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Parasites and plumage in Steller's jays: an experimental field test of the parasite-mediated handicap hypothesis

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Parasites and plumage in Steller's jays: an experimental field test of the parasite-mediated handicap hypothesis

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The handicap hypothesis broadly argues that ornamental traits and displays are costly to produce and are a function of individual quality and condition. Consequently, the extent of ornament expression can act as an honest indicator of quality, condition or susceptibility to parasites, and influence the behavior of mates or competitors. We used reflectance spectrometry to quantify non-iridescent, ultraviolet (UV) and blue structurally-based plumage color and character size in relation to individual condition (feather growth rate) and occurrence of disease caused by a parasite infestation (knemidokoptic mange) in wild male Steller's jays (*Cyanocitta stelleri*). We then attempted to experimentally reduce parasite load prior to molt and quantified the relative change in plumage and condition. Those birds with faster feather growth rates (i.e., in better condition) had lower hues (i.e., reflected shorter wavelengths, displaying a more intense, brilliant UV-blue color), suggesting the possibility of condition or feather growth rate-dependent production of color. We found that UV reflectance (UV chroma) was positively related to the occurrence of disease. We detected no effect of experimental treatment on plumage or condition. In conclusion, our results are suggestive of possible condition-dependent development of structurally-based plumage, and the positive relationship between macro-parasite–caused disease intensity and UV blue plumage color, demonstrated for the first time in this study, did not support the parasite-mediated handicap hypothesis.

KEY WORDS: condition-dependent, *Cyanocitta stelleri*, handicap, parasites, ptilochronolgy, Steller's jay, structural color, ultraviolet reflectance.

INTRODUCTION

In many species, ornamental traits and displays function in predator-prey interactions, agonistic encounters, intra-sexual interactions and often mate selection, where females choose mates with elaborate, ornamental traits (Darwin 1871; Fisher 1915; M. Andersson 1982; S. Andersson 1994; M. Andersson & Iwasa 1996). Several

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attempts have been made to explain the evolution and maintenance of this preference for the most exaggerated ornaments (FISHER 1915; RYAN 1990; RYAN & KEDDY-HECTOR 1992; S. ANDERSSON 1994). One group of proposed explanations, the "good genes" collection of hypotheses (see M. ANDERSSON 1982; KODRIC-BROWN & BROWN 1984), includes the handicap (ZAHAVI 1975, 1977) and the closely associated parasite-mediated handicap hypothesis (HAMILTON & ZUK 1982).

The handicap principle asserts that costly secondary sexual traits, including elaborate patterns, colors or displays, may act as honest indicators of intrinsic individual quality or condition. Exceptionally healthy or fit individuals can achieve maximum expression of these energetically costly traits. Intrinsic individual quality can therefore be assessed by potential mates or competitors via condition-dependent development of traits, and influence mate selection or conspecific behavior (ZAHAVI 1975, 1977). HAMILTON & ZUK's (1982) hypothesis explicitly incorporated disease as the potential proximate mechanisms regulating development of ornamental traits. Disease can impart heavy costs on the nutritional state and ultimately the health and condition of individuals (HAMILTON & ZUK 1982; FOLSTAD & KARTER 1992; PROCTOR & OWENS 2000). The parasite-mediated handicap hypothesis posits that individuals with "good genes" for pathogen resistance can better afford to produce and display elaborate traits without suffering diminished health and ultimately fitness. In addition, high quality individuals can acquire more resources to meet daily energy requirements, maintain condition and fight disease. HAMILTON & ZUK (1982) argued that ornamental traits can reliably signal current infection or susceptibility to parasites. By assessing the degree of trait expression, potential mates can assess parasite load or susceptibility and can avoid direct exposure to parasites for themselves and their offspring. More importantly, they may benefit from acquisition of superior genes for parasite resistance in future offspring (HAMILTON & ZUK 1982; FOLSTAD & KARTER 1992).

