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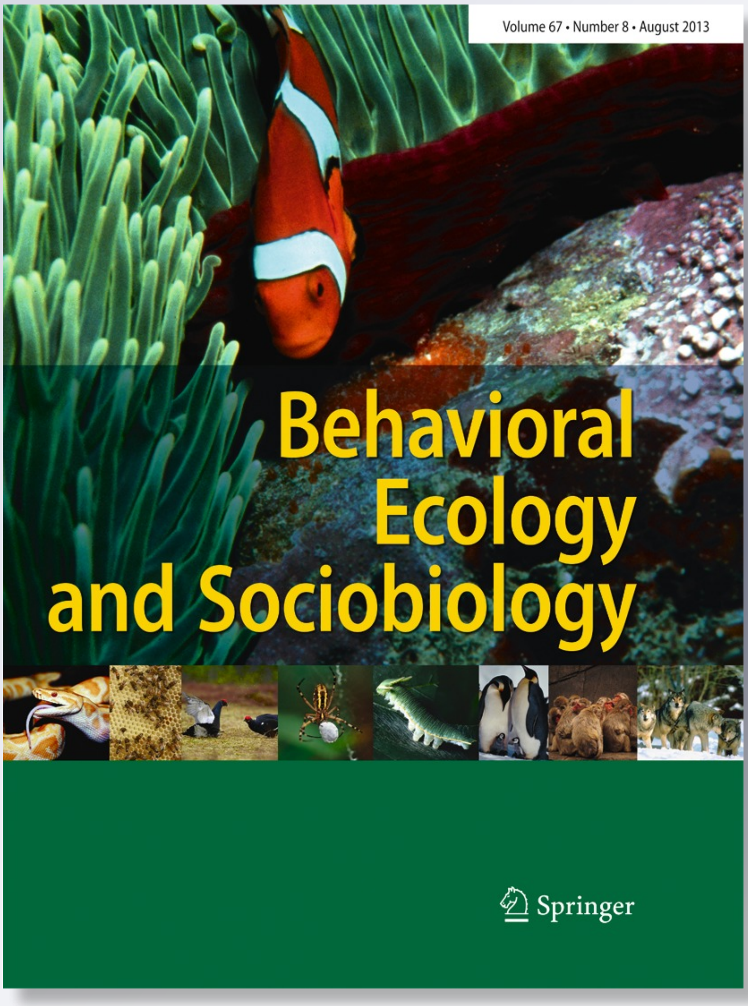

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ORIGINAL PAPER

Vivid birds respond more to acoustic signals of predators

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Abstract Because conspicuous morphology such as colorful plumage may increase predation risk, we aimed to see if variation in plumage coloration could explain variation in avian anti-predator behavior. We included several measures of plumage coloration: human perception of vividness from images in field guides, total intensity from reflectance spectra of museum skins, contrasts calculated from physiological models of these spectra parameterized for both raptors and humans, chroma, and spectral saturation. We investigated how well these measurements predicted risk assessment in ten species of birds in St. John, U.S. Virgin Islands. We quantified how each species responded to playbacks of a predator's calls and compared this response to that elicited by songs from a non-predatory, sympatric bird. We found that human-determined measures of vividness best predicted anti-predator responses of birds—more vividly colored species responded more to predators than duller species. No spectrophotometric variable explained variation in species reactions to a predator call. Our results suggest that vivid birds may compensate for their conspicuousness by being more responsive to the sound of predators and that more work is needed to better evaluate how animal coloration is quantified in comparative studies.

Keywords Anti-predator behavior · Coloration · Spectrophotometry · Playback · Behavioral plasticity · Plumage vividness

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Introduction

Many of the early critics of natural selection (Darwin 1859) argued that natural selection could not explain the evolution of showy phenotypes (such as peacock trains), given that they increase the likelihood of predation. Darwin (1871) expanded his initial outline of sexual selection to respond to these critics, and we now view showy plumage as a potential burden, and many investigators have noted that cryptic prey should be less vulnerable to visual hunting predators than conspicuous prey (Cott 1940; Merilata 1999; Merilata and Lind 2005). Indeed, much empirical work supports this claim (e.g., Götmark 1993; Stuart-Fox et al. 2003; Husak et al. 2006), yet ornamented plumage could signal unpalatability (aposematism) or unprofitability to predators (Cott 1940, 1946; Baker and Parker 1979; Guilford 1986).

