



Multiple signaling in a variable environment: expression of song and color traits as a function of ambient sound and light

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ABSTRACT

Many animals communicate using more than one signal, and several hypotheses exist to explain the evolution of multiple signals. However, these hypotheses typically assume static selection pressures, and previous work has not addressed how spatial and temporal environmental variation can shape variation in signaling systems. In particular, environmental variability, such as ambient lighting or noise, may affect efficacy (*e.g.*, detectability/perception by receivers) of signals. To examine how signal expression varies intraspecifically as a function of habitat characteristics, we evaluated relationships between spatial environmental variation and song and plumage color expression in a tropical songbird, the Red-throated Ant-tanager (*Habia fuscicauda*) in Panama. We recorded male ant-tanager song, plucked feathers to measure coloration, and quantified the acoustic and light environments from each male's territory. In addition, we took several morphological measurements from each male to assess the potential information content of song and plumage color. We found that males with redder and more saturated crown plumage occurred on darker territories, and males that sang shorter and lower frequency songs occurred on noisier territories. We also found that more colorful males tended to sing longer and lower frequency songs. Finally, we found that song and color correlated similarly with male morphology (*e.g.*, tarsus length, body mass). Altogether, these results indicate that spatial variation in the environment is related to male coloration and song, and that males might be optimizing color and song expression for their particular territorial environment.

Abstract in Spanish is available with online material.

Key words: birdsong; coloration; environmental variation; *Habia fuscicauda*; multi-modal signals; signal efficacy.

MANY ANIMALS COMMUNICATE USING A DIVERSITY OF SIGNALING TRAITS (*E.G.*, SONG, COLOR, VIBRATIONS). There are several proposed hypotheses to explain the function and evolution of multiple signals, both in terms of information content and signal efficacy (Endler 1992, Hebets & Papaj 2005). Hypotheses centered on the information content of multiple signals test whether the signals relay the same or different messages about individual quality (*e.g.*, aggression, health, parental effort: (Jawor & Breitwisch 2004, Jawor *et al.* 2004; food quality: Hölldobler 1999; or prey defense: Rowe & Halpin 2013)). In contrast, studies of signal efficacy have evaluated how properties of the environment, such as light (Endler & Thery 1996) or acoustics (Preininger *et al.* 2013), influence the transmission effectiveness and perceptibility of different signals independent of any information contained in the traits.

Many researchers have tested how environmental conditions affect the use of multiple signals (reviewed in Bro-Jørgensen 2010), but they have typically considered the environment to be static and paid little attention to environmental variability. Although some environments can be relatively static and signals in static environments may quickly evolve toward an optimum (Bro-Jørgensen 2010), animals often exist in dynamic environments that vary either spatially and/or temporally (*e.g.*, in

temperature, light availability, resource abundance). Environmental variation can strongly shift signal presentation/conspicuousness (Bortolotti *et al.* 2011, Sicsú *et al.* 2013, Hutton *et al.* 2015), receiver evaluation/choice (Chaine & Lyon 2008, Robinson *et al.* 2012, Hutton *et al.* 2015), and ultimately the costs and benefits of signaling with different traits (Robinson *et al.* 2008). Therefore, it is vital to account for environmental spatiotemporal variability when studying multiple signals (Bro-Jørgensen 2010). For example, understanding how environmental variation shapes the evolution of multiple signals could clarify why multiple signals evolve to reveal redundant information—*i.e.*, each signal could be a backup against environmental constraints on the other (Bro-Jørgensen 2010, Gordon & Uetz 2011, Uetz *et al.* 2013). Furthermore, signal efficacy can be greatly impacted by environmental variation, in that certain signals may be effectively transmitted only under specific conditions (*e.g.*, bright light, little background noise; Endler & Thery 1996, Uetz *et al.* 2010).

Birds serve as a useful system for studying how environmental variability can affect the expression and use of multiple signals, because many species possess multi-modal signals (*i.e.*, using different sensory modalities; Hebets & Papaj 2005). For example, many passerine birds have elaborate coloration and vocalizations, each of which can be greatly affected by environmental variation (*e.g.*, color: Endler & Thery 1996, Heindl & Winkler 2003a,b; song: Kirschel *et al.* 2009, Ríos-Chelén *et al.* 2012, Slabbekoorn 2013). Species with multi-modal signals permit investigation of

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how different environmental pressures influence each signal, because different signal modalities may not be affected by the same environmental pressure (Smith *et al.* 2008, Uetz *et al.* 2013). For example, light availability can vary considerably in space for both terrestrial and aquatic habitats (Endler 1993) and plays a critical role in color perception and communication (Endler 1992, Cronin *et al.* 2014). Spatial variation in light has caused some bird species to occupy different light environment niches within a similar geographic area to maximize each species' plumage color conspicuousness (Endler & Thery 1996, Heindl & Winkler 2003b, Gomez & Thery 2004). Ambient sound/noise can also vary spatially in environments such as tropical forests (Kirschel *et al.* 2009) and urban centers (Rfos-Chelén *et al.* 2012). Sustained, loud, and diverse background sounds can alter the length (Slabbekoorn & den Boer-Visser 2006), frequencies (Slabbekoorn & Peet 2003, Kirschel *et al.* 2009), and loudness (Brumm & Todt 2002) of acoustic signals in animals. Thus, by studying the influences of spatial changes in both light environment and ambient noise on visual and acoustic signaling, we can understand how dynamic environments influence multiple signal function and evolution.