It has been suggested that individual quality in animals can only be honestly signaled by secondary sexual characteristics which are costly to produce and maintain (ZAHAVI 1975, 1977; HAMILTON & ZUK 1982; IWASA & POMIANKOWSKI 1994; but see SZÁMADÓ 2010). In birds there are large energetic costs associated with the annual regrowth of feathers and associated ornamental plumage and colors, such as immune system function, thermoregulatory stability and nutritional demands (LINDSTRÖM et al. 1993; FITZPATRICK 1998; S. ANDERSSON 1999; HILL 2011). Additional costs associated with displaying exaggerated plumage may include increased competition and predation risks (ROHWER & EWALD 1981; HAMILTON & ZUK 1982; FOLSTAD & KARTER 1992; LINDSTRÖM et al. 1993; S. ANDERSSON & PRAGER 2006).

Coloration in feathers can be produced by pigment or structurally-based mechanisms. Pigment-, including melanin-, based colors are responsible for most of the red, orange, yellow, black, and brown colors found in feathers (HILL 2006; MCGRAW 2006). Structural colors are produced by the interaction of feather microstructure and light and are responsible for blue, iridescent and most green of feathers (PRUM et al. 1998; PRUM 2006). Non-iridescent, blue structural coloration is produced through ordered scattering of light by microscopic air vacuoles of the keratin layer and light-absorbing melanin (PRUM et al. 1998; PRUM 2006; SHAWKEY & HILL 2006). Structurally-based feathers can reflect light in the wavelengths (color) visible to humans (400–700 nm) and in the ultraviolet range (UV; 315–400 nm), which is within the visible range of birds (BURKHARDT 1989; BENNET & CUTHILL 1994; CUTHILL et al. 2000). While individual variation, condition dependency, and behavioral influence of pigment-based color is well documented (reviewed in JOHNSTONE 1995; HILL 2002), variation of reflectance in the UV range of structurally-based colors has only more recently been studied (DALE

2006; Hill 2006; Prum 2006). Recent research has revealed some links between UV coloration and various indices or measures of quality (Doucet 2002; Doutrelant et al. 2008, 2012; Siefferman et al. 2008; Griggio et al. 2010b). In addition to plumage coloration, the size and symmetry of plumage ornaments, such as crests or elaborate patterning, may also be condition-dependent and under selective pressure (S. Andersson 1994).

Our objectives were to experimentally test the parasite-mediated handicap hypothesis in a wild population of adult male Steller's jays, *Cyanocitta stelleri*. We quantified individual variation in non-iridescent structural plumage color (brightness, chroma, hue), the width of blue-black wing bars, and the size of crest plumage in relation to condition (quantified by measuring the alternating light and dark bands on the feather, which signify daily feather growth rates) and disease caused by infestation of *Knemidokoptes* mites. Parasite loads were then experimentally reduced using a parasiticide prior to the post-breeding molt. Subsequently, we tested for a change in plumage characteristics following the molt. Based on the handicap and parasite-mediated handicap hypotheses, we tested whether secondary sexual traits were positively related to individual condition or negatively to the occurrence of disease. We also determined whether potential plumage ornament quality and individual condition improved in individuals with experimentally reduced parasite loads.

METHODS

Species and general methods

We conducted the experiment on a population of Steller's jays, as part of an ongoing, long-term study of behavior and ecology (Black 1998) in Humboldt County, CA (USA, 40°59′N, 124°06′W), which was characterized by mild wet winters and cool, dry summers (Barnhart et al. 1992). The approximately 70 ha study area was composed of suburban neighborhoods and the Humboldt State University campus bordering a coastal redwood (*Sequoia sempervirens*) forest. Steller's jays are common, conspicuous members of the corvid family with blue and black plumage, found across much of the western United States (Greene et al. 1998). Adult birds in our population are non-migratory and undergo a full molt between June and September (Pyle 1987; Greene et al. 1998). Jays in this population have black crests with paired blue stripes on the crest, which are often erected and displayed during agonistic and sexual behaviors (Brown 1964). Their flight feathers have a sexually dichromatic, non-iridescent structurally-based blue color with dark banding which reflects light in the UV spectrum (Fig. 1; Shawkey & Hill 2006). The dorsal sides of the wings (i.e., the blue color and banded pattern) are displayed and visible to potential mates and competitors during sexual display and agonistic encounters (Brown 1964).

