ORIGINAL ARTICLE

Juvenile coloration of Florida Scrub-Jays (*Aphelocoma coerulescens*) is sexually dichromatic and correlated with condition

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Abstract The Florida Scrub-Jay is a monogamous cooperative breeder in which both males and females display extensive structurally based blue plumage. Juveniles of this species exhibit blue tail and wing feathers that they begin growing as nestlings, and some of these feathers are retained throughout their first year. Although the birds appear to be sexually monochromatic, we assessed whether cryptic dichromatism exists in both the magnitude and pattern of coloration in tail feathers of juvenile Florida Scrub-Jays. We then determined whether variation in plumage coloration is associated with nutritional condition during molt. Tails of juvenile male Florida Scrub-Jays exhibit a greater proportion of UV reflectance than those of females. Mass at age 11 days and ptilochronology of the juvenile tail feathers were used as measures of individual nutritional condition during feather growth, and the latter was found to be positively associated with UV chroma. These data demonstrate that Florida Scrub-Jays are sexually dichromatic and suggest that variation in plumage color may be condition dependent, although we cannot rule out alternative explanations. Juvenile plumage coloration, therefore, has the potential to function as a signal of individual quality in both males and females.

Keywords Condition-dependent traits · Ptilochronology · Sexual dichromatism · Structural color · UV coloration

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Introduction

A large body of literature suggests that sexual selection is responsible for much of the diversity in ornamental plumage coloration in birds (Andersson 1994; Hill and McGraw 2006). Consequently, colorful ornaments, such as those in feathers, are mainly found in adults. Juvenile plumage tends to lack bright coloration and is often cryptically colored brown or gray by melanin pigments (reviewed in Kilner 2006). Cryptic coloration is thought to give young birds fitness advantages in the nest or after fledging (reviewed in Kilner 2006). In some bird species, however, conspicuous coloration is expressed in the plumage of nestlings, but the signal content of such coloration is largely unknown. In most species with nestling ornamentation, chicks remain ornamented only during the period of intense parental care, suggesting that chick color evolved to signal hunger or individual quality to parents or to competing siblings (Krebs and Putland 2004). Although most juveniles of passerine species molt the entire body plumage before the first breeding attempt (post-juvenile molt), in some species, like the Florida Scrub-Jay (*Aphelocoma coerulescens*), most remiges are not molted and instead are retained throughout the first year. In such species, it is possible that coloration could function as a signal to parents or siblings in the nest environment or to convey information to potential mates or same-sex competitors.

Hypotheses of reliable signaling propose that, because ornaments covary positively with condition, ornamentation can be used by conspecifics to evaluate individual quality (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Andersson 1994). Reliable signaling of health and sex by juveniles may be adaptive in at least two, non-mutually exclusive ways. First, parents might preferentially care for certain offspring if parents are likely to benefit from discriminating among offspring. Evidence for parental preference of colored ornaments during food provisioning has been found in American Coots (*Fulica americana*; Lyon et al. 1994) and the Great Spotted Cuckoo (*Clamator glandarius*) (Rowe 1999; Soler et al. 1995). Parents may also benefit from choosiness in feeding if one sex is more valuable than the other (Trivers and Willard 1973). Many bird species that appear sexually monochromatic to the human eye may be dichromatic to the UV-sensitive avian eye (e.g. Mennill et al. 2003; Eaton 2005), and parents may use this information to adjust feeding rates. Second, variation in juvenile coloration also could be used to signal information to siblings in the nest (Kilner 1999) or to signal dominance in juvenile flocks (Rohwer 1975).