To overcome the cost of being conspicuous, species may evolve compensatory behavior (Castilla and Bauwens 1991; Hedrick 2000; Cuadrado et al. 2001). For example, large bird species compensate for the drawbacks associated with large size by initiating flight at greater distances than smaller species (Blumstein 2006). One such compensatory behavior is increased wariness by which individuals may increase vigilance or be more likely to initiate flight (e.g., Adams et al. 2006). In this study, we tested the prediction that more colorful birds (i.e., more vivid, brighter, more chromatic, more saturated) will be more responsive to predator sounds because they are more conspicuous. We tested this by broadcasting the sounds of an aerial predator and a non-predatory heterospecific to several species of birds and quantifying their responses.

We measured color using human observers as well as using spectrophotometric methods. Several studies question the adequacy of human observers, given that birds perceive colors differently than humans (Burkhardt 1989; Maier and Bowmaker 1993), and this difference in perception has serious consequences for studies of sexual dichromatism birds (e.g., Andersson et al. 1998; Vorobyev et al. 1998;

Cuthill et al. 1999; Eaton 2005, 2007; Håstad and Ödeen 2008; Burns and Shultz 2012). Other studies, however, have found that human perception can adequately decipher sexual dichromatism (e.g., Armenta et al. 2008; Seddon et al. 2010). However, to our knowledge, no study has explicitly compared the use of human scores of field guides and spectrophotometric measures of overall conspicuousness rather than just sexual dichromatism.

Methods

Study area

We conducted this study in the Virgin Island National Park, U.S. Virgin Islands, St. John, (18° 19′ 19.45″N 64° 43′ 22.58″ W) from 10 to 30 October 2009. We collected data between 0600 and 1200 hours, and again between 1500 and 1800 hours. We performed our playback experiments along multiple park trails covering ~15 km. Vegetation varied from moist forest to sub-tropical dry forest to semi-arid cactus scrublands (National Park Service U.S. Department of the Interior 2008). To minimize the potential of pseudoreplication, we walked paths in one direction within a single day. We performed playbacks on focal subjects (virtually all were initially perched and relaxed when we began our experiments) from ten different species (Table 1). We aimed to conduct playbacks on solitary birds (0 conspecifics within 10 m) and for those in or close to cover.

Playback protocol

We acquired vocalizations from Xeno-Canto (www.xeno-canto.org) and a commercial compact disk (Oberle 2008). We edited and normalized these to 95 % peak amplitude with Sound Edit 16 (Version 2, Macromedia 1996; Fig. 1) and uploaded aif files to an iPod (Apple, Cupertino, CA, U.S.A.). We broadcast calls through a Sony SRS-77G speaker, at 85 dB SPL (measured at 1 m with a SPER Scientific 840029 digital sound meter, weighting level A, fast response). We designed the playback to simulate a nearby but not immediately adjacent, raptor (broad-winged hawk, *Buteo platypterus*).

We approached subjects by walking 0.5 m/s until we came within playback distance (no further than 20 m, averaging 7.5 m (± 3.8 SD) from the focal subject), waited briefly, and began playback. We conducted a 75-s focal animal observation divided into a 15-s baseline period, which we observed the initial state of the subject, immediately followed by a 60-s period that began with a stimulus playback (all playback stimuli were 2 s) (Table 1). For our predator stimulus, we used calls of broad-winged hawks (*B. platypterus*—five exemplars) because they hunt in the interior of the forest (Johnsgard 1986) and have diet that includes various avifauna (Rusch and Phillip 1972). For the non-predatory control stimulus, we used calls of bananaquits (*Coereba flaveola*—five exemplars). When observing bananaquits, we used calls of lesser Antillean bullfinches (*Loxigilla noctis*—five exemplars). Our ethogram included the following behaviors: look (head fixated, scored with each head movement), call (emitting vocalizations), forage (feeding with head down), preen (contact of beak with body parts), walk (forward movement greater than two steps), hop (in air without wing movement), flight (in air with wing movement), and out of sight. We dictated behaviors into a microcassette recorder, and then transcribed and quantified our focal observations using JWatcher 1.0 (Blumstein and Daniel 2007).

