Male Red-winged Blackbirds (Agelaius phoeniceus) respond with greater intensity to epaulets with UV reflectance

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Male Red-winged Blackbirds (*Agelaius phoeniceus*) respond with greater intensity to epaulets with UV reflectance

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ABSTRACT—Male Red-winged Blackbirds (*Agelaius phoeniceus*) have red epaulets that are used as badges for intrasexual competition for territory acquisition and defense. Red epaulets reflect very little across ultraviolet (UV) wavelengths (300–400 nm) yet most birds, including Red-winged Blackbirds, are visually sensitive to UV light. Here, we conducted a field experiment to test if adding UV reflectance (UV+) to epaulets changed the effectiveness of signals to receivers relative to control epaulets. We constructed blackbird models with an epaulet made from red felt that reflected both long-wavelength (i.e., red) and UV wavelengths (UV+). To half of the models we applied sunscreen over the epaulets to block UV reflectance (UV–) and therefore mimic reflectance spectra of natural epaulets. UV+ and UV– models, along with small playback recorders playing *oak-a-lee* calls, were presented in established territories of male Red-winged Blackbirds. UV+ models received significantly more song flight displays (2017) and song spread displays (2019) from territorial males. Two territorial males physically attacked UV+ models but none attacked UV– models. To our knowledge, this is the first field experiment to add UV color to a plumage signal, resulting in a behavioral response from wild birds, raising questions for future research to explore a potential pre-existing visual bias for UV coloration in Red-winged Blackbirds and potential phylogenetic constraints on expression of UV reflectance of epaulets. *Received 18 October 2018. Accepted 12 March 2020.*

Key words: signal evolution, territory defense, ultraviolet color

Los machos del tordo *Agelaius phoeniceus* responden con mayor intensidad a charreteras con reflectancia ultravioleta

RESUMEN (Spanish)—Los machos del tordo *Agelaius phoeniceus* tienen charreteras rojas que utilizan como distintivos en la competencia intrasexual por adquisición de territorio y defensa. Las charreteras rojas reflejan muy poco de las longitudes de onda ultravioleta (UV, de 300–400 nm) si bien la mayoría de las aves, incluidos estos tordos, son visualmente sensibles a la luz UV. Llevamos a cabo un experimento de campo para probar si la adición de reflectancia ultravioleta (UV+) a las charreteras cambia la efectividad de las señales hacia sus receptores con relación a charreteras control. Construimos modelos de tordo con charreteras hechas de fieltro rojo que reflejaban rojos con longitudes de onda largas y longitudes de onda UV+. A la mitad de estos modelos les aplicamos bloqueador solar sobre las charreteras para impedir la reflectancia ultravioleta (UV–) y con ello imitar la reflectancia espectral de charreteras naturales. Los modelos UV+ y UV–, junto con pequeñas grabadoras que tocan los llamados *ouc-a-lii*, fueron expuestos en territorios de tordos machos establecidos. Los modelos UV+ recibieron un número significativamente mayor de despliegues "canto en vuelo" (2017) y despliegues "canto extendido" (2019) por parte de machos territoriales. Dos machos territoriales atacaron físicamente los modelos UV+ aunque ninguno atacó a los modelos UV–. Por lo que sabemos, este es el primer experimento de campo para agregar color UV a una señal de plumaje para obtener una señal de comportamiento de aves silvestres, lo que genera nuevas preguntas a investigarse en el futuro como explorar el potencial sesgo visual por la coloración UV y las potenciales limitaciones filogenéticas en la expresión de la reflectancia UV de sus charreteras.

Palabras clave: color ultravioleta, defensa de territorio, evolución de señales

Bird plumage has been intensively studied for communication in displays of resource holding potential, mate quality, and social status (e.g., Hill 1991). Carotenoid-based pigments signal successful foraging history and immunocompetence, and detection of these signals relies on sensory biology (Hill 1991, Hill et al. 2002). Most birds have 4 classes of cone cells conferring color vision, with peak sensitivities in long, medium, short, and ultraviolet (UV) wavelengths (Chen et al. 1984, Chen and Goldsmith 1986, Hart and Hunt 2007). Carotenoid-based pigments generally reflect strongly in the long wavelengths (i.e., appearing red/orange/yellow), with a secondary peak of reflectance in the UV (Shawkey and Hill 2005).

An exception to this general pattern is the red epaulet of Red-winged Blackbirds (*Agelaius phoeniceus*). Feathers that contribute to red epaulets of Red-winged Blackbirds contain 5 carotenoids (in trans form): canary xanthophyll

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A, astaxanthin, lutein, zeaxanthin, and canthaxanthin (McGraw et al. 2004). Epaulet feathers also contain 2 melanin pigments: eumelanin and phaeomelanin that absorb across visible light, and also in UV wavelengths (McGraw et al. 2004). The combination of carotenoids and melanins produce feathers that reflect strongly in the long wavelength part of the spectrum (600–700 nm), but reflect very little in the UV (<400 nm) part of the spectrum (Götmark 1996, Eaton 2006, Yasukawa et al. 2009b).