In this study, we evaluated how spatial variation in sound and light environments was associated with the expression of song and color traits in a colorful neotropical songbird species, the Red-throated Ant-tanager (*Habia fuscicauda*). Red-throated Ant-tanagers are common, year-round, territorial, and socially monogamous passerines (Chiver *et al.* 2014) that reside in edges and understories of tropical rain forests from Mexico to Columbia. These habitats are environmentally heterogeneous in terms of both available light (due to canopy cover) and to noise coming from a variety of natural sources (*e.g.*, insects, birds, wind). They are sexually dimorphic in body size (males are larger) and plumage, with males possessing a red throat and crown and females possessing a yellow throat and brown crown; both sexes typically molt after the breeding season. While males and females aggressively defend territories together throughout the year, only males sing (*pers. obs.*). We tested if and how spatial environmental variation predicted song and color characteristics of resident male ant-tanagers. Specifically, we evaluated relationships between male ant-tanager plumage color and song and the noise and light environments of their territories. To further understand variation in these ant-tanager traits, we also tested for associations between song and plumage color parameters in individual males and compared the expression of each trait to various morphological measurements (*e.g.*, body mass, tarsus length), as a means of examining the potential information content of these traits (*e.g.*, redundancy, multiple messages) if they serve as signals.

If plumage color signals are difficult to transmit in low-light environments, we predicted that males with brighter, redder, and more saturated plumage would occupy darker territories, to maximize their conspicuousness/contrast (Gomez & Thery 2004, Gomez *et al.* 2007). Alternatively, if more colorful males are of higher quality, as in other red passerines (*e.g.*, house finches: Hill 1990, northern cardinals: Jawor *et al.* 2003), and if territories with more light gaps are highly prized (*i.e.*, more opportunity to

display in bright lighting conditions; Endler & Thery 1996), then brighter, redder, and more saturated males may be found on well-lit territories. In terms of vocal communication, we predicted that males found on territories with more ambient noise would sing lower frequency songs to maximize song efficacy against the higher frequency insect sounds (Kirschel *et al.* 2009, Hart *et al.* 2015), which are commonly found in tropical rain forests. Longer ant-tanager songs would also provide greater opportunities for the song to be heard through the background noise (Brumm & Slabbekoorn 2005, Brumm & Zollinger 2013). Habitat structure may also influence song characteristics, as lower frequency sounds are thought to travel further in the forest (Morton 1975, Marten & Marler 1977, Wiley & Richards 1978); thus, male ant-tanagers in more dense/closed (*i.e.*, greater canopy cover) territories may sing lower frequency songs.

In addition, we tested for relationships between the expression of the two male traits and various morphological measurements (*i.e.*, body mass, tarsus length, wing chord), to understand the potential information content (*i.e.*, current, developmental, and molting conditions, respectively) of song and plumage coloration. If the redundant signaling hypothesis is true, we predict that song and color will possess similar relationships to morphology, which could ensure successful information transfer to the intended receiver by at least one modality through the variable environment (Bro-Jørgensen 2010). Alternatively, if the forest understory presents different challenges to visual (Endler 1993) and acoustic communication (Morton 1975, Marten & Marler 1977, Wiley & Richards 1978), then song and plumage color expression may relate to different aspects of morphology, which would be more consistent with the multiple messages hypothesis.

METHODS

STUDY SYSTEM AND FIELD SITES.—We studied Red-throated Ant-tanagers during their breeding season (February–May 2013) in Soberania National Park, located in central Panama along the Panama Canal (9°07'N 79°42'W). Here, ant-tanagers primarily occur along forest edges, with territories along roads or trails. We used mist nets, male song playback, and a stuffed male model to capture adult males ($N = 13$) from their territories (note that we recorded songs and territory background noise for 18 males, but only had all sound/color data for 12 males total; further details below). At capture, we measured wing chord, tarsus length, and body mass for each male. Due to correlations between the three variables, we compressed them using principal components analysis (PCA; see Appendix S1 for additional details). Higher values of Morphology PC1 indicated males with smaller tarsi that weighed less, while higher values of Morphology PC2 indicated males that had shorter wings (Table S1). In addition, from each bird, we plucked nine throat feathers and three crown feathers from standardized positions on the body (see Appendix S2 for additional details).