Analyses

We calculated the rate of looking and locomotive behavior (walk, hop, flight) in the 15-s interval before and after the

Table 1 Number of predator and control calls broadcast to each species and change in locomotive behavior

Common name	Scientific name	No. of control	No. of predator	Mean change in rate of locomotive behavior
Antilean crested hummingbird[a]	*Orthorhyncus cristatus*	6	5	−0.0678
Bananaquit	*Coereba flaveola*	50	49	0.0282
Bridled quail-dove	*Geotrygon mystacea*	6	8	0.002
Caribbean elaenia	*Elaenia martinica*	8	7	0.0006
Green-throated carib	*Eulampis holosericeus*	6	9	0.0736
Lesser Antillean bullfinch[a]	*Loxigilla noctis*	17	11	−0.0387
Mangrove cuckoo	*Coccyzus minor*	7	7	0.0359
Pearly eyed thrasher	*Margarops fuscatus*	31	30	−0.0000116
Yellow warbler[a]	*Setophaga petechia*	7	6	0.067
Zenaida dove	*Zenaida aurita*	21	21	0.0194

All other species are not sexually dichromatic

[a] Only data for males are reported

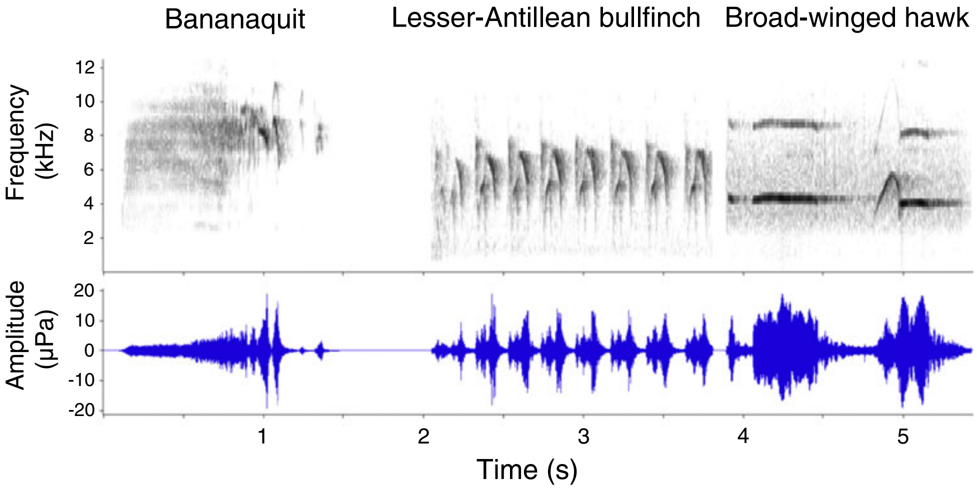

Fig. 1 Spectrograms and waveforms of representative exemplars of acoustic stimuli used. Sampling rate 44 kHz, 256-point FFT (frequency resolution 172.3 Hz), *gray scale* represents −80 dB from peak amplitude

playback stimulus. We analyzed the rate of looking because studies have noted increased vigilance as an anti-predator behavior (Searcy and Caine 2003; Adams et al. 2006; Fernández-Juricic et al. 2011). Increased locomotion, or increased activity, may act as a pursuit-deterrence signal to predators whereby the prey makes itself obvious to communicate to the predator that its presence has been detected (Woodland et al. 1980; Caro 2005). Alternatively, decreases in locomotion might improve a prey's ability to scan their environment and assess risk (Underwood 1982; McAdam and Kramer 1998; Kramer and McLaughlin 2001).

