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FLANGE COLOR DIFFERENCES OF BROOD PARASITIC BROWN-HEADED COWBIRDS FROM NESTS OF TWO HOST SPECIES

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ABSTRACT.—We compared the red, green, and blue color values from digital photographs of the rictal flanges of nestling Brown-headed Cowbirds (*Molothrus ater*), a generalist obligate brood parasite, in sympatric Yellow Warbler (*Setophaga petechia*) and Song Sparrow (*Melospiza melodia*) nests at Mono Lake, California, USA. We detected significant differences in all three color components across nestlings of different species (R: $P < 0.0001$; G: $P < 0.0001$; B: $P < 0.0001$), but differences among cowbird nestlings from the nests of these two hosts were not significant (R: $P = 0.543$; G: $P = 0.737$; B: $P = 0.319$). Principal components results were mixed: Principal Component I described brightness and accounted for 84% of the variance. It did not differ among cowbird nestlings from nests of different hosts ($P = 0.319$). Principal Component II described chromaticity and accounted for 14% of the variance, which differed significantly among cowbird nestlings from the two different hosts' nests ($P = 0.026$). Color differences between cowbird nestlings from nests of different host species may result from selective parasitism by female parasites based on host nestling flange morphology, or ontogenetic effects on cowbird nestlings reared by different host species. Received 25 January 2011. Accepted 21 July 2011.

Evidence of recognition and discrimination of parasitic nestlings is relatively rare among hosts of avian brood parasite species (Redondo 1993; Grim et al. 2003; Langmore et al. 2003, 2009; Schuetz 2005b; Sato et al. 2010; Shizuka and Lyon 2010). Patterns of parasite chick's visual and/or acoustic similarity of host nestlings in a handful of brood parasite lineages (Anderson et al. 2009, Sato et al. 2010, Langmore et al. 2011) imply mimicry to avoid rejection (Langmore et al. 2003, Payne 2005, Tokue and Ueda 2010, Langmore et al. 2011). Hosts may discriminate not only by directly rejecting foreign nestlings, but by providing better care or higher quality prey (Schuetz 2005a, Soler 2008) for nestlings with particular attributes (Rothstein 1978, Lichtenstein 2001, Dugas 2009), resulting in variation among nestlings in growth rate and condition (Hauber

and Kilner 2007). Nestling discrimination among cowbird hosts has been documented for Rufous-bellied Thrushes (*Turdus rufiventris*) parasitized by the non-evicting generalist Shiny Cowbird (*Molothrus bonariensis*) (Lichtenstein 2001), but is not yet known to occur in any hosts of the Brown-headed Cowbird (*M. ater*).

Hosts may recognize parasitic nestlings using variation in size, color, vocalization, brood size, and length of time before fledging (Langmore et al. 2003, Schuetz 2005b, Grim 2007). Variable coloration of both gapes and rictal flanges may have a signaling function, conveying nestling identity, need, health or other indicators of quality (Thorogood et al. 2008, Dugas 2010), which would need to be matched by parasitic nestlings (Nicolai 1974, Payne 2005, Hauber and Kilner 2007). Flange color is typically monomorphic within species, but Brown-headed Cowbird nestlings appear polymorphic across the species so that a nestling has either distinctly yellow or white flanges with few intermediates (Rothstein 1978). Polymorphic flange color occurs in only two phylogenetically distant New World oscine genera, *Geospiza* and *Molothrus*. It is plausible this polymorphism in cowbirds is the outcome of selection for preferential parasitism of certain host species by female cowbirds to match the host-specific flange color by the parasitic nestling (Ellison et al. 2007).

Alternatively, the differences in human-perceived flange phenotype of cowbird nestlings may not result from genetic polymorphism, but from differences in carotenoid consumption and

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provisioning to chicks across different hosts. Carotenoid pigments are derived entirely from diet, and their concentration is known to modulate nestling mouth color (Thorogood et al. 2008). Carotenoid concentration is widely hypothesized to indicate nestling quality, as demonstrated in House Sparrows (*Passer domesticus*) (Loiseau et al. 2008) and Barn Swallows (*Hirundo rustica*) (Saino et al. 2000, 2003).

We investigated whether cowbird nestlings differ in flange coloration when reared by one of two host species, Song Sparrows (*Melospiza melodia*) and Yellow Warblers (*Setophaga petechia*) using quantitative measures of coloration. Birds have a fourth violet- or ultraviolet-sensitive photoreceptor type, and human color perception is an insufficient proxy for avian color perception (Cuthill et al. 2000). We provide the first objective assessment of cowbird nestling flange colors based on measures of color using digital photographs and imaging software (Dale 2000). However, this remains a preliminary analysis because imaging software is designed for human vision and has limited value for avian perceptual studies (Stevens et al. 2007).