The epaulet of male Red-winged Blackbirds is used in intrasexual contests over territory acquisition and defense. Epaulet length is an important determinant of social dominance (Searcy 1979, Eckert and Weatherhead 1987). Males with blackened epaulets lose their territory (Peek 1972, Smith 1972) but ultimately may do just as well as control males (Westneat 2006, Yasukawa et al. 2009b, 2010), whereas males with reddened epaulets receive more attention from females and more displays from males (Yasukawa et al. 2009a), and models with enlarged epaulets are avoided by intruders (Røskraft and Rohwer 1987).

Underlying selective causes for the atypical biochemical composition of Red-winged Blackbirds resulting in red-colored epaulets without any peak reflectance of UV wavelengths are not well understood (McGraw et al. 2004). Here, we conducted a field experiment to test for a behavioral response to adding UV reflectance to Red-winged Blackbird epaulet coloration. We presented territorial males with models representing male intruders with "normal" epaulet coloration (UV–, hereafter referred to as "controls") and enhanced-UV epaulet coloration (UV+). Given the visual sensitivity of these birds to UV wavelengths (Chen et al. 1984, Chen and Goldsmith 1986, Hart and Hunt 2007, Ödeen and Håstad 2013), responses of males to UV+ models could be more, equally, or less aggressive relative to controls, indicating a commensurate perception of threat to territory defense by the resident male. For example, if UV+ models are not recognized as potential intruders because of their novel appearance (i.e., different species), or are perceived as an individual with a maladaptive color signal, we would predict little to no response from territorial males. On the other hand, an increased aggressive response to UV+ models compared to controls (UV–) might indicate visual recognition of an honest signal of social status (e.g., a super-normal stimulus of plumage color). If, indeed, UV+ epaulet coloration represents a visual signal with increased efficacy in territorial interactions, this raises interesting questions about evolutionary scenarios for it lacking in the plumage repertoire of this species.

Figure 1. Model Red-winged Blackbirds used in this study, and the pole and plastic bag apparatus for presenting the model and playback recorder in territories in the field. Photo by Laura Domine.

Methods

Construction of two models

Black cotton socks were stuffed with paper towel and sewn to crudely resemble male Red-winged Blackbirds. Epaulets were created by sewing on red and yellow felt (Fig. 1). These models were affixed atop 3 m lengths of polyvinyl chloride (PVC) poles with stainless steel wire. In addition, a playback recorder (VN-8100 PC, Olympus Digital Voice Recorder) was inserted into a plastic bag and suspended immediately below the model. The recorder played a recording of an *oak-a-lee* call in a continuous loop. The recording used in 2017 contained 6 *oak-a-lee* calls in a 25 s period. The recording used in 2019 sampled a different male that performed the *oak-a-lee* call 8 times over 42 s (additional calls from neighboring males can be heard faintly in the background). We acknowledge that our use of a single individual male call may have pseudoreplication implications.

We collected representative color data from a sample of the red felt, a sample of the red felt treated with 50-SPF sunscreen, and red epaulet feathers from a Red-winged Blackbird study skin.

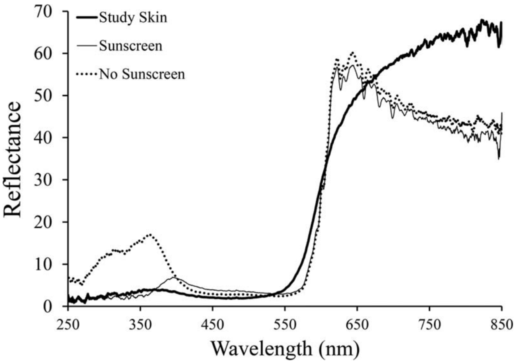

Figure 2. Epaulet reflectance from a Red-winged Blackbird study skin (solid heavy line), the model without sunscreen applied, UV+ (dotted line) and the model with sunscreen applied, UV– (solid thin line).