We included species for which we broadcast at least five playbacks of each stimulus type (predator and control). For each species, we compared responses to a predator call (broad-winged hawk) vs. control call (bananaquit or lesser Antillean bullfinch). To do so for each species, we first calculated the average difference from baseline in the rate of looking and rate of locomotion in response to a predator call vs. non-predatory calls. We then subtracted a species response to a predator from the control to develop an index of response. Thus, more responsive species have a larger difference between how they responded to a predator compared to a non-predatory bird.

To measure vividness based on human perception we employed a numerical scale system. For the Virgin Islands species we included in our study (Table 1), we used QuestionPro (2009) to create a survey with clear illustrations from seven field guides (Raffaele 1989; Ridgely and Gwynne 1989; Stiles and Skutch 1989; Fjeldså and Krabbe 1990; Sibley 2000; Raffaele et al. 2003; Dunn and Alderfer 2006).

Ten undergraduate observers ranked the vividness of the plumage of each species from the field guides by giving a score from a range of 1–5 [(1) dull; entirely neutral colors, (2) overall dull, but some small amount of color that stands out slightly against neutral background, (3) slightly bright; mostly neutral/dull colors, but fair amount of subtle coloration or prominent amounts of white, (4) bright; plumage mostly bright colors, but some dull/neutral colors, (5) very bright; no dull/neutral plumage, all plumage bright/neon]. The participants were naïve to the spectrophotometric definition of brightness, which is distinct from its colloquial use (e.g., Lovely cotinga (*Cotinga amabilis*) females have whitish-brown plumage, whereas males have brilliant blue and violet plumage. To the lay public, a male would be brighter than a female of this species, but using the spectrophotometric definition, females would be brighter than males). An average vividness score was calculated for each species (Supplementary Table 1). For the three dichromatic species (Table 1), we only included males in the analyses.

To measure reflectance spectra of plumage, we obtained bird skins from museums (Supplementary Table 2), choosing specimens nearest to our study location when possible. We measured reflectance spectra of plumage with an Ocean Optics USB-2000 spectrometer equipped with a pulsed xenon light source (Ocean Optics PX-2). We measured reflectance as the proportion of reflectance relative to a Labsphere certified reflectance standard using Ocean Optics' OOI Base 32 software. We averaged three reflectance measurements for each patch measured: crown, throat, ventral surface of the retrices, dorsal surface of the retrices, the ventral surface of the bird (just below the breast), and the back. For some species with iridescent patches or a cheek stripe (e.g., the crown of *Orthorhyncus cristatus*), we took additional measurements.

We measured total intensity as the sum of reflectance values measured at 0.37-nm intervals across the entire avian visual range (300–700 nm) and the human visual range (400–700 nm). For each individual, we calculated the mean total intensity across all patches measured, and the maximum single total intensity score across all regions (see Supplementary Table 2). In our analyses, we calculated a mean total intensity for each species, which is the mean of the individual measures of mean total intensity. The standard regions for each species included the crown, throat, retrices (dorsal side), belly, and back. For species with additional measurements (e.g., an iridescent patch on the scapulars), the additional region was substituted for the nearest standard region (e.g., the back). We did this to maintain the same number of patches averaged for each species. Since the conspicuousness of individuals may be the result of a single small patch, we also calculated a maximum total intensity score for each species, which was the mean of the maximum total intensity scores for all individuals of that species.

To calculate chromatic and achromatic contrasts, two measures of the conspicuousness of a given color patch (Endler 1990), we used AVICOL (Gomez 2006) to run Vorobyev and Osorio physiological models for tetrachromatic vision (Vorobyev et al. 1998). Since raptors studied so far have violet sensitive visual systems (Ödeen and Håstad 2003), we parameterized the model using the default VS settings in AVICOL for relative cone densities and Weber fraction (ω= 0.05) and average avian VS photoreceptor sensitivity curves from Endler and Mielke (2005).

We ran the models to calculate contrasts in both full sun and shade environments. We parameterized the background reflectance spectra, against which the contrasts of color patches are calculated in AVICOL, with measurements from the same spectrophotometer and probe used to measure plumage reflectance spectra by pointing it at a 45° angle toward the sky and randomly rotating the probe, taking several measurements in the full sun and in the shade (Fernández-Juricic et al. 2012). Since we did not have access to a spectrophotometer in St. John, we measured these reflectance spectra on campus in Los Angeles, California. We used the irradiance spectra of sunny and shade-canopy conditions from Endler (1993).

