similar to the definitive female plumage. During the non-breeding season, less-conspicuous median-crown stripes could help formative birds join already established territories (Willis 1960a, 1960b; Chiver et al. 2024), thus increasing winter survival (Berggren et al. 2004). During the breeding season, furthermore, formative males may reduce aggression from territorial definitive males (Senar

Fig. 3 Latitudinal trend in median-crown stripe development (0= no stripe, 1= intermediate, and 2= full stripe) per age/sex group in the red-crowned and the red-throated ant-tanagers. Sample sizes are small (see Table 2)

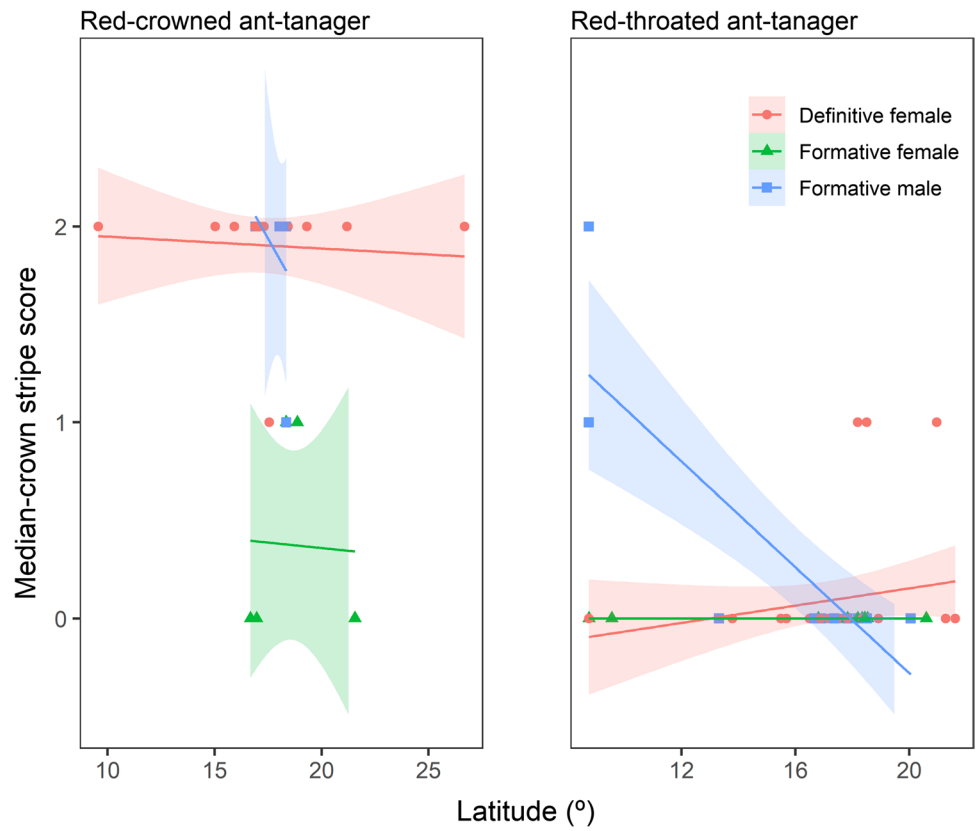


Table 2 Number of specimens per subspecies and plumage used in the analyses ($n=106$). Two specimens from Mexico lacked geographic information. Our dataset only contains definitive males of *Habia rubica nelsoni*, which therefore were excluded from analyses

(supplementary material table S1). Each cell contains the number of specimens assigned to the three median-crown stripe variants ordered by development: no stripe, intermediate, and full stripe

	Formative female	Formative male	Definitive female
<i>Habia rubica</i>			
<i>affinis</i>	1,1,0	0,0,2	0,1,9
<i>alfaroana</i>			0,0,2
<i>holobrunnea</i>	0,1,0	0,1,2	0,0,2
<i>peruviana</i>		0,1,0	0,0,1
<i>rosea</i>	2,0,0		0,0,2
<i>rubicoides</i>	2,1,0	0,0,1	0,1,4
<i>Driophlox fuscicauda</i>			
<i>fuscicauda</i>	3,0,0	0,1,1	3,0,0
<i>insularis</i>	5,0,0	3,0,0	3,1,0
<i>salvini</i>	11,0,0	7,0,0	25,2,0

et al. 1993), likely increasing their chances of benefitting from extra-pair copulations (Chiver et al. 2024), as predicted by the female-mimicry hypothesis. However, the formative plumages in males of both species largely lack the predicted transition toward more definitive male plumage that would reflect differences in fighting ability and dominance rank (Table 3). The latter transition is lacking even in those individuals that undergo a prealternate molt

(limited to a small percentage of the body feathers; Guallar et al. 2016; 2020). Therefore, the striking differences in the frequency of occurrence of the median-crown stripe in the formative plumage of ant-tanagers, especially in males, could combine camouflage and social interaction. The more pronounced variation of median-crown stripe in the red-crowned ant-tanager suggests a greater diversification of social strategies (e.g., reproductive helpers,

Table 3 Transition from juvenile to formative plumage in red-crowned (RC) and red-throated (RT) ant-tanagers and consistency with three hypotheses of delayed plumage maturation. Support varies between males (M) and females (F) and among median-crown stripe variants

Hypothesis	Transition predicted	Consistency
crypsis	no transition	RC: only no-stripe variant RT: yes (all F and more than 75% M)
female mimicry	to definitive F	RC: yes (M); only intermediate variant (F) RT: yes
status signaling	to definitive M	RC: no RT: no

territory defenders during winter, male intruders) in this species than in the red-throated ant-tanager.

Further studies are needed to infer the role of the median-crown stripe of ant-tanagers. The large variation across ant-tanagers (from an ill-defined patch in the black-cheeked ant-tanager *Driophlox atrimaxillaris* to a crest in the crested ant-tanager *Driophlox cristata*) suggests a diversification of roles. Also, experiments should be designed to elucidate how median-crown stripe variants fit in each species' social system (Chaine et al. 2018), and how they interact with overall coloration and with other plumage traits (e.g., the throat patch of the red-throated ant-tanager likely conveys a different information since it is lacking in other plumages; Boves et al. 2014). Although many other passerines show mark variants in formative and definitive female plumages, including species as diverse as bluethroat *Luscinia svecica* (Amundsen et al. 1997) and crescent-chested warbler *Oreothlypis superciliosa* (Guallar et al. 2009), the complex natural histories of ant-tanagers make them an interesting model for behavioral studies of passerine social systems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s43388-024-00223-y>.

Acknowledgements We are grateful to Dr. Adolfo Navarro and to MSc. Fany Rebón for allowing access to the specimen collection at Museo de Zoología Alfonso Herrera; We thank Carla Cicero at the Museum of Vertebrate Zoology, Berkeley, California, and Maureen Flannery of the California Academy of Sciences, San Francisco, California, for assistance and access to specimen collections. We are grateful to Dra. Patricia Escalante and MSc. Marco Gurrola of the Colección Nacional de Aves in Mexico City. We are also thankful to two anonymous reviewers and the editor for their comments.

Author contributions S.G. conceived the study analyzed the data and wrote the first manuscript. All authors collected data, commented on

previous versions of the manuscript, and read and approved the final manuscript.

Funding We do not have any funds to declare.

Data availability The data that support the findings of this study have been included as Supplementary Material Table S1.

Declarations

Ethical approval Data were obtained under authorization from natural reserves and museums.

Competing interests The authors declare no competing interests.

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