We measured plumage characteristics and parasite load from January–March 2007–2010 (blue-black wing bars and feather growth rates 2009–2010 only). Male birds captured in 2009 were administered the experimental treatment in June–July 2009 and captured again from January–March 2010 (before-after control-impact design). Plumage traits were quantified when mate selection and bond formation occurs (Brown 1964; J.M. Black & P.O. Gabriel unpub.). Birds were sexed via observations of sex-specific vocalizations (Brown 1964; Greene et al. 1998; J.M. Black & P.O. Gabriel unpub.) and genetic analysis (K. Overeem, unpub.). To quantify plumage reflectance and condition, secondary flight feather 7 was removed and stored in a climate controlled environment. All birds were held for approximately 30 min from time of capture and were immediately released upon completion of data collection.

Preliminary analysis indicated that adult male Steller's jay body mass at the time of molt, independent of body size, was positively related to feather growth rates ($r_{22} = 0.50$, 95% CI = 0.12–0.75, Pearson's correlation, $P < 0.02$). Passerine body weights can fluctuate over short time

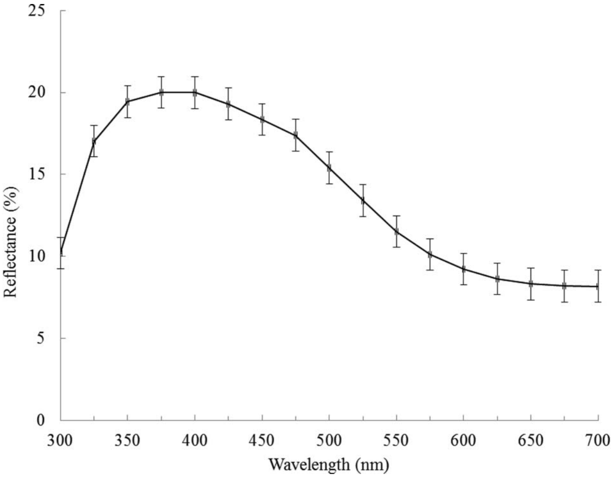

Fig. 1. — Average reflectance curve (relative to a white standard) of an adult male Steller's jay ($n = 32$; ± standard error) structurally-based blue secondary flight feather, Arcata, CA 2009.

periods (Lehikoinen 1987; Haftorn 1989); therefore we examined feather growth rates, which are static, temporally stable representations of individual nutritional, conditional and physical state during molt (Grubb 2006). Quantifying growth bars taken from birds in the non-breeding season allowed us to create an index of individual condition during the post-breeding molt, when feather structures responsible for color are developed. Using methods described by Grubb (2006), we quantified growth rates on one secondary flight feather by measuring the pairs of alternating bands of color on the inner vane, which each represent 24 hr of growth (6 light-dark bands per bird). We only measured feathers which had well-defined growth bars throughout the entire vane. Average daily growth bar width was calculated to create an index of bird condition, where larger daily growth rates (i.e., faster feather growth) signified better condition during molt (Grubb 2006).

We quantified structural feather color using an Ocean Optics S2000 spectrometer, a PX-2 xenon pulse lamp and a fiber-optic probe (Endler 1990; S. Andersson & Prager 2006; Ocean Optics, Dunedin, Florida, USA). We restricted the analysis to wavelengths between 300 and 700 nm and extracted the original reflectance spectra with CLR software, version 1.05 (Montgomerie 2008). We placed feathers on black paperboard and held the fiber-optic probe at 90° to the feather. Feather reflectance was measured at six random points, within the three central segments between the dark bars on the outer vane. The reflectance spectra were averaged to calculate three standard descriptors of reflectance for each individual: brightness, UV chroma and hue (Montgomerie 2006). We calculated feather brightness as the total amount of light reflected, relative to a white standard (300–700 nm). Ultraviolet chroma, or the spectral purity, is the ratio of total reflectance over the UV range and reflectance of the total spectrum (R300–400/R300–700 nm), where a higher percentages equates to reflected wavelengths more restricted to UV range (i.e., more pure UV reflectance). Hue, the principal color reflected, was the wavelength at peak reflectance, where reflection of shorter wavelengths indicate a more UV-shifted color (i.e., more reflectance in the UV range) (Montgomerie 2006).