The Florida Scrub-Jay is a cooperatively breeding, socially and genetically monogamous species (Woolfenden and Fitzpatrick 1996; Quinn et al. 1999) with extensive structurally based (i.e. created largely without pigments through the coherent scattering of light by highly ordered tissues; see Hill and McGraw 2006) blue plumage that appears monochromatic to the human eye (Woolfenden and Fitzpatrick 1996). Florida Scrub-Jays live in permanently defended territories and ownership is passed on to a sequence of replacement breeders, some of which are offspring heirs. With few exceptions (e.g. for widowed birds), only males obtain territories and only males that possess territories obtain mates (Woolfenden and Fitzpatrick 1986). Approximately one-half of males obtaining territories inherit them (either through inheriting the entire territory or gaining part of that territory through 'territorial budding'; Woolfenden and Fitzpatrick 1996). Thus, competition for territories is intense. During territorial encounters, Florida Scrub-Jays display a stereotypic 'lateral display' in which birds within 1 m of a rival will hop sideways toward the rival with the tail spread and tilted toward the opposing bird. During mutual encounters, two jays will orient toward the other's tail and circle one another (Woolfenden and Fitzpatrick 1996). These displays suggest that males may use tail color in competition for territories.

Our objectives were to document the extent of natural variation in plumage coloration in juvenile Florida Scrub-Jays, to determine the extent of dichromatism and investigate potential relationships between body condition and plumage coloration.

Methods

Field methods

All data were collected as part of a long-term on-going study of the behavior and ecology of Florida Scrub-Jays at Archbold Biological Station, Highlands County, Florida, USA (27°10′N, 81°21′W, elevation 38–68 m a.s.l.). Since 1970, in a study tract of approximately 500 ha, every jay has been individually color-banded and all events pertinent to survival, movement and reproduction recorded (Woolfenden and Fitzpatrick 1984). All nests were monitored, and nestlings were weighed and banded on day 11 after hatching. In July, recently independent young-of-the-year (mean ± SD, range; 72.1 ± 12.7, 50–191 days post-fledging; Woolfenden 1978) were trapped and measured, and the fully grown outermost right (R6) rectrix of each bird was plucked and stored in envelopes in a climate-controlled room. Sex was assigned either by the observation of a juvenile female-specific 'hic' call or incubation behavior and, in later years, by genetic analysis (Woolfenden and Fitzpatrick 1996) following the protocol of Griffiths et al. (1998).

Young Florida Scrub-Jays begin to grow tail feathers while still in the nest (mostly in May) and complete feather growth as fledglings at approximately 3–4 months old (Woolfenden 1978). Although young undergo a molt (Prebasic I) in late summer to early fall, only body feathers are molted, and most rectrices and all primary coverts are retained until their second summer (Bancroft and Woolfenden 1982). Only about 4% of the yearlings breed; most remain in their natal territory and help the resident breeders (Woolfenden and Fitzpatrick 1996).

Feather growth rates were estimated by measuring the width of alternating dark and light bars on the right outer rectrix. Each pair of dark/light bands represents 1 day's growth (Michener and Michener 1938), and wider bars are associated with faster growth rates and with better nutritional condition (Grubb 1989; Hill and Montgomerie 1994; Jenkins et al. 2001). The outer rectrix extends <2 cm beyond the body at the time of fledging, and growth to 12–14 cm is complete before nutritional independence (Woolfenden 1978); therefore, the rate of feather growth can be used as an index of dependent fledgling nutrition. Using methods detailed in Grubb et al. (1998), we measured the average width (mm) of ten growth bars centered on a point two-thirds of the distance from the proximal end of each rectrix.

Plumage reflectance was quantified using an Ocean Optics S2000 spectrometer (Ocean Optics, Dunedin, FL), a PX-2 xenon pulse lamp and a single, bifurcated fiber-optic probe. The measurements were obtained from an illuminated area 2 mm in diameter and were taken at a 90° angle to the feather surface. We measured tail coloration at three points on each feather—1, 2 and 3 cm from the distal tip of the feather—and then averaged the reflectance spectra from the three points. Repeatability among the three measurements was high; spectrometer readings from the same body region (i.e. the three described above) were strongly correlated (all $r > 0.95$, all $P < 0.01$). We summarized reflectance data by calculating three standard descriptors of reflectance spectra: UV chroma, mean brightness and hue. Ultraviolet chroma, a measure of spectral purity, is the ratio of the reflectance in the UV range to total reflectance ($\Sigma R_{300-400}/(\Sigma R_{300-700})$). Mean brightness, or the amount of light reflected by the feather, is the mean of the summed reflectance from 300 to 700 nm. Hue, the principal color reflected by the feather, is the wavelength (nm) corresponding to maximal reflectance (λ_{max}).