For each species, we calculated mean chromatic and achromatic contrast in both sun and shade environments by taking the mean of the means of patches (only including a set number of patches used in the reflectivity analysis). We used the same particular patches as in the reflectivity analysis. Furthermore, we calculated maximum chromatic and achromatic contrasts in both sun and shade environments by taking the mean of the highest contrast value for each individual.

We also calculated chromatic and achromatic contrasts with the models parameterized for human vision, using a photoreceptor sensitivity curves from Table 8 of Stockman et al. (1993) and a Weber fraction of ω=0.3. Again, we ran the models to calculate contrasts in both full sun and shade environments using the same background and irradiance spectra as above.

Additionally, we calculated the chromatic and achromatic contrasts between plumage patches within each bird and averaged the mean and maximum within-bird contrasts for each species. For species with iridescent patches, we only included the measurements from the single patch that had the highest contrast. Since the outcome for sun and shade irradiance was qualitatively similar in our preceding analyses, we only calculated within-bird contrasts using the sunny irradiance spectrum from Endler (1993). We parameterized these analyses with both avian and human photosensitivities, as above.

Finally, we measured spectral saturation and chroma (Montgomerie 2006). To calculate the mean spectral saturation (calculated as $R_{\max}/(R_{\min}+0.0000001)$, where R is reflectance) and chroma ($R_{\max}-R_{\min}/R_{\mathrm{avg}}$) measures for each individual, we included only the most saturated and chromatic measurements for iridescent patches with several measures. For spectral saturation, there were a few outliers so we calculated the median of these individual mean and individual maximum spectral saturation measures for each species. We calculated the mean of the mean and maximum scores for chroma measures of each species.

To control for body mass, we obtained body mass for each species from Dunning (2008). Where there were several means for each species (from different regions), we used the mean from the location nearest to St. John. For monomorphic species with different mass values for males and females, we averaged the male and female means. We log10-transformed mean mass prior to analysis.

There is the chance that species may resemble each other because of shared ancestry. Thus, we calculated phylogenetically independent contrasts (Felsenstein 2004). We constructed a phylogeny (Fig. 2) using topologies from Jønsson and Fjeldså (2006) and Hackett et al. (2008). We used a fully bifurcated phylogeny, where branch lengths were set to 1. We calculated contrasts using the ape package

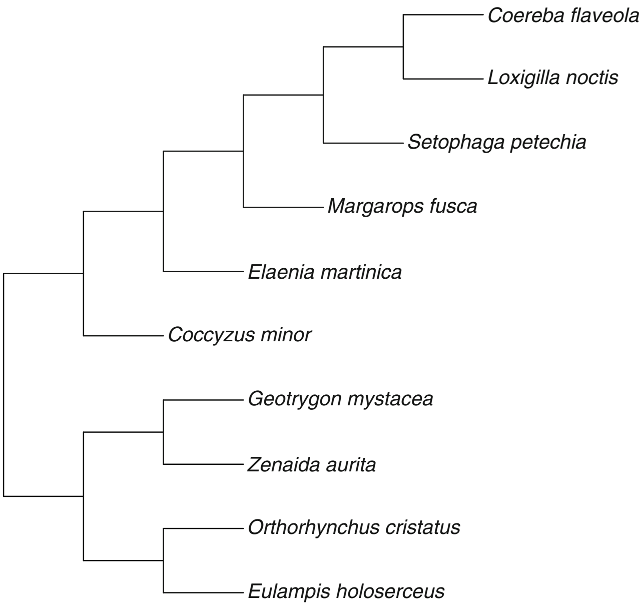

Fig. 2 Phylogenetic topology of species studied

in R (Paradis et al. 2004). We acknowledge that we calculate many correlations, an inevitable outcome of using many measures to quantify conspicuousness. Strictly our results should be viewed as exploratory and suggestive, rather than confirmatory.