PLUMAGE COLOR ANALYSIS.—Feathers from the throat and crown were separately stacked on top of each other to mimic their

natural, overlapping appearance on the bird and mounted on black matte cardstock, following methods similar to previous studies (Saks *et al.* 2003, McGraw *et al.* 2004, Meadows *et al.* 2011, Dakin & Montgomerie 2014, Lantz & Karubian 2016). To quantify plumage coloration of each patch, we used an Ocean Optics USB2000 spectrometer and a PX-2 pulsed xenon lamp (Dunedin, FL) with a probe perpendicular to the surface of the feather patch. We collected reflectance data for the throat and crown feathers of every male at approximately 0.4 nm intervals across the avian visual spectrum (300–700 nm). We took three measurements per plumage patch, and because all color variables were repeatable across the three measurements (interclass correlation (ICC) for all >0.8, $P < 0.001$), we averaged the three spectra to get an average spectrum for both the throat and crown of every male through the R package *pavo* (Maia *et al.* 2013). We then used visual models to assess each individual's throat and crown color through the eyes of a passerine bird with ultraviolet (UV) visual sensitivity (Vorobyev & Osorio 1998, Vorobyev *et al.* 1998, Govardovskii *et al.* 2000, Hart 2001, Hart & Vorobyev 2005). We used the average UV chromatic visual system and the European starling (*Sturnus vulgaris*) achromatic visual system, with ideal illumination and an idealized background, and employed the R package *pavo* (Hart 2001, Maia *et al.* 2013) to measure chromatic (see below) and achromatic (*i.e.*, luminance) characteristics of each color patch. Each color was plotted in tetrachromatic color space (Goldsmith & Butler 2003, Endler & Mielke 2005, Stoddard & Prum 2008), and we measured hue theta (ranges from π to $-\pi$, with orange around -0.15 and red around -0.5 ; thus increases from -0.15 to 0.5 indicate a redder hue), hue phi (ranges from $\pi/2$ to $-\pi/2$, with higher numbers indicating more UV coloration), and chroma (specifically $r_{vectors}$ with larger numbers meaning greater color saturation/purity; see Stoddard & Prum 2008 for details). We found that the variation in crown and throat coloration among males was biologically relevant and visually discriminable by the birds (see Appendix S3 for results).

We then used PCA to compress the four variables for crown and throat coloration independently into two non-correlated PC's (see Appendix S1 for additional details). Higher values of Crown PC1 indicate males with less chromatic, more orange crowns that reflect more UV light, while higher values of Crown PC2 indicate males with darker and less chromatic crowns (Table S1). Higher values of Throat PC1 indicate males with redder, more chromatic, and brighter throat patches, while higher values of Throat PC2 indicate males with less bright throats that reflect more UV (Table S1).

SONG ANALYSIS.—We used a Sennheiser ME66 shotgun microphone (Hanover, Lower Saxony, Germany) connected to a Marantz PMD670 digital recorder (sampling rate 44.1 kHz, 16-bit accuracy; Kanagawa, Japan) to record song of male ant-tanagers that we elicited by playing back one of two consistent recordings of a conspecific male song, chosen at random, on their territory throughout March and April 2013 (*sensu* Koloff & Mennill 2013, Ficken *et al.* 2002, Slabbekoorn *et al.* 2002, Feng *et al.* 2006, Uy & Safran 2013). Songs were recorded from a distance of 5–10 m

throughout the day, as the ant-tanagers would sporadically sing all day (pers. obs.). We presented the playback for 30–120 s (until a male started singing) and then recorded song from the territory-owning male for 5 min, which was enough time to capture the full repertoire of ant-tanager song (pers. obs.). This was repeated at least twice per male (average = 2.6 recording sessions per male) either within the same day or across a few days. We quantified minimum song frequency, maximum song frequency, peak song frequency (frequency with most power), song bandwidth, and song duration of every complete and clear song in each recording, using RavenPro v.1.4 (Cornell Laboratory of Ornithology, Ithaca, NY, USA; Spectrogram: Hann Window, DFT size = 256 samples), and then calculated an average for each metric per male (see Appendix S4 for additional song variable selection and processing details). To avoid redundancy among our correlated song frequency variables (see Table S2), we ran PCA on all frequency metrics (leaving song duration as an independent variable, due to lack of correlation with all frequency variables; Table S2), which resulted in two PC's. Higher values of Song PC1 indicated males that sang songs with lower maximum and peak frequencies and had smaller bandwidths, while higher values of Song PC2 indicated males that sang songs with higher minimum and maximum frequencies (Table S1).

MEASURES OF ENVIRONMENTAL VARIATION.—To broadly measure environmental lighting conditions, we quantified canopy cover on each male's territory (see Appendix S5 for justification). We took three skyward photographs in the same position using a Nikon D3100 DSLR camera (Tokyo, Japan) and fish-eye lens for three locations per territory (see Appendix S5 additional details), during either dusk or dawn, so that bright sunlight would not wash out the canopy in the photo. The camera was mounted on a 1-m tall tripod, so that all photos were taken at the same height from the ground. These nine photographs (three photos per location) were analyzed using Gap Light Analyzer (Frazer *et al.* 1999), which computes percent canopy cover of each photograph, and then we calculated an average canopy cover for each male. Canopy cover measurements were significantly repeatable across the three areas (ICC = 0.39, $P < 0.001$).