The objective of our study was to test the hypothesis that rictal flange color of host and cowbird nestlings varies between nestlings and parasites of two sympatric hosts. We predicted measures of flange colors would differ among: (1) nestlings of different species (Yellow Warbler, Song Sparrow, and Brown-headed Cowbird), and (2) cowbird nestlings in nests of different host species.

METHODS

Study Site and Species.—This study was conducted in the riparian corridors of four tributaries of Mono Lake (38° 1' N, 119° 3' W) on the eastern slope of the Sierra Nevada, California, USA: Lee Vining, Mill, Rush, and Wilson creeks. We located Song Sparrow and Yellow Warbler nests and monitored nests during the 2004 breeding season following Martin and Geupel (1993) and Ralph et al. (1993). The ranges of nest initiation dates for Yellow Warbler and Song Sparrows were similar in 2004 (Tonra et al. 2009).

Nestling Photographs.—We photographed nestlings on day 6 (hatching day = day 0) of the cowbird nestling cycle. This day was chosen because it coincided with the age at which nestlings are sufficiently large to band and allowed for incorporation of carotenoid pigments

from host-provisioned diet into tissues. Photographs were taken with a Hewlett Packard Photosmart 215 digital camera, set to ISO 200 and 'fine' quality (1,280 × 960 pixels). We photographed all cowbirds in each nest and, if hosts were present, we also randomly selected one individual to photograph. Sixteen Brown-headed Cowbird, three Yellow Warbler, and three Song Sparrow nestlings were included in the analysis. Both cowbird and host chicks were photographed in two Song Sparrow and two Yellow Warbler nests, and one Yellow Warbler and two Song Sparrow nests each contained two cowbird nestlings. Each photograph was taken of the right side of the head against a background of gray paper with a strip composed of six 1-cm² sections cut from paint store color sample cards (red, blue, green, white, yellow, and black) (Home Depot, Reno, NV, USA) as a color standard, and stored in a dark box between photography sessions. This allowed us to make direct comparisons of colors under varying light conditions in the field. The photographs were saved and subsequently analyzed as jpeg images using the histogram function in Adobe Photoshop Elements 8.0 (Adobe Systems Inc., San Jose, CA, USA). Storing images as jpeg compresses both image and color data (Stevens et al. 2007); color compression in this software obscures rather than enhances differences in color and would result in our failure to reject the null hypothesis (despite its falsehood: Type II statistical error). Thus, use of jpeg images made our analyses more conservative.

Flanges were divided into three portions for color measurement; A at the apex of the flange, site B at the fleshy middle, and site C at its most rostral point. Three replicate measures of red, green, and blue values were made at each flange site for each nestling. Red, green, and blue measures represent the intensity levels (saturation) for 24-bit color; these measures range in intensity from 0 (black) to 255 (white, totally saturated color). Measurements were also made from the center of the yellow standard present in each photograph to allow for direct comparison of the standard and biological colors.

Data Analysis.—We compared red (R), green (G), and blue (B) values, while accounting for variation in light conditions associated with field work in each photograph, by first scaling according to the RGB values of the yellow standard in that photograph *i*. Thus, $F_I/Y_I * 100$, where *I* = R, G, or B value, F_I = flange color

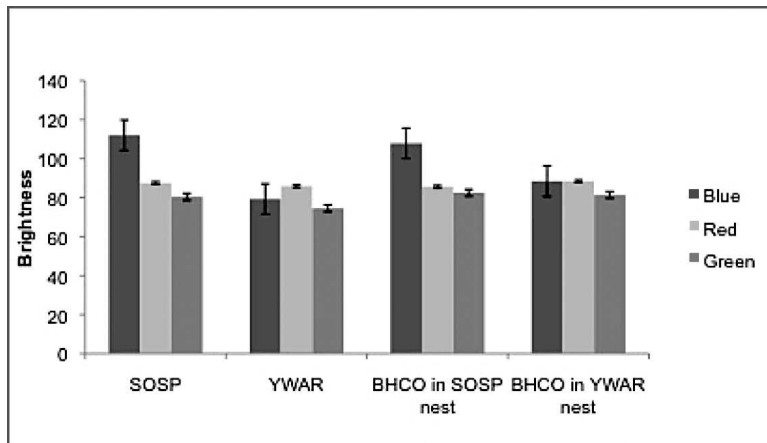


FIG. 1. Differences in flange color saturation values by species and host. SOSp = Song Sparrow, YWAR = Yellow Warbler, and BHCO = Brown-headed Cowbird. Bars represent mean saturation values of red, green, and blue across flange sites and replicates. Error bars represent standard error.