We quantified the width of the repeating blue-black barring on the secondary feathers collected. We averaged the width of 5 bi-colored patches, centered on a line located 2/3 of the length of the entire feather from the proximal end (morphologic data was collected to the nearest 0.1 mm) (Grubb 2006). We measured crest size as the maximum raised crest feather height from top of the skull. We quantified crest stripe height by measuring the height of both stripes and calculating an average stripe height.

Visible evidence of chronic mange or scaley-leg mite (*Knemidokoptes* spp.) infestation in this population of Steller's jays was regularly encountered and documented during routine trapping efforts (J.M. BLACK & P.O. GABRIEL unpub.). The results of necropsy confirmed the presence of *Knemidokoptes* spp. (UNITED STATES GEOLOGIC SURVEY 2000). The disease caused by *Knemidokoptes* mites can range from mild cases of inflammation to severe leg and digit inflammation, digit malformation, hemorrhaging wounds and secondary infections (BAKER et al. 1956; KIMERSE 1966; SHANTA et al. 2006). Severe cases of mange can result in interference with food consumption by giving continuous irritation, ultimately reducing health, reducing condition and increasing morbidity (SOULSBY 1982; PENCE et al. 1999; LATTA 2003). Knemidokoptic mange was quantified by creating a binomial variable of non-infested (sub-clinical infestation, no visible signs of inflammation) and infested (clinically diseased, observable signs of inflammation, scale loss, and nail or digit malformation).

Experimental procedure

We randomly assigned birds to either treatment or control groups. The treatment group received ivermectin (Ivomec® Merial, Boise, Idaho, USA), a broad-spectrum anti-parasite medication recommended for the treatment of knemidokoptic infestation (KAHN 2005; ULLAH et al. 2005). Ivermectin was diluted with propylene glycol (0.25mg/ml) and administered subcutaneously at 0.4 mg/kg body weight (KAHN 2005; ULLAH et al. 2005). Control birds received sterile water injected subcutaneously at 0.4 ml/kg.

Data analysis

All variables and residuals were tested for deviation from normality and homoscedacity with Shapiro-Wilk and Bartlett's tests, respectively. To control for body size, we used residuals from a linear regression of wing chord versus crest height ($F_{1,31} = 3.789$, $P = 0.057$) and crest stripe ($F_{1,31} = 2.356$, $P = 0.131$) to create indices of ornament size. Two-tailed Pearson's correlations were used to assess the relationship between average feather growth rate and plumage characteristics. Preliminary analysis indicated no effect of year on all feather color or crest variables from data collected in 2007, 2008 and 2009 [analysis of variance (ANOVA), $P > 0.6$], and therefore these data were pooled to test for differences in expression of plumage and feather growth rate of non-infested and infested individuals using two-tailed t-tests. We used paired *t*-tests to examine changes in secondary sexual characteristics and feather growth rates in treatment and control groups after experimental treatment. This was calculated as the difference in a given variable before and after the treatment. Two-tailed t-tests were used to compare absolute change in treatment versus control group (i.e., test for difference in extent of change), only when a significant change was found for a given variable. We confined tests to male birds aged as 3rd year or older as preliminary analysis indicated that juvenile plumage coloration differed from adult plumage.