To measure environmental background noise (*i.e.*, sounds produced by local animals, wind), we recorded ambient sound on each male's territory for four hours in the morning (starting 30 min before sunrise) and for two hours in the afternoon (between 1600–1800 h) on the same day using an automated SongMeter device that contains two non-directional microphones (sample rate: 24 kHz, 16 bit; Wildlife Acoustics Inc., Concord, MA, USA). We selected these times of day to record noise based on behavioral observations (see Appendix S5), as we found these to be the times with the greatest ant-tanager vocal activity. The SongMeter was placed at the same locations used for photography described above, attached to the trunk of a tree, approximately 1-m off the ground. This device captures a 1-min recording every 15-min for the duration of the set recording time. Using RavenPro v.1.4 (Cornell Laboratory of Ornithology, Ithaca, NY, USA), we calculated average power (because ambient

noise frequencies overlapped with song frequencies—see Results) and peak frequency, to have similar measures to previous studies (e.g., Slabbekoorn & Peet 2003, Brumm & Slater 2006, Kirschel *et al.* 2009, Francis *et al.* 2011, Montague *et al.* 2012, Ríos-Chelén *et al.* 2012), of each 1-min recording and then calculated an average peak frequency and average power across all recordings per territory per day. All territories were recorded on at least one day throughout March and April (average = 1.6 days/territory). Average power and peak frequency measures for individual territories among days were significantly repeatable (average power ICC = 0.88, $P < 0.001$; peak frequency ICC = 0.74, $P = 0.016$); thus, for territories with multiple measurements, we averaged the peak frequency and average power of the two or more days. Although a male ant-tanager's songs could be part of the background noise recordings on his territory, we found that male song rate did not significantly co-vary with noise level on his territory (linear regression: $R^2 = 0.19$, $P = 0.14$). Finally, to account for temporal variation in ambient noise, we calculated the variation (standard deviation) in average power and peak frequency throughout the day for each territory.

STATISTICAL ANALYSES.—All statistical analyses were conducted using the statistical platform R (R Development Core Team 2012). For every intended correlation and multiple linear regressions, we tested the residuals for adherence to normality, and in cases where the assumption of normality was violated, we transformed the data using either logarithmic or square root transformations, which alleviated each violation of normality. We first tested for a correlation between canopy cover and ambient noise. For only 12 males did we have data for song, color, and morphology, so $N = 12$ for all analyses comparing the two signals and the signals with morphology. Ideally, we could have collapsed all variables into fewer multivariate tests, but due to our small sample size, we conducted separate analyses for the influence of the environment (spatial and temporal also separate) and morphology on color and song; as this avoids having too few animals/data points per explanatory variable in our analysis. Given our small sample size, we conducted power analyses for all multiple linear regressions to determine if any significant relationships found were likely to be true or false positives (Table S7).

To understand how spatial differences in sound and light environment predicted male ant-tanager traits, we used multiple linear regressions to test for relationships of song and color to ambient noise and canopy cover. We compared each male signal PC to the average power and peak frequency of the ambient noise and the average canopy cover percentage of each male's territory. Additionally, in a separate regression, we compared each male signal PC to the variation in average power and peak frequency of the ambient noise on each male's territory throughout the day. We also ran multiple linear regressions between male song and color variables, to assess potential relationships between the two signals. We did not control for the co-variation among male traits due to the opposite ways that song and color related to the environment and the lack of correlations between song

frequency and duration and crown and throat coloration. To understand if these signals were conveying information about body size, we used multiple linear regressions to test for relationships between a male's morphological traits and his song and color variables.

ETHICAL APPROVAL.—We obtained permits from all applicable international, national, and institutional levels to study these animals. All animal care and use on this project was conducted with approval from both Arizona State University and Smithsonian Tropical Research Institute International Animal Care and Use Committees. Permission to work with the ant-tanagers in Panama and to transport their feathers was granted by the Ministerio de Ambiente, Republic of Panama.

RESULTS

NOISE AND LIGHT LEVELS ACROSS TERRITORIES.—Average power of ambient sound across male territories ranged from 45.6 dB on the quietest territory to 60.4 dB on the loudest (mean \pm SE: 50.7 ± 1.06 dB). Peak frequency of ambient sound had an interquartile range from 516.8 Hz to 6374.0 Hz (3544.92 ± 111.0 Hz; max range: 172.3 Hz to 19810.0 Hz; Fig. 1I) and greatly overlapped with male Red-throated Ant-tanager song frequencies, which ranged from the lowest minimum frequency of 592.0 Hz to the highest maximum frequency of 3667.1 Hz (minimum frequency: 966.4 ± 7.3 Hz; maximum frequency: 2867.3 ± 11.1 Hz; Fig. 1I). Furthermore, the average standard deviation for noise average power on a territory was 4.7 dB, which is less than the range for noise average power across territories (range = 14.8 dB; max = 60.4 dB; min = 45.6 dB). Average standard deviation within a territory for noise peak frequency was 3000 Hz, which is also less than the range for noise peak frequency across territories (range = 4538.5 Hz; max = 5890.2 Hz, min = 1351.6 Hz). Canopy cover across male territories ranged from 78.4 percent on the least covered (*i.e.*, brightest) territory to 95.7 percent on the most covered (*i.e.*, darkest) territory (mean \pm SE = $87.0 \pm 1.42\%$). There was no significant relationship between canopy cover and ambient noise variables on individual territories (Correlation: $r < 0.3$ or $r > -0.3$, $P > 0.1$).