For each sample, spectral reflectance data were acquired using an Ocean Optics S-2000 fiber-optic spectrometer and OOIBase32 software (Dunedin, Florida, USA), equipped with an R200-7-UV/VIS reflectance probe (fiber diameter = 200 μm) and a PX-2 pulsed xenon light source, and were calibrated against a Spectralon white reflectance standard with the following settings: msec = 100, average = 10, boxcar = 5. The reflectance probe was housed in a black rubber tube, which blocked ambient light, and maintained a constant distance (~2 mm) from the probe to the measured surface, and maintained a constant 90° measurement angle relative to a sample's surface. Raw spectral reflectance data from these 3 samples were then imported into Excel and plotted (Fig. 2). Red felt used on models reflected strongly in the long-wavelength part of the spectrum (i.e., "red"), but also had a secondary peak of reflectance in the UV part of the spectrum (Fig. 2). The long-wavelength (red) end of reflecting spectra of our models did not perfectly match the red of the natural epaulet but, we assume, was close enough to the natural epaulet to evoke responses, and in any case, the red of the felt models was present in both UV+and UV– treatment and therefore did not contribute to differential responses to model types. When sunscreen was applied to the felt, UV reflectance was largely blocked, rendering a reflectance spectrum of felt that is very similar to that of a natural epaulet, in reflecting strongly only in the long wavelength part of the spectrum (Fig. 2). Thus, red felt was treated with sunscreen (UV–) on half the models (*n* = 10 in 2017; *n* = 18 in 2019), and left untreated (UV+) on half of the models (*n* = 10 in 2017; *n* = 18 in 2019).

Study site and field protocol

Our study site was a wetland of approximately 48 ha in an area located in Two-Inlets State Forest, north-central Minnesota, USA (47°02′43.2″N, 95°18′05.3″W, elevation 470 m). Male Red-winged Blackbird territories were approached by canoe, and a PVC pole bearing a model and a playback recorder was planted in the approximate center of the territory. We recorded behaviors (based on an ethogram in Yasukawa and Searcy [1995]) for 10 min, including responses by resident territory holders (song spread, song flight, and physical attack) and by resident females (approaches) (Table 1). Each territorial male was tested twice, one presentation following immediately after the other, with half of the males receiving the UV+ model first, and the other half receiving the UV– model first to control for an effect, if any, of order of presentation. We tested responses from 10 territorial males in June 2017 (i.e., 5 UV+ with call playback followed by UV– with call playback, and 5 UV– with playback followed by UV+ with call playback), and an additional 18 territorial males in May 2019 (i.e., 9

Table 1. Description of behavioral responses recorded for territorial Red-winged Blackbirds to blackbird models presented as intruders (descriptions after Yasukawa and Searcy 1995).

Actor	Behavior	Description
Territorial male	Song spread	Epaulets exposed as song is delivered, epaulet feathers partially or fully erected, wings extended partially or fully and curved downward
	Song flight	Male erects contour feathers, especially epaulet feathers, spreads and lowers tail, and beats wings slowly and deeply so that he flies at minimum speed
	Physical contact	Contacting the model with either the bill or feet
Resident female	Approach	Approach to within 1 m of the model

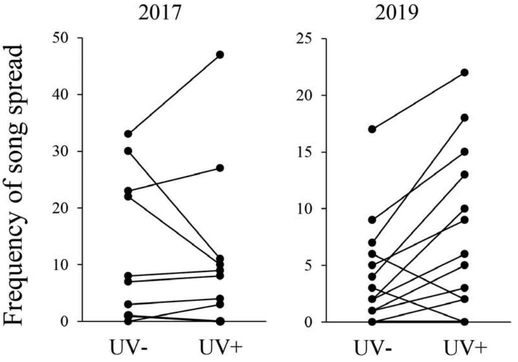

Figure 3. Reaction norms for song spread displays in response to model males without (natural mimic control) and with ultraviolet reflectance for each year of the study. Heavy lines indicate 2 reactions norms superimposed upon each other.

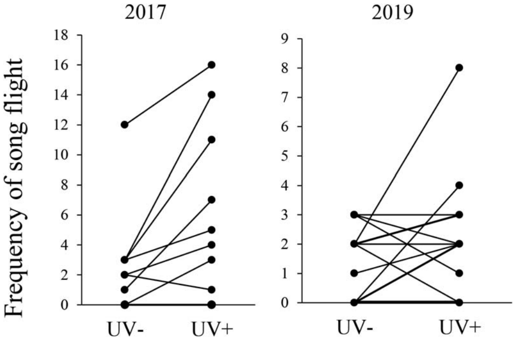

Figure 4. Reaction norms for song flight displays in response to model males without (natural mimic control) and with ultraviolet reflectance for each year of the study. Heavy lines indicate 2 reactions norms superimposed upon each other.

UV+ with call playback followed by UV– with call playback, and 9 UV– with playback followed by UV+ with call playback).

Data analysis

We used male and female residents on each territory as their own controls by comparing differences in responses to each model type within each territory using a Wilcoxon matched-pairs signed-ranks test (SPSS 23, IBM Corp., Armonk, New York, USA). All reported *P* values are based on 2-tailed probability distributions.