Statistical analyses

We used SPSS ver. 15.0 (SPSS, Chicago, IL) software to analyze the data, and all statistical tests were two-tailed. We tested for normality using Shapiro–Wilk tests and compared multiple measures of plumage coloration using Pearson's correlations. Pseudoreplication due to common nest origin was eliminated by randomly selecting one nestling from each brood for analysis. Although we collected 8 years of data from 1990 to 2001, in this study we only included the 5 years for which we had sample sizes larger than ten broods per year. We used General Linear Models to test for the influence of sex, year, hatch date, growth bar width and mass at age 11 days on juvenile coloration. Sex was included as a fixed factor, year was included as a random factor and hatch day of year, growth bar width and mass at age 11 days were included as covariates. In all models, we first included all interaction terms. However, as no interaction terms were significant (all $P \geq 0.4$), we then re-ran models with no interaction terms.

Results

The relationships among multiple measures of structural coloration

As in other studies of blue structural color (e.g. Shawkey et al. 2003; Siefferman and Hill 2003), measures of color were highly correlated. Tails with greater UV chroma had lower wavelength hues (Pearson correlation $r = -0.72$, $P < 0.001$, $n = 186$) and were brighter ($r = 0.27$, $P < 0.001$, $n = 186$). Tails with lower wavelength hues were also brighter ($r = -0.27$, $P < 0.001$, $n = 186$). Some studies have used principal components analysis (PCA) on color data to reduce the number of correlated variables in analyses (Siefferman and Hill 2003), but previous studies on this type of blue structural color have used these individual color measures and found important differences in both the mechanisms of their variation (Shawkey et al. 2003) and their signaling properties (Sheldon et al. 1999) so we maintained their use in our study.

Effects of sex, year, hatching date and body condition on coloration

Males expressed greater UV chroma than females (Table 1), suggesting that Florida Scrub-Jays are dichromatic in bird-visible wavelengths. This pattern appears to be primarily driven by female feathers reflecting greater proportions of light in the longer wavelengths (Fig 1).

We also found an effect of year on all measures of plumage coloration (Table 2). These differences were probably not caused by differences in storage time, as one study has shown little influence of storing time on structural coloration of specimens less than 60 years old (SM Doucet, personal communication), and we found no significant correlations between time of storage and color (Pearson correlation $r = 0.74$, $n = 5$, $P = 0.15$; $r = -0.65$, $n = 5$, $P = 0.24$; $r = -0.43$, $n = 5$, $P = 0.48$).

Table 1 Mean (±SD) of measures of juvenile tail color for male and female Florida Scrub-Jays in each year of the study

Year	Sex	n	UV chroma	Hue	Brightness
1991	Male	15	0.250 ± 0.031	398.7 ± 16.9	8.481 ± 1.02
1991	Female	21	0.239 ± 0.036	406.0 ± 17.9	8.325 ± 1.068
1993	Male	18	0.271 ± 0.011	380.1 ± 15.5	8.875 ± 0.570
1993	Female	24	0.266 ± 0.013	380.2 ± 22.7	8.986 ± 0.463
1999	Male	22	0.265 ± 0.013	392.0 ± 15.7	7.955 ± 0.680
1999	Female	29	0.259 ± 0.010	395.3 ± 16.4	8.541 ± 0.677
2000	Male	14	0.286 ± 0.015	359.8 ± 24.2	8.233 ± 0.643
2000	Female	18	0.271 ± 0.013	374.2 ± 18.	8.540 ± 0.923
2001	Male	13	0.276 ± 0.007	392.5 ± 30.0	7.576 ± 0.653
2001	Female	12	0.265 ± 0.005	386.1 ± 31.7	7.869 ± 1.190