RELATIONSHIPS BETWEEN SIGNALING TRAITS AND ENVIRONMENTAL VARIATION.—Song frequency (Song PC2) was significantly negatively related to the average power of ambient sound on territories (Table 1; Fig. 1A), meaning that males on louder territories sang songs with lower maximum and minimum frequencies. Additionally, song length was significantly negatively related to average power of background sound on territories (Table 1; Fig. 1B). There were no other significant relationships between song and environmental characteristics (Tables 1 and S3).

Crown coloration (Crown PC1) was significantly negatively related to average canopy cover (Table 1, Fig. 1C), such that males with redder, more chromatic, and less UV-colored crowns were found on darker, more covered territories. There were no

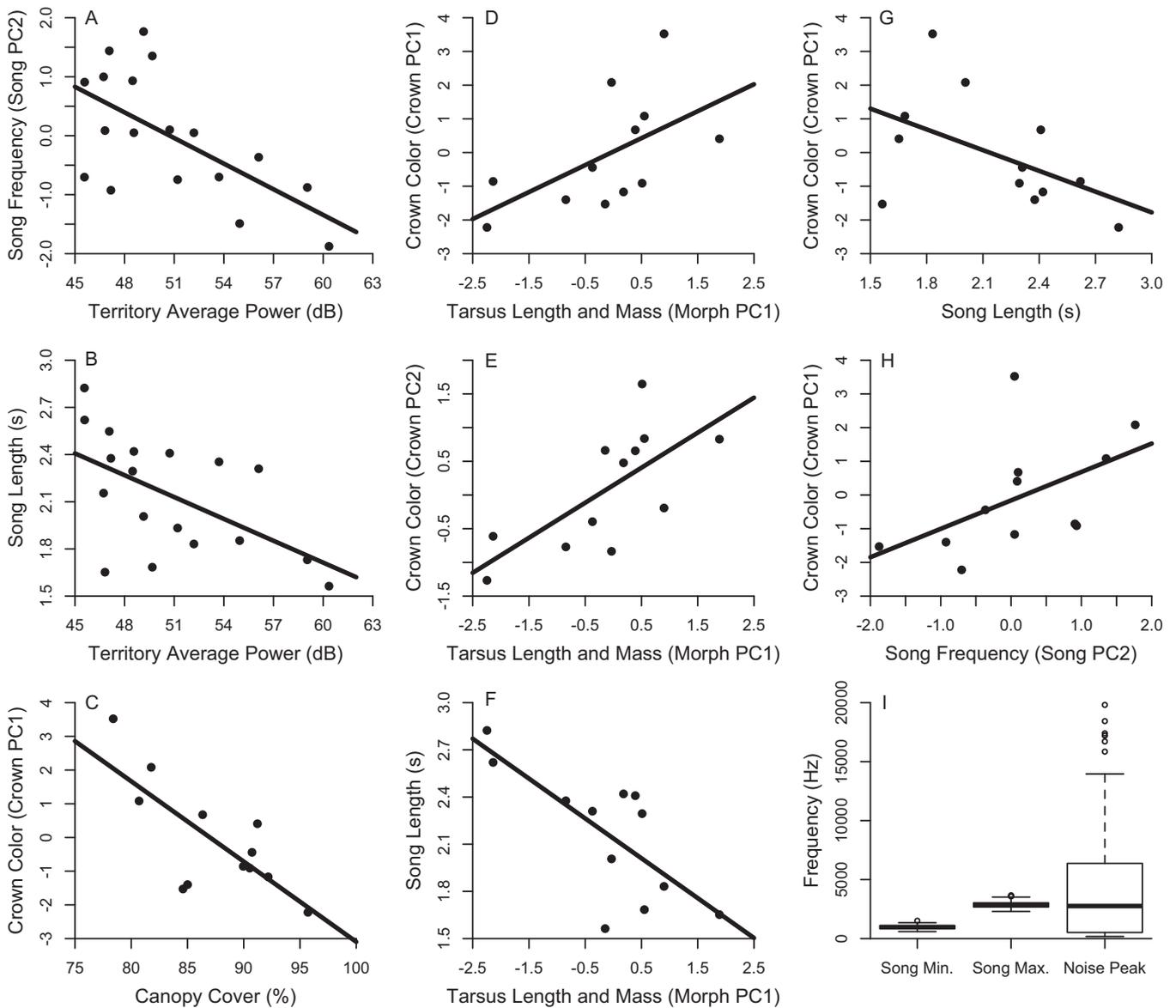


FIGURE 1. Results from multiple linear regressions (A-H) and summary data on song minimum frequency, song maximum frequency, and ambient sound peak frequency on individual territories (I). The average power of ambient sound on individual territories was (A) negatively related to male song frequency (Song PC2) and (B) average male song length. Higher values of Song PC2 indicate males with higher minimum and maximum frequencies. Males on louder territories sang shorter, lower frequency songs. (C) The average percent canopy cover on individual territories was negatively related to crown color (Crown PC1). Higher values of Crown PC1 indicate males with less red, more UV, and less chromatic crowns. Male tarsus size and mass (Morphology PC1 D and E) was positively related to male crown color (Crown PC1 and Crown PC2) and (F) negatively related to male song length. Higher values of Crown PC2 indicate males with less bright and less chromatic crowns. Higher values of Morphology PC1 indicate males with smaller tarsi and lower mass. Male crown color (Crown PC1) was (G) negatively related to song length and (H) positively related to song frequency (Song PC2). (I) Finally, male song frequencies (both the range of minimum and maximum frequencies) overlapped with the peak frequencies of ambient sound on individual territories. Boxes represent the inter-quartile range, with the black bars representing the median; whiskers represent the maximum and minimum values, without outliers, and the open circles represent the outliers.

significant relationships between canopy cover and other crown variables (Tables 1 and S3) or throat coloration (Table S4).