value for i , and Y_1 = the yellow standard for i . Repeated measures at each flange site within color group (R, G, and B) were averaged across replicates. Data were analyzed using three separate univariate analyses of variance (Mixed Effects ANOVA), where each color value was the dependent variable, nestling species (Yellow Warbler, Song Sparrow, or Brown-headed Cowbird) and cowbird nestling host species (Yellow Warbler or Song Sparrow) were fixed effects, and nestling metal-band ID and flange site were random effects. Color variables R, G, and B are necessarily correlated and we also used principal components analysis (PCA) to recombine color variables into uncorrelated scores describing brightness and chromaticity (following Endler and Thery 1996). Mean PC scores were compared among host nestling species and cowbird nestling species groups using ANOVA. All analyses were conducted in JMP Version 8.0 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Color values were significantly different among nestling species in all three univariate analyses of red, green, and blue color components (R: $F_{2,48} = 11.67$, $P < 0.0001$; G: $F_{2,50} = 11.14$, $P < 0.0001$; B: $F_{2,50} = 16.61$, $P < 0.0001$), but not between cowbird nestlings of different host species (R: $F_{1,17} = 0.84$, $P = 0.543$; G: $F_{1,16} = 0.12$, $P = 0.737$; B: $F_{1,17} = 1.06$, $P = 0.319$; Fig. 1).

The first two Principal Components (PC) together explained 97% of the variation in

nestling flange color (Table 1). The first Principal Component (PC I) explained 84% of variance in the combined RGB variables and described variation in brightness for all three color components, as implied by the consistently positive eigenvalue loadings of all three red (0.575), green (0.613), and blue (0.541) chromatic values. PC I differed across nestling species ($F_{2,47} = 24.96$, $P < 0.0001$), but did not differ between cowbird nestlings from different host species nests ($F_{1,16} = 0.004$, $P = 0.950$). Principal Component II (PC II) explained 14% of variance and described the color content or chromaticity of the RGB variables (i.e., hue and saturation), where blue was a positively loaded (0.793) eigenvector and red was negatively loaded (-0.591). Green was also negatively loaded, although this value was low (-0.145). Higher values of PC II reflected higher values for blue and lower values for red. PC II did not differ by nestling species ($F_{2,56} = 0.84$, $P = 0.436$), but differed significantly between cowbird nestlings from different host species nests ($F_{1,19} = 5.89$, $P = 0.026$) (Fig. 2).

DISCUSSION

Flange colors of two species serving as hosts for Brown-headed Cowbird nestlings were different in most univariate and PC analyses of physical coloration measures, confirming the assumptions of species-specificity of these visual traits. Univariate measures of flange colors revealed no differences between cowbird nestlings from the two host species' nests. However, most univariate

TABLE 1. Eigenvalues from the principal components analysis of variation in nestling flange color. The first two principal components explained 97.4% of the total variance.

Parameter	Eigenvalue	Eigenvector	Variance explained (%)
Principal Component I	2.51	red 0.58 green 0.61 blue 0.54	83.7
Principal Component II	0.41	red -0.59 green -0.15 blue 0.79	13.7
Principal Component III	0.08	red 0.56 green -0.78 blue 0.28	2.7

analyses of color traits are confounded with variation in brightness (Endler and Thery 1996). PC analysis, in contrast, revealed differences in PC II describing the relative saturation of red and blue among cowbird nestlings. Thus, parasitic offspring in nests of the two sympatric host species differ in physical measures of coloration, as recorded on digital photographs of live nestlings in the field. These differences may be behaviorally relevant for host discrimination, as recent studies of hosts of brood parasitic birds have demonstrated the avian-specific role of particular chromatic elements influencing egg rejection behavior (Honza et al. 2007; Cassey et al. 2008, 2009).

The host-specificity of the chromatic variation of cowbird nestling flange color detected suggests a potential signaling function in the context of parasitic nestling discrimination. A mechanism

may exist by which female cowbirds preferentially parasitize hosts whose nestling flange color matches that of their own chicks, despite the vast diversity of cowbird host species (Friedmann 1929). This mechanism may be similar to female parasites' host-specific egg color matching, documented in Common Cuckoos (*Cuculus canorus*) (Cherry et al. 2007, Aviles 2008).