UV chroma, Ratio of the reflectance in the UV range to total reflectance ($\Sigma R_{300-400}/(\Sigma R_{300-700})$); brightness (amount of light reflected by the feather), mean of the summed reflectance from 300 to 700 nm; hue (principal color reflected by the feather), wavelength (nm) corresponding to maximal reflectance (λ_{max})
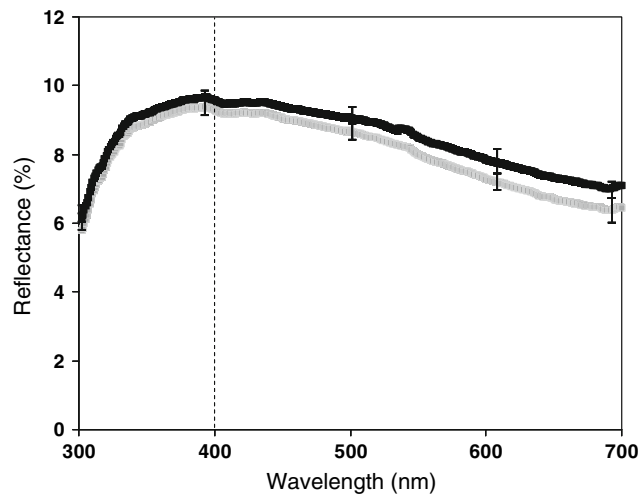
Fig. 1 Average reflectance (with standard *error bars* at 100-nm intervals) of the UV-blue tail feathers of male (*gray line*) and female (*black line*) Florida Scrub-Jays in 1999. *Dashed line* separates UV and human-visible wavelengths

Mass was significantly positively correlated with growth bar width (Pearson correlation $r = 0.23$, $P = 0.002$, $n = 174$) and hatch date (Pearson correlation $r = 0.16$, $P = 0.04$, $n = 177$). Ultraviolet chroma was significantly related to growth bar length (Table 2). Juveniles that grew feathers faster had tails with greater UV chroma (Fig. 2), suggesting that UV chroma could be a condition-dependent trait. We found no significant relationships between measures of plumage coloration and mass at day 11 (Table 2). Moreover, neither hue nor brightness was significantly related to growth bar length (Table 2). Hatching date influenced the brightness of juvenile tail coloration; the tails of offspring that hatched earlier in the year were brighter (Table 2).

Discussion

Reflectance spectrometry revealed significant variation in UV-blue plumage coloration of juvenile Florida Scrub-Jays

Table 2 Relationships between sex, year, hatching day and body condition (growth bar width and body mass) on plumage coloration of juvenile Florida Scrub-Jays

Trait	Factor	B	Standard error	df	F	P
UV chroma (%)	Sex	−0.011[a]	0.008	1	20.13	0.006
	Year					
	1991	−0.029[b]	0.007	4	40.49	<0.001
	1993	−0.006[b]	0.007			
	1999	−0.011[b]	0.007			
	2000	0.012[b]	0.008			
	Hatch day of year	−1.84e−005	0.000	161	0.38	0.85
	Growth bar width	0.015	0.007	161	5.00	0.02
	Mass at 11 days	−3.59e–005	0.000	161	0.03	0.87
Hue (nm)	Sex	−6.731[a]	8.354	1	1.13	0.34
	Year					
	1991	5.39[b]	8.236	4	16.49	0.007
	1993	−11.63[b]	7.861			
	1999	1.41[b]	7.608			
	2000	36.28[b]	8.391			
	Hatch day of year	−0.024	0.104	161	0.06	0.82
	Growth bar width	−9.910	0.279	161	1.85	0.17
	Mass at 11 days	0.095	0.239	161	0.16	0.69
Brightness (%)	Sex	0.337[a]	0.319	1	1.77	0.25
	Year					
	1991	1.136[b]	0.315	4	9.16	0.02
	1993	1.519[b]	0.300			
	1999	0.567[b]	0.291			
	2000	0.871[b]	0.321			
	Hatch day of year	0.010	0.004	161	5.92	0.02
	Growth bar width	0.310	0.278	161	1.25	0.27
	Mass at 11 days	−0.013	0.009	161	2.10	0.15

All interaction terms were non-significant ($P > 0.4$)