RELATIONSHIPS BETWEEN SONG AND COLOR.—Song frequency (Song PC2) was significantly positively correlated with crown

coloration (Crown PC1; Table 2; Fig. 1G), meaning that males with redder, more chromatic, and less UV-colored crowns sang songs with lower maximum and minimum frequencies. Additionally, song duration was significantly negatively correlated with crown coloration (Crown PC1; Table 2; Fig. 1H), meaning that

TABLE 1. Results from multiple linear regressions comparing environmental variables with song/crown color principal components; significant relationships are marked in bold.

Dependent variable	Independent variables	β	F/t	df	p
Song PC1	Whole model ($R^2 = 0.23$)		1.40	3,14	0.29
	Noise average power	0.06	0.73	1,14	0.48
	Noise peak frequency	<0.01	1.09	1,14	0.29
	Canopy cover	-0.12	-1.57	1,14	0.14
Song PC2	Whole model ($R^2 = 0.49$)		4.50	3,14	0.02
	Noise average power	-0.16	-3.40	1,14	<0.01
	Noise peak frequency	<0.01	0.50	1,14	0.63
	Canopy cover	-0.07	-1.72	1,14	0.11
Song	Whole model ($R^2 = 0.46$)		3.91	3,14	0.03
	Duration	0.04	-2.63	1,14	0.02
	Noise peak frequency	<0.01	0.16	1,14	0.87
	Canopy cover	0.03	1.79	1,14	0.10
Crown PC1	Whole model ($R^2 = 0.73$)		7.21	3,8	0.01
	Noise average power	-0.05	-0.63	1,8	0.55
	Noise peak frequency	<-0.01	-2.00	1,8	0.08
	Canopy cover	-0.22	-3.40	1,8	<0.01
Crown PC2	Whole model ($R^2 = 0.20$)		0.66	3,8	0.60
	Noise average power	0.03	0.47	1,8	0.65
	Noise peak frequency	<0.01	1.21	1,8	0.26
	Canopy cover	-0.02	1.22	1,8	0.79

males with redder, more chromatic, and less UV-colored crowns sang longer songs. There were no other significant associations among our other song and plumage metrics (Tables 2 and S5).

RELATIONSHIPS BETWEEN SONG/COLOR AND BODY SIZE.—Crown coloration (Crown PC1) was significantly positively related to body mass and tarsus length (Morphology PC1; Table 3; Fig. 1D), meaning that males with redder, more chromatic, and less UV-colored crowns weighed more and had longer tarsi. Crown PC2 was also significantly positively related to body mass and tarsus length (Morphology PC1; Table 3; Fig. 1E), meaning that males with more chromatic and brighter crowns weighed more and had longer tarsi. Additionally, song length was significantly negatively related to morphology PC1 (Table 3; Fig. 1F), meaning that males who weighed more and had longer tarsi sang longer songs. No other significant relationships were observed between male signaling traits and morphology (Tables 3 and S6).

DISCUSSION

We mapped the expression of song and plumage coloration in male Red-throated Ant-tanagers onto spatial environmental variation to test predictions about the efficacy of these putative signaling traits in a tropical forest songbird. We found that variation in some song and color parameters was linked to properties of the environment that are known to influence signal transmission. For

TABLE 2. Results from multiple linear regressions comparing song and crown color principal components; significant relationships are marked in bold.

Dependent variable	Independent variables	β	F/t	df	p
Crown PC1	Whole model ($R^2 = 0.64$)		4.74	3,8	0.04
	Song duration	-1.80	-2.75	1,8	0.03
	Song PC1	-0.21	-1.24	1,8	0.25
	Song PC2	-0.62	2.49	1,8	0.04
Crown PC2	Whole model ($R^2 = 0.25$)		0.90	3,8	0.48
	Song duration	-0.93	-1.35	1,8	0.21
	Song PC1	0.08	0.42	1,8	0.68
	Song PC2	0.11	0.40	1,8	0.70
Song PC1	Whole model ($R^2 = 0.49$)		0.49	4,7	0.20
	Crown PC1	-0.37	-1.34	1,7	0.22
	Crown PC2	0.51	1.04	1,7	0.33
	Throat PC1	-0.17	-0.58	1,7	0.58
Song PC2	Whole model ($R^2 = 0.52$)		1.92	4,7	0.21
	Crown PC1	0.20	1.13	1,7	0.30
	Crown PC2	0.18	0.58	1,7	0.58
	Throat PC1	-0.30	-1.63	1,7	0.15
Song	Whole model ($R^2 = 0.49$)		1.69	4,7	0.26
	Duration	-0.10	-1.38	1,7	0.21
	Crown PC2	-0.22	-1.73	1,7	0.13
	Throat PC1	0.05	0.68	1,7	0.52
Throat PC2		0.04	0.40	1,7	0.70

example, we found that more colorful males resided on darker territories, and males that sang shorter and lower frequency songs occurred on louder territories. These results are consistent with the signal efficacy hypothesis—that animals optimize signal contrast and conspicuousness against their territory's lighting conditions and/or background sounds.