Results

The 2 most common behavioral responses to models by territorial males were song spreads and song flights. In 2017, UV reflectance did not affect the frequency of song spread behavior but it did increase frequency of song spreads in 2019 (Fig. 3, Table 2). In 2017, territorial males performed significantly more song flights to UV+ models but this result did not surpass the threshold of statistical significance in the 2019 data set (Fig. 4, Table 2). There were 2 instances of physical contact with models in 2017, in both cases to UV+ models. Physical contacts with models did not occur in 2019. Female approaches to models were not affected by the presence of UV reflectance in the epaulet (Table 2).

Discussion

Resident territorial males responded more intensively to UV+ models than they did to the UV– models that mimicked natural reflectance of Red-winged Blackbird epaulets. This occurred over 2 field seasons. The current study is the first to our knowledge to add, or enhance, UV reflectance to a carotenoid-based signal and demonstrate increased aggression from free-living wild birds.

Table 2. Frequency of behavioral responses of territorial Red-winged Blackbirds to models. Outcome of Wilcoxon signed ranks tests for data collected 2017, 2019, and for both years combined for song flights, song spreads, and female approaches. Tests with $P < 0.05$ are bolded.

	2017			2019			2017 + 2019		
	z	*n*	*P*	*z*	*n*	*P*	*z*	*n*	*P*
Song flight	2.838	10	**0.017**	1.239	18	0.215	2.740	28	**0.006**
Song spread	0.361	10	0.718	2.403	18	**0.016**	1.888	28	0.059
Female approach	0.184	10	0.854	1.378	18	0.168	0.982	28	0.326

Previous tests of the effect of UV on efficacy of plumage to evoke an effect in receivers has been to reduce or eliminate the UV component of plumage color with an already existing UV signal (see Remy et al. 2010 for an exception). Visual detection of UV color signals, and behavioral response to manipulation of these, are well documented among animal taxa, including fish (e.g., Macías-Garcia and de Perera 2002, Rick and Bakker 2008, Sabol et al. 2017), lizards (e.g., Stapley and Whiting 2006), spiders (e.g., Lim and Li 2006), and birds (e.g., Cuthill et al. 2000, Eaton and Lanyon 2003, Alonso-Alvarez et al. 2004, Delhey et al. 2007, Zampiga et al. 2008). The application of sunscreen rendered the felt to pure "red" (by blocking the UV reflectance), similar in color to the real feathers of a Red-winged Blackbird epaulet. (It is worth noting that, to the human eye, epaulet color of the models was not affected by application of sunscreen.) This new "UV + red" color evoked a more intense behavioral response than did pure red, indicating its potential to signal information. UV+ models might then indicate a pre-existing bias favoring signals that include the UV portion of the spectrum (Endler and Basolo 1998, Ninnes and Andersson 2014). The biochemistry underlying epaulet coloration in the *Agelaius* clade represents a constraint on the evolution of a carotenoid–melanin plumage signal that has a UV-color component. Ancestral state reconstruction of plumage colors indicates that the common ancestor of the *Agelaius* clade possessed epaulet coloration defined by high levels of "long-wavelength" reflectance (red, yellow, or brown epaulets) and low levels of "UV reflectance" (McGraw et al. 2004, Eaton 2006).

Many studies have documented the role of epaulet coloration and size in relation to successful territory defense in Red-winged Blackbirds, which is the main determinant of reproductive success in terms of within-pair mates and total number of fledglings from within-pair and extra-pair fertilizations (Røskaft and Rohwer 1987, Westneat 1995, Yasukawa and Searcy 1995, Yasukawa et al. 2009a, 2009b).

Alternatively, intrasexual territorial interactions among males could explain the lack of UV color in Red-winged Blackbirds. If UV+ models were perceived as subnormal and relatively weak rivals that emboldened territorial males to confront them more frequently relative to controls with song flight and song spread displays, and on 2 occasions, physical attack, this increased aggression could represent a selective mechanism against UV reflectance as a component of color in epaulets. Furthermore, in some species, males bear a badge that honestly indicates dominance status in which subordinates can pay a cost in terms of harassment from dominant males (e.g., Tibbets 2014).

A number of studies in the Red-winged Blackbird have shown cost (e.g., eliciting increased aggression) associated with enhancement of the epaulet size, and coloration (Røskaft and Rohwer 1987, Metz and Weatherhead 1991, Yasukawa et al. 2009b), again suggesting selection against UV color in epaulets if it is perceived as an indicator of dominance status.

While the selective mechanisms underlying the evolution of Red-winged Blackbird epaulet coloration remain speculative, our experiment does demonstrate a behavioral response to manipulation of the ultraviolet aspects of this visual signal. In fact, our study represents the first field experiment on wild birds to show a behavioral response to adding UV color to a plumage signal, thus creating a novel "UV + red" color. Our results add to growing evidence for the role of ultraviolet vision in signal efficacy among birds, and indicate the potential for UV components of plumage coloration to respond to selective pressures and evolutionary constraints in much the same way as for other plumage color signals.

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