Results

We collected 312 playback observations from ten species (Table 1). Although specimens were collected between 1886 and 1987, specimen age had no effect on reflectance values (maximum total intensity $r=-0.068$, $P=0.525$; mean total intensity $r=0.043$, $P=0.692$). Body masses ranged from 5.7 to 211.0 g. The contrast values for total intensity and mass were neither highly, nor significantly correlated ($r=-0.436$, $P=0.241$).

Overall, 61 % of the variation ($F_{2,7}=8.193$, $P=0.015$) in the difference in the rate of locomotion was explained in a model that included human scored vividness ($t=4.041$, $P=0.005$) and body mass ($t=2.089$, $P=0.075$). Neither human nor spectrophotometric indices of plumage color explained any variation in the difference in the rate of looking (all P values>0.295).

There were significant differences between species for the distance at which we broadcast stimuli to species ($F_{9,272}=4.817$, $P<0.0001$). Average distances per species ranged from 4.3 to 10.6 m. However, no variation in the rate of looking ($r^2=0.002$, $P=0.886$), or the rate of locomotion ($r^2=0.027$, $P=0.673$) was explained by distance to speaker in a linear regression analysis of independent contrasts. Thus, distance to speaker was not a confounding variable in our analyses. For the playback experiments, animals were typically close to cover ($n=315$, mean=0.2 m, SD=0.762), and subjects were typically alone (i.e., there were no other conspecifics within 10 m of the focal individual; $n=315$, mean=0.35, SD=1.329), so it is unlikely that these variables contributed to variation in anti-predator behavior.

Though not significant, the models including chromatic contrast values, both between the background spectra and between patches within birds, were better than the models that used total intensity values (Table 2). Vividness assessed by humans was significantly correlated with chromatic contrast values (e.g., avian mean chromatic contrast [sun]: $r=0.83$, $P=0.01$, avian within-bird max chromatic contrast [sun]: $r=0.69$, $P=0.04$) but was not correlated with total intensity values (e.g., maximum total intensity: $r=0.55$, $P=0.122$).

Overall, the models for spectral saturation and chroma were not significant. However, the paramater value for the model including the species mean of the maximum chroma value for each individual skin was marginally significant and was negatively correlated with change in locomotive behavior (Table 2). However, this apparent correlation appears to be driven by an influential point (DFFITs=2.07, Cook's distance=1.48), without which the relationship is no longer significant ($t=-0.622$, $P=0.56$). None of the spectral saturation or chroma variables were correlated with human-determined vividness (e.g., max chroma: $r=0.06$, $P=0.87$).

Total intensity calculated over the visible range for humans was correlated with the total intensity calculated over the avian visual range (mean total intensity: $r=0.998$, $P<0.001$; maximum total intensity: $r=0.935$, $P<0.001$). Contrast values calculated using human vision parameters were also highly correlated with those parameterized for raptor vision (Fig. 3).

Discussion

Many, but not all, species respond to predator vocalizations (Blumstein et al. 2008). Previous studies on other species have treated this response as a dichotomous trait (e.g., Magrath et al. 2007; Neal 2009); however, we quantified it continuously. We found substantial variation in the degree to which our ten bird species modified their locomotion in response to predator sounds.

Degree of vividness, scored by human observers, explained the difference in the rate of locomotion: vivid birds were warier than duller birds. Since the colloquial use of the word "vividness" is a measure of ornamentation, we infer that due to their vivid coloration, showy birds compensate for their conspicuousness by altering their behavior compared to more cryptic species. This is another example of organisms using anti-predator behavior to compensate for increased vulnerability due to increased conspicuousness (Lind and Cresswell 2005; Husak et al. 2006; Husak and Rouse 2006). Our results are inconsistent with the unprofitable prey hypothesis—which states that brightly colored prey are difficult to catch (Baker and Parker 1979), and the aposematism hypothesis—which states that brightly colored birds are distasteful and thus warn off predators (Cott 1946).

The discrepancy between different methods could reflect our use of museum specimens for spectrophotometry analysis. Studies show that the specimen age and preservation agents can influence reflectance values (McNett and Marchetti 2005; Pohland and Mullen 2006). However, in our study there was no influence of specimen age on reflectance values. Furthermore, a study comparing reflectance spectra from wild and museum specimens of long-tailed manakins (*Chiroxiphia linearis*), found no significant difference in coloration (Doucet and Hill 2009). Thus, we believe that the museum specimens we used in this study were appropriate for spectrophotometric analyses.