Our findings that redder and more saturated males were found on darker territories corroborates previous comparative work that found that understory birds were more likely to be red, as colors rich in long wavelengths contrast better with the understory background in the forest-shade light environment (Endler 1992, Gomez & Thery 2004, Gomez *et al.* 2007). However, this previous work focused on interspecific comparisons of color conspicuousness and contrast across different light environments, whereas we detected similar dynamics between the light environment and coloration within a species. Other work has found that some understory birds seek forest gaps in which to display their colorful plumage (Endler & Thery 1996, Heindl & Winkler 2003a,b), but this would not explain our relationship where more colorful males have more covered territories, as more covered territories should have fewer light gaps. We propose two possible explanations for our observed relationship. One is that territories with more canopy cover offer some alternative benefit, such as more food (*e.g.*, fruit, insects) or safety from predators, and that more colorful males are better able to secure these territories. Alternatively, males might be under a

TABLE 3. Results from multiple linear regressions comparing song/crown color principal components with morphological principal components; significant relationships are marked in bold.

Dependent Variable	Independent variables	β	F/t	df	p
Crown PC1	Whole model ($R^2 = 0.56$)		5.65	2,9	0.03
	Morphology PC1	0.79	2.51	1,9	0.03
	Morphology PC2	0.79	2.19	1,9	0.06
Crown PC2	Whole model ($R^2 = 0.51$)		4.72	2,9	0.04
	Morphology PC1	0.52	3.01	1,9	0.01
	Morphology PC2	-0.14	-0.67	1,9	0.52
Song PC1	Whole model ($R^2 = 0.28$)		1.79	2,9	0.22
	Morphology PC1	0.14	0.37	1,9	0.72
	Morphology PC2	-0.81	-1.86	1,9	0.10
Song PC2	Whole model ($R^2 = 0.36$)		2.54	2,9	0.13
	Morphology PC1	0.15	0.63	1,9	0.54
	Morphology PC2	0.57	2.15	1,9	0.06
Song Duration	Whole model ($R^2 = 0.66$)		8.54	2,9	<0.01
	Morphology PC1	-0.26	-3.79	1,9	<0.01
	Morphology PC2	0.14	1.74	1,9	0.12

receiver-imposed handicap (proposed in Hutton *et al.* 2015), where males that contrast better in less optimal light environments (and potentially are singing in territories with more noise–song frequency overlap) are in better condition or more preferred by females. Additionally, the negative relationship between canopy cover and UV coloration makes sense due to the reduction in UV light in the forest understory and corroborates previous work (Endler 1992, Gomez *et al.* 2007, Gomez & Thery 2004, but see Smith *et al.* 2008). Interestingly, we found no relationship between canopy cover and throat coloration, and crown and throat color do not correlate (see methods). We suggest that throat color might be more of a short-distance signal (*e.g.*, for up close presentation ventrally to mates during courtship), whereas crown color is more detectable from afar and thus shaped by general environmental conditions; however, further work is needed to test this hypothesis.

Previous work evaluating environmental impacts on birdsong has focused on constraints on song transmission (*e.g.*, Morton 1975, Wiley & Richards 1978) or ambient noise in urban environments (see Table 7.3 in Brumm & Zollinger 2013). More recently, ambient noise in natural environments has been studied by comparing species (Tobias *et al.* 2010, Weir *et al.* 2012) or populations (Slabbekoorn & Smith 2002) across habitats, where different noise regimes lead to different shifts in song frequency. In the present study, we focused on a single population of birds and found that males on louder territories sang lower frequency songs in a natural, tropical rain forest environment. Our results are consistent with other work on forest-dwelling birds (*e.g.*, Green Hylia, *Hylia prasina*; Kirschel *et al.* 2009), but the work in *H. prasina* evaluated changes in frequencies across larger environmental gradients (*i.e.*, elevation, rainfall). Insect and other animal sounds were loud and constant at our field sites (unpubl. data), although we did not specifically

identify each source of noise, and previous work has suggested that these biotic sounds, especially those in tropical forests such as cicada song frequencies (Hart *et al.* 2015), can shape song frequency adjustments in birds (Lengagne *et al.* 1999, Brumm & Zollinger 2013, Lenske & La 2014, Hart *et al.* 2015). While the peak frequency of the ambient noise did not relate to male song frequency, we found that peak frequencies of ambient noise did overlap with male ant-tanager song frequencies, suggesting that louder ambient noise could affect ant-tanager songs. Cicadas and other insects typically produce high frequency songs (Hart *et al.* 2015), so we would expect selection to favor lower frequency songs in birds that share this sound space, to avoid overlap or being drowned out (Kirschel *et al.* 2009); thus, the louder the insects, the stronger the selective pressure on song of male ant-tanagers. While we did not measure song amplitude in ant-tanagers, passerine birds that sing louder songs also tend to sing with higher frequencies, due to the relationship between frequency and amplitude (Nemeth *et al.* 2013), so it seems that these forest-dwelling birds are not simply increasing their amplitude to escape competition with ambient noise. The reduction in song frequency might be an alternative strategy for birds to avoid noise competition, or this may be the only successful strategy for tropical forest-dwelling birds to escape ambient noise. Finally, we found no relationships between song frequency and canopy cover, suggesting that forest density or closure is not a strong driver of song frequency variation in these birds.