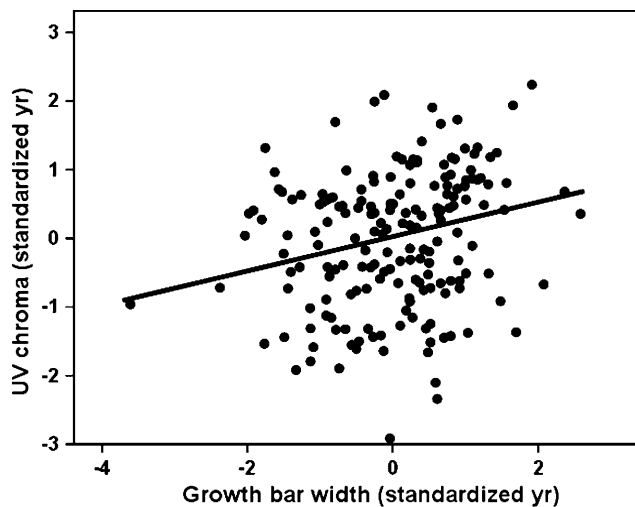[a] Relative to male

[b] Relative 2001

Fig. 2 Relationship between UV chroma and mean growth bar width of fledgling Florida Scrub-Jays (data have been standardized for year)

with respect to sex and body condition. Juvenile Florida Scrub-Jays are sexually dichromatic in avian-visible UV wavelengths, with males expressing greater UV chroma than females. The reflectance curves of males and females (Fig. 1) indicate that these differences in chroma are caused primarily by the female feathers reflecting proportionally more light in the longer wavelengths. Male feathers, therefore, reflect more pure UV-blue coloration.

Tail feathers of birds in better condition during feather growth had greater UV chroma than those of birds in poorer condition. The correlation between plumage color and nestling condition, as measured by growth bar width, suggests that ornamentation is condition dependent and could convey honest information about individual quality in both sexes. Plumage coloration of juvenile Florida Scrub-Jays was also influenced by year and correlated with day of hatching. Juveniles that fledged earlier in the season expressed more exaggerated plumage coloration (i.e. brighter tail feathers). The effects of year and hatch date on color further suggest that coloration is influenced, at least in part, by environmental variation.

Ornamentation in juvenile Florida Scrub-Jays may be a condition-dependent trait; however, two other mechanisms could explain the relationship between plumage coloration and body condition. First, the covariation of plumage coloration and body condition may have a genetic basis. Genetic correlations between coloration and condition may arise if genes responsible for coloration and body condition are located close on the genome or when a gene has pleiotropic effects on coloration and body condition. Genetic correlations between a polymorphic color trait and condition occur in the Tawny Owl (*Strix aluco*; Roulin et al. 2004). Second, coloration could be strongly heritable, and "more-ornamented" parents could provide more

resources to their offspring and influence juvenile body condition. The heritability of plumage coloration has been shown in the Barn Owl (*Tyto alba*; Py et al. 2006), and both theoretical (Hoelzer 1989) and empirical (e.g. Hill 1991) data suggest that, in some species of birds, more-ornamented parents provide more resources to their offspring. On the basis of our results we cannot differentiate between these three non-mutually exclusive mechanisms at this time. In the future, pedigree data or a cross-fostering experiment in conjunction with animal model analyses could disentangle the genetic and environmental effects on plumage coloration and condition of Florida Scrub-Jays.

Although sexual dichromatism and condition-dependent coloration in juvenile birds is relatively under-studied and the adaptive significance largely unknown, the relationship between plumage coloration and condition of Florida Scrub-Jays is consistent with studies in juveniles of two other species of birds. The UV-blue structural coloration of juvenile Blue Tits (*Parus caeruleus*; Johnsen et al. 2003) and Eastern bluebirds (*Parus caeruleus*; Siefferman and Hill 2007) is sexually dichromatic. Measures of structural coloration correlate with feather growth rates of both male and female nestling Blue Tits (Johnsen et al. 2003) and with blood protein levels of male nestling Blue Tits (Peters et al. 2007). Further, Blue Tit and Eastern Bluebird nestlings reared in enlarged broods grew tails with less elaborate plumage than those reared in reduced brood sizes (Jacot and Kempenaers 2007, Siefferman and Hill 2007). Finally, variation in structural coloration associated with hatch date has been demonstrated in juvenile Eastern Bluebirds (Siefferman and Hill 2007). Our data thus add to a growing body of literature suggesting that non-iridescent structural coloration is often condition dependent and may thus function as a signal.