Although results are presented with traditional test statistics and *P* values, interpretation based solely on these values may not reveal the true biological significance of relationships (NAKAGAWA 2004; GARAMSZEGI 2006). Furthermore, to reduce the probability of committing Type II errors while conducting multiple comparisons we did not employ any Bonferroni corrections to our critical values (NAKAGAWA 2004; GARAMSZEGI 2006). To evaluate the biological significance of our results, we assessed the direction and strength of relationships among variables, in place of simply evaluating based on critical values by calculating effect sizes and 95% confidence intervals. We used effect sizes and 95% confidence intervals to infer the magnitude of relationships and the precision and certainty with which the data indicate those relationships (GARAMSZEGI 2006; NAKAGAWA & CUTHILL 2007; GARAMSZEGI et al. 2009). We calculated correlation coefficients (i.e., effect sizes) from regressions either directly (Pearson's r_S) or from two-sample tests (calculated as d and converted into r; COHEN 1988). We interpreted results with 95% confidence intervals that did not overlap zero with an effect size of r = 0.1 as small, r = 0.3 as medium, and r = 0.5 as large (COHEN 1988).

RESULTS

Plumage and feather growth rate

The color hue in male Steller's jay plumage was inversely related to feather growth rates with a medium effect, meaning birds which grew feathers faster reflected shorter and bluer, UV wavelengths ($r_{22} = -0.41$, 95% CI = from – 0.69 to – 0.008, $P = 0.05$; Fig. 2). Feather growth rates were not correlated to brightness and UV chroma ($r_{22} = -0.13$, 95% CI = from – 0.50 to 0.28, $P = 0.53$; $r_{22} = 0.08$, 95% CI = from – 0.33 to 0.47, $P = 0.73$, respectively). The size of the blue-black wing barring, crest and crest stripe was not related to feather growth rates ($r_{22} = -0.06$, 95% CI = from – 0.37 to 0.43, $P = 0.79$; $r_{22} = 0.07$, 95% CI = from – 0.32 to 0.48, $P = 0.75$; $r_{22} = 0.29$, 95% CI = from – 0.13 to 0.62, $P = 0.16$, respectively).

Plumage and parasites

Forty-two percent of adult male Steller's jays ($n = 63$) had visible signs of knemidokoptic mange. Ultraviolet chroma was greater in birds with mange than birds with no mange with a medium effect ($r_{59} = 0.31$, 95% CI = from 0.06 to 0.51, *t*-test, $t = -2.56$, $P = 0.013$; Fig. 3). Feather brightness and hue was not related to occurrence of mange ($r_{59} = -0.12$, 95% CI = from – 0.35 to 0.13, *t*-test, $t = 0.95$, $P = 0.35$; $r_{59} = -0.08$, 95% CI = from – 0.32 to 0.17, *t*-test, $t = 0.67$, $P = 0.5$, respectively). The blue-black wing bars, crest height and crest stripe height were not related to occurrence of mange ($r_{28} = -0.27$, 95% CI = from – 0.58 to 0.10, *t*-test, $t = 1.41$, $P < 0.02$; $r_{60} = 0.23$, 95% CI = from – 0.02 to 0.45, *t*-test, $t = -1.91$, $P = 0.06$; $r_{55} = 0.02$, 95% CI = from – 0.23 to 0.26, *t*-test, $t = -0.26$, $P = 0.79$, respectively). Feather growth rates were similar for birds with and without signs of mange ($r_{27} = 0.11$, 95% CI = from – 0.30 to 0.50, *t*-test, $t = -0.58$, $P = 0.57$).

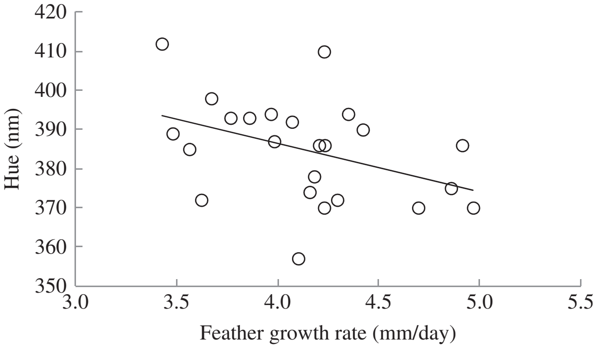

Fig. 2. — Average feather growth rates and hue (wavelength at peak reflectance) of adult male Steller's jays' secondary flight feathers in Arcata, CA 2009.