Interestingly, we found that males on louder territories also sang shorter songs, which is not what we predicted and contradicts other work from natural environments (Brumm & Slabbekoorn 2005, Smith *et al.* 2008, Brumm & Zollinger 2013). In fact, humans, mammals, and birds have all been found to increase the duration of their songs/speech with noise (see Brumm & Slabbekoorn 2005, Brumm & Zollinger 2013, and references therein). However, our results parallel what is often found in birds affected by anthropogenic noise (see Table 7.3 from Brumm & Zollinger 2013). For example, previous work on great tits (*Parus major*) and European robins (*Erithacus rubecula*) found that birds sang shorter songs in cities or forests near busy highways, respectively (Slabbekoorn & den Boer-Visser 2006, Montague *et al.* 2012). Therefore, singing shorter songs in louder environments may be an alternative tactic to convey short packets of information through periodic noise gaps.

The relationships we uncovered between song and plumage color expression in male ant-tanagers suggest that, while transmission properties of the environment might influence these traits, there may also be some trade-offs between song and color expression. Redder and more saturated males sang lower frequency songs, which suggests that both traits are under selection for successful transmission in the environment based on previous work demonstrating that longer-wavelength colors and lower frequency songs are more conspicuous in forest understories (Morton 1975, Marten & Marler 1977, Wiley & Richards 1978, Endler 1992, Gomez & Thery 2004, Gomez *et al.* 2007). However, males with redder and more saturated plumage also sang longer songs, which, based on our finding that males on louder territories sang shorter songs, suggests an efficacy trade-off between

color and song. These contradicting results demonstrate the complexity of the relationships between signals and the environment and merit further exploration to tease apart the synergistic or antagonistic selection pressures on the efficacy of visual and acoustic signals.

We found several relationships between male ant-tanager song and color and our measures of body size, which align with predictions of the redundant signal hypothesis (Hebets & Papaj 2005), although not in the way we originally predicted. Males that weighed more and had longer tarsi had redder, more saturated, and brighter crowns and sang longer songs. These relationships suggest that both song and crown color might convey similar information about male size and potentially male quality, although controlled tests of signal content and use are needed to confirm this. If birds in noisier environments sing shorter songs as a way to communicate effectively through the noise, then these results also suggest that larger males are more successful at visual signal efficacy over acoustic signal efficacy, because they sing longer songs but have brighter, more chromatic, longer-wavelength colors, which should be more conspicuous in the understory (Endler 1992, Gomez & Thery 2004, Gomez *et al.* 2007). However, if longer songs help birds effectively communicate through noise, which has been found in several species (Brumm & Slabbekoorn 2005, Brumm & Zollinger 2013) or in individuals occurring in less disturbed and more mature forests (Smith *et al.* 2008), then males that are brighter, more colorful, and sing longer songs would be more effective in both modalities. Either way, our results provide some support for the idea that animals in dynamic environments may have evolved multiple signals to ensure signal transmission under variable environmental conditions.

In conclusion, we demonstrate the importance of understanding how spatial variation in the environment can affect the expression of multiple signaling traits. Variation in song and color signals of male Red-throated Ant-tanagers closely tracked variation in both ambient light and sound among territories. By studying a single species/population, we provide finer-scale resolution of the link between environmental variation and signaling trait expression than prior comparative work. We hope that future studies on multiple signals will incorporate spatial and temporal variability in the environment, so that we can continue to improve our understanding of how environmental changes, many of which are rapid and human-induced, can influence communication systems of wild animals.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1j81k> (Simpson & McGraw 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Principal components analyses.

APPENDIX S2. Feather plucking details.

APPENDIX S3. Plumage just noticeable differences.

APPENDIX S4. Song variable selection and processing.

APPENDIX S5. Canopy cover justification and methods.

TABLE S1. *Principal components used from independent analyses on song frequency, throat color, crown color, and morphological variables.*

TABLE S2. *Correlation coefficients among song metrics for individual males.*

TABLE S3. *Results from multiple linear regressions comparing within-territory noise variation with male song and crown-color variables.*

TABLE S4. *Results from multiple linear regressions comparing light and sound environmental variables and male throat-color variables.*

TABLE S5. *Results from multiple linear regressions comparing between male song and throat-color variables.*

TABLE S6. *Results from multiple linear regressions between throat color variables and morphological measurements.*

TABLE S7. *Results from power analyses of each multiple linear regression.*

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