One potential function of sexually dichromatic and condition-dependent juvenile coloration is to signal individual quality to caregivers in the nest or during the post-fledging period. Signaling to parents may be advantageous if caregivers adjust feeding patterns according to the traits of the offspring. Given that the tail feathers of Florida Scrub-Jays are relatively short during the nestling stage (only 10% grown), signaling in the nest seems unlikely. Moreover, because brood sizes are relatively small in Florida Scrub-Jays, competition among siblings may not be strong. Young Florid Scrub-Jays, however, remain in their natal territory for approximately 1 year and may establish dominance hierarchies with other members of their cohort (Woolfenden and Fitzpatrick 1996). Consequently, it is possible that the coloration of juveniles is important for establishing social hierarchies (i.e. status signaling hypothesis, Rohwer 1975).

An alternative function of sexually dimorphic and condition-dependent coloration is to signal information to

potential mates and competitors. However, because very few Florida Scrub-Jays (4%) retain these feathers for the first year that they breed, i.e. their first nuptial plumage, this explanation seems unlikely. For the relationship between body condition and plumage coloration to be causally linked to mechanisms of sexual selection (i.e. mate choice or within sex competition for breeding resources), relative coloration and body condition need to remain consistent from juvenile (Basic 1) to adult (Definitive) plumage. If the plumage color of individual scrub-jays remains consistent throughout their lifetime, then color as a juvenile could indicate color as an adult.

Although we detected sexual dichromatism and condition-dependent coloration using a spectrometer, we do not know that Florida Scrub-Jays perceive this variation in coloration. Further, because these data are correlative, it remains uncertain whether the structural coloration of Florida Scrub-Jays functions as a condition-dependent signal of individual quality. However, if dichromatism was caused by arbitrary preferences (e.g. Fisher 1958), then we would not expect to see correlations between bright colors and condition. Our data suggest the potential for some role for selection on plumage coloration in this cooperatively breeding species, and signaling hypotheses should be tested further through direct experiments.

Zusammenfassung

Die Jugendfärbung von Buschhähern (*Aphelocoma coerulescens*) unterscheidet sich zwischen den Geschlechtern und korreliert mit der Kondition

Der Buschhäher ist ein monogamer kooperativer Brüter, bei dem sowohl Männchen als auch Weibchen ein intensiv blaues Gefieder auf der Basis von Strukturfarbe haben. Jungvögel dieser Art haben blaue Schwanz- und Flügelfedern, die im Nestlingsstadium zu wachsen beginnen, und einige dieser Federn werden während des ersten Jahres beibehalten. Obwohl hier beide Geschlechter gleichfarbig erscheinen, haben wir untersucht, ob ein kryptischer Sexualdichroismus in Bezug auf Ausmaß und Muster der Färbung in den Schwanzfedern juveniler Buschhäher vorlag. Wir haben dann ermittelt, ob die Variation in der Gefiederfärbung mit dem Ernährungszustand während der Mauser assoziiert war. Schwanzfedern juveniler männlicher Buschhäher zeigten einen größeren Anteil ultravioletten Reflexionsvermögens als die von Weibchen. Die Körpermasse am elften Nestlingstag und die Ptilochronologie der juvenilen Schwanzfedern wurden als Maße des individuellen Ernährungszustandes während des Federwachstums verwendet, und letzteres stand in positivem Zusammenhang

mit der UV-Chrominanz. Diese Daten zeigen, dass beim Buschhäher die Geschlechter unterschiedlich gefärbt sind, und deuten darauf hin, dass die Variation in der Gefiederfärbung konditionsabhängig sein könnte, wobei wir alternative Erklärungen allerdings nicht ausschließen können. Jugendliche Gefiederfärbung hat daher das Potential, als ein Signal individueller Qualität bei Männchen wie auch Weibchen zu funktionieren.

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