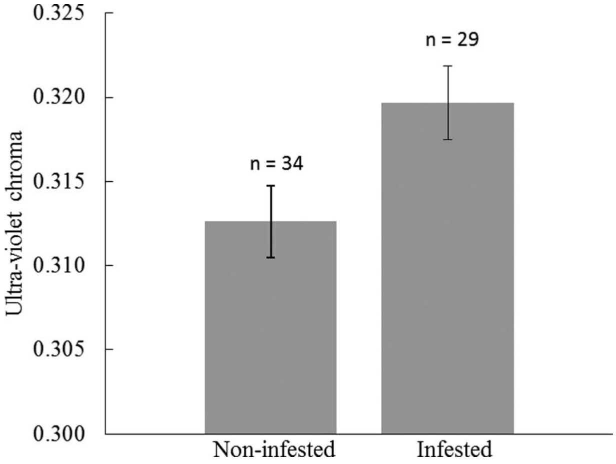

Fig. 3. — Average plumage ultraviolet chroma (± standard error; ratio of reflectance in the ultraviolet range over total spectrum; 300 – 400/300 – 700 nm) of secondary flight feather in adult male Steller's jays with visible signs of knemidokoptic mange (infested) and with no signs of mange (non-infested), Arcata, CA 2007–2009.

Experimental treatment

We recaptured 11 treatment and 10 control male Steller's jays. Brightness in the recaptured treatment group was higher than the recaptured control group prior to treatment, but the original randomly selected group had similar values. Only one bird that received the experimental treatment had visible signs of healing from wounds caused by knemidokoptic mite infestation (e.g., reduced inflammation, re-growth of scales on legs).

Regarding the relative change of feather characteristics after administering the parasiticide, treatment birds grew feathers which were 10% brighter with a strong effect (i.e., reflected more light) ($r_9 = 0.62$, 95% CI = from 0.24 to 0.83, paired *t*-test, $t = -5.23$, $P < 0.0005$; Table 1), while control birds had a 5% increase in brightness after their experimental treatments with a strong effect ($r_9 = 0.56$, 95% CI = from 0.16 to 0.80, paired *t*-test, $t = -2.29$, $P = 0.023$; Table 1). However, the extent of absolute change was similar in the treatment and control groups ($r_{18} = 0.27$, 95% CI = from – 0.63 to 0.20, two-tailed *t*-test, $t = -1.59$, $P = 0.12$). Ultraviolet chroma did not change in the treatment or control group ($r_{10} = 0.08$, 95% CI = from – 0.35 to 0.49, paired *t*-test, $t = -0.85$, $P = 0.20$; $r_9 = -0.09$, 95% CI = from – 0.51 to 0.36, paired *t*-test, $t = 0.883$, $P = 0.80$, respectively; Table 1). Plumage hue also did not change in treatment or control groups ($r_{10} = 0.004$, 95% CI = from – 0.42 to 0.42, paired *t*-test, $t = -0.018$, $P = 0.50$; $r_9 = 0.15$, 95% CI = from – 0.31 to 0.56, paired *t*-test, $t = -0.840$, $P = 0.41$, respectively; Table 1). The width of the blue-black barring did not change in either treatment or control groups ($r_{10} = 0.09$, 95% CI = from – 0.34 to 0.49, paired *t*-test, $t = -1.18$, $P = 0.13$; $r_9 = 0.33$, 95% CI = from – 0.13 to 0.68, paired *t*-test, $t = -1.54$, $P = 0.13$, respectively; Table 1). Crest stripe height in the treatment group increased by 14 % with a strong effect ($r_9 = 0.63$, 95% CI = from 0.25 to 0.84, paired *t*-test, $t = -5.19$, $P < 0.0003$; Table 1), while control birds increased by 10 % after experimental treatment ($r_{10} = 0.33$, 95% CI = from 0.15 – 0.69, paired *t*-test, $t = -2.86$, $P = 0.014$; Table 1).

Table 1.

Male Steller's jay color components, secondary sexual traits and average daily feather growth rates (± SD) of treatment and control groups before and after experimental parasite reduction, Arcata, CA 2009–2010.