The ontogenetic basis of host-parasite flange color matching requires additional study, as it may involve genetic and maternal effects of host-specific parasitism by female cowbirds. Alternatively, it may be the result of host-specific plasticity of cowbird chicks' coloration during development. Experimental manipulation of cowbird nestling flange color, and cross-fostering studies of parasitic eggs between different host species should provide experimental tests of some of these alternatives, as demonstrated in

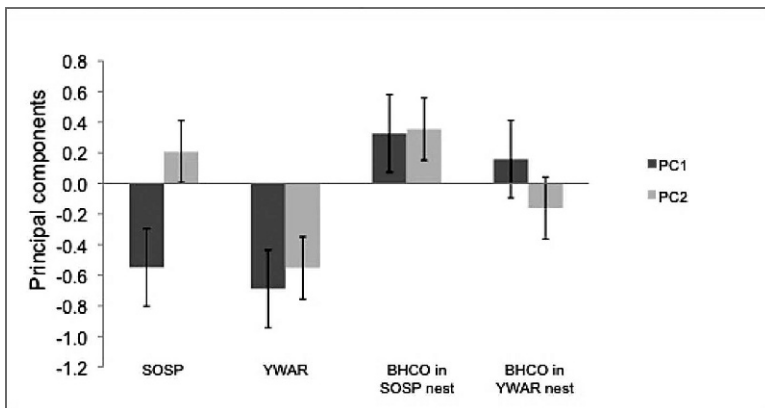


FIG. 2. Values of the first two Principal Components (PC) by species and host. PC I represents overall intensity including red, green, and blue values, and is significantly different across species. PC II describes blue as a positively loaded Eigenvector and red as negatively loaded. PC II is significantly different across cowbird nestlings from different host species nests. Bars represent mean values for PC I and PC II, and error bars represent standard error.

the host-specific begging call matching by cuckoos of Australian songbirds (Langmore et al. 2008).

The difference in chromatic reflectance of flange colors (PC II) across cowbird nestlings from the two hosts may also be a developmental result of carotenoid concentration based on the diets of our two host species. Carotenoids in birds are derived entirely from diet, and are known to modulate variation in nestling mouth color by blocking the reflectance of short-wavelength (blue/green) light and cause the mouthparts to appear orange, yellow or reddish (Thorogood et al. 2008). Thus, nestlings with carotenoid-rich mouthparts are favored in species where parents exhibit a feeding preference based on nestling mouth coloration (Dugas 2009). Nestling flanges are significantly brighter, more UV reflective, and more chroma rich in the part of the flange visible during begging than hidden parts (the sides), lending support for the signaling hypothesis in the function of flange coloration (Dugas 2010). However, measurements in our study were made on the sides of the flange, and would be less visible during begging. Differences in the coloration of these two regions may be the combined result of signaling during begging and decreasing conspicuousness when not, resulting in decreased UV reflectance on sides compared to insides (Dugas 2010). The inside and side flange colors were weakly correlated (Dugas 2010), but we might expect to find even better color matching based on the inner part of the flanges. Future studies would benefit from comparing these two regions using UV-sensitive spectrophotometric measures as opposed to the human-visible only color measurements available to us from digital photographs.

We did not measure ambient light at the nest. Thus, our results of species-specific differences in the color variables contributing to PC I and host-specific differences in the relative amount of blue reflectance of cowbird nestlings (PC II) may be an adaptive result of nestlings optimizing their own detection in the specific ambient light environments of the different host species' nests (Ficken 1965). Nestlings in dark nests increase conspicuousness through the relative color and size of the flange (Kilner and Davies 1998), and open-nesting species show higher achromatic contrast with the nest than cavity-nesting species (Aviles et al. 2008). Both Yellow Warblers and Song Sparrows nest in open cups, albeit typically at different heights and in different plant substrates (Tonra et al. 2009), and differences in nestling

coloration based on detection under ambient light conditions are an unlikely causal explanation for the pattern of differences in cowbird flange color diversity.

Our results support predictions of the host-parasite flange color matching hypothesis for Brown-headed Cowbirds and their hosts. Further experimentation is necessary to examine the role of flange color in the host-brood parasite coevolutionary arms race, including nestling mimicry and discrimination (Fraga 1998, Lichtenstein 2001). These studies have the potential to shed light on the evolution of host use strategies in cowbirds, revealing the extent to which specialization may exist in individual cowbird females. This information would have important and broadly applicable implications for both coevolutionary theory and conservation.

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