Assessing plumage vividness using field guides also has potential weaknesses. For one, field guides typically ignore

Table 2 Results of models of rate of change in locomotive behavior explained by different measures of conspicuousness as predictor variables

Response variable	Overall model *P* value (*F* statistic)	Response variable *P* value	Mass *P* value	Adjusted r^2
Human-determined vividness	0.02 (8.19)*	0.01 **	0.08	0.62
Mean total intensity	0.87 (0.15)	0.62	0.97	−0.23
Max total intensity	0.96 (0.04)	0.81	0.87	−0.27
Mean chromatic contrast	0.28 (1.54)	0.12	0.35	0.11
Max chromatic contrast	0.55 (0.65)	0.30	0.42	−0.09
Mean achromatic contrast	0.86 (0.16)	0.60	0.96	−0.23
Max achromatic contrast	0.86 (0.16)	0.60	0.88	−0.23
Mean within-bird chromatic contrast	0.31 (1.41)	0.14	0.21	0.08
Max within-bird chromatic contrast	0.16 (2.35)	0.07	0.16	0.23
Mean within-bird achromatic contrast	0.81 (0.22)	0.54	0.96	−0.21
Max within-bird achromatic contrast	0.98 (0.02)	0.87	0.92	−0.28
Human mean chromatic contrast	0.40 (1.04)	0.20	0.42	0.01
Human max chromatic contrast	0.61 (0.53)	0.34	0.43	−0.12
Human mean achromatic contrast	0.71 (0.36)	0.43	0.82	−0.17
Human max achromatic contrast	0.67 (0.43)	0.39	0.55	−0.14
Human within-bird mean chromatic contrast	0.51 (0.75)	0.26	0.33	−0.06
Human within-bird max chromatic contrast	0.30 (1.44)	0.14	0.24	0.09
Human within-bird mean achromatic contrast	0.78 (0.26)	0.50	0.90	−0.20
Human within-bird max achromatic contrast	0.96 (0.04)	0.80	0.94	−0.27
Max spectral saturation ($R_{\max}/R_{\min}$)	0.31 (1.39)	0.14	0.85	0.08
Mean spectral saturation ($R_{\max}/R_{\min}$)	0.72 (0.35)	0.44	0.97	−0.17
Max chroma ($((R_{\max}-R_{\min}/)R_{\mathrm{av}})$)	0.12 (2.92)	0.05*	0.18	0.30
Mean chroma ($((R_{\max}-R_{\min}/)R_{\mathrm{av}})$)	0.97 (0.03)	0.85	0.97	−0.28

All models are no-intercept models calculated using independent contrast data. Only results calculated with sunny irradiance spectra are presented

$*P=0.05$; $**P=0.01$

visual signals not evident to humans, such as coloration that is only visible during displays, which birds can detect (Bennett et al. 1994). Similarly, drawings in field guides do not provide information about non-visual ornamentation such as song, behavior, or olfactory cues. Field guides are also highly typological, ignoring intraspecific and geographic variation.