	Treatment ($n = 11$)		Control ($n = 10$)	
	Before	After	Before	After
Brightness (%)	**58.5 ± 3.8**	**64.5 ± 4.42**, $n = 10$	**53.84 ± 2.1**	**56.7± 3.96**
UV chroma	0.315 ± 0.015	0.318 ± 0.012	0.318 ± 0.011	0.316 ± 0.005
Hue (nm)	387.45 ± 12.89	387.54 ± 9.98	386.84 ± 13.9	391.3 ± 13.1
Wing bar width (mm)	7.9 ± 1.08	8.1 ± 0.6	8 ± 0.54	8.38 ± 0.49
Crest stripe height (mm)	**16.1 ± 4.5**	**18.3 ± 4.6**, $n = 10$	**17.53 ± 2.7**	**19.43 ± 2.7**
Crest height (mm)	46.03 ± 2.5	46.18 ± 2.5	45.32 ± 1.77	44.8 ± 1.4
Feather growth rate (mm/day)	4.34 ± 0.44	4.12 ± 0.36, $n = 7$	4.16 ± 0.46	4.26 ± 0.48, $n = 9$

Brightness (total reflectance relative to white standard, 300–700 nm), ultraviolet chroma (ratio of reflectance in UV range over total range; 300–400/300–700 nm), hue (wavelength at peak reflectance), significant within group differences are bolded (significance based on effect sizes and 95% confidence intervals, see text for further description of statistical methods).

The extent of absolute change in crest stripe height was similar in the treatment and control groups ($r_{18} = -0.009$, 95% CI = from – 0.45 to 0.43, one-tailed *t*-test, $t = 0.36$, $P = 0.35$). Crest feather height did not change in treatment or control groups ($r_{10} = 0.03$, 95% CI = from – 0.40 to 0.45, paired *t*-test, $t = -0.30$, $P = 0.39$; $r_9 = -0.15$, 95% CI = from – 0.55 to 0.32, paired *t*-test, $t = 1.19$, $P = 0.26$, respectively; Table 1). Feather growth rates did not change in either the treatment or control groups ($r_6 = -0.243$, 95% CI = from – 0.65 to 0.28, paired *t*-test, $t = -0.92$, $P = 0.80$; $r_8 = 0.10$, 95% CI = from – 0.37 to 0.54, paired *t*-test, $t = -4.6$, $P = 0.66$, respectively; Table 1).

DISCUSSION

Male jays which had higher feather growth rates displayed lower color hues, meaning they had bluer feathers with greater reflectance of shorter, UV wavelengths. Variation in feather color may be attributed in part to the energetic costs of producing precise feather microstructure; specifically, reflection at shorter wavelengths may require more fine-scaled structures which are potentially costly to produce (FITZPATRICK 1998; S. ANDERSSON & PRAGER 2006; but see DUFRESNE et al. 2009). Although their results were inconclusive for hue, SHAWKEY et al. (2003) found that microscopic structures within the feather predicted variation in other color attributes. We found that individuals in the best condition during molt, indicated by faster feather growth rates, may have developed the finest-scaled and most precise microstructure, indicated by bluer feathers. These results suggest that feather color may fit the handicap model of condition-dependent production and may honestly signal individual quality to mates or competitors. Similar results were found in blue grosbeaks (*Guiraca caerulea*) (KEYSER & HILL 1999), blue-black grassquits (*Volatinia jacarina*) (DOUCET 2002), blue tits (*Parus caeruleus)* (PETERS et al. 2007; but see PETERS et al. 2011) and juvenile Florida scrub-jays (*Aphelocoma coerulescens*) (SIEFFERMAN et al. 2008).

The parasite-mediated model of sexual selection suggests that ornamental characters should co-vary inversely with parasite load (HAMILTON & ZUK 1982). Our results did not support this prediction and were in contrast with some recent findings (DOUCET & MONTGOMERIE 2003; FIGUEROLA et al. 2003; HILL et al. 2005; MOUGET et al. 2005). We found that male Steller's jays with knemidokoptic mange had higher