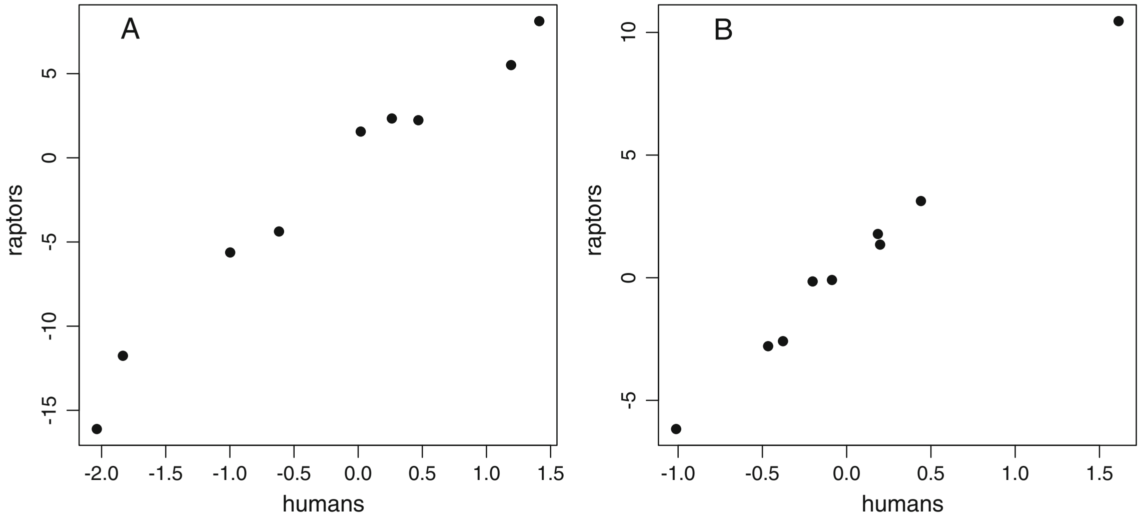

Fig. 3 Relationship between **a** maximum and **b** mean chromatic contrasts using models parameterized for human and raptor vision (sun values shown, though shade values are similar). Independent contrast values shown

Nevertheless, these factors should not systematically bias data from field guides in such a way as to render our results irrelevant.

The difference between methods could also result from assumptions of our spectrophotometric analyses (e.g., our background reflectance spectra, irradiance spectra, and model parameters were not measured in the field but obtained elsewhere). However, the degree to which variation in the contrasts calculated using physiological models of spectral data influences perception and consequently, behavior, is still a black box.

Total intensity values for the human visual range (400–700 nm) and the avian visual range (300–700 nm) were highly correlated. Moreover, the contrasts calculated for human and raptor vision were also correlated (Fig. 3). This may indicate that the discrepancy in results calculated when we used humans to quantify vividness compared to those values derived from spectrophotometry-determined measurements is not a function of the differences between human and avian visual systems. This discrepancy could either be a result of our methodology (e.g., a difference between field guides and museum skins, which we did not address), or it could be because of differences between perception of colors and spectrophotometric measurements. In other words, this result may indicate that the ornamentation of birds is more than the sum of spectral measurements for individual patches since higher-level neural processes act to create a gestalt or search image (e.g., Montgomerie 2006; Miller and Bee 2012). Indeed, field guides likely provide a caricature of this gestalt, which may have also influenced our results. Future investigations would benefit from research on ways of incorporating neural processes and spectral data.

Like humans, predators likely form a gestalt when searching for prey. The large literature on search image formation (see review in Shettleworth 1998) suggests that this is a common mechanism employed. Although spectrophotometry is more objective in that spectral measurements are calculated from explicitly parameterized models, our study suggests that human perception may be a valid proxy when measuring an overall index of vividness of bird plumage. Huhta et al. (2003), for example, collected 63 species of dead birds preyed on by sparrowhawks (*Accipiter nisus* L.) over 33 years and found that prey vividness, determined by humans, explained variation in predation frequency; vivid birds were preyed upon more frequently.

Increased response to predators may be an adaptive response to the costs of conspicuousness. Previous studies examining behavioral responses due to conspicuous coloration have focused on polymorphic species (e.g., Brodie 1989; Forsman and Appelqvist 1998) or made comparisons between sexes of the same species (e.g., Scudder and Burghardt 1983; Zinner 1985). There are few interspecific studies examining behavioral responses to variable coloration or conspicuousness. For instance, Cabido et al. (2008) exposed two species of ornamented male Iberian rock lizards (*Iberolacerta monticola* and *Iberolacerta cyren*) to different predator densities, and the lizards varied their behavior according to their degree of conspicuousness; a finding consistent with ours. Future comparative studies may provide further support that animals compensate for increased vulnerability associated with costly traits.

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Ethical standards This study was conducted under UCLA ARC Protocol no. 2000-147-31, and permits from the National Park Service (no. VIIS-2009-SCI-0028). All experiments comply with the current laws of the country in which they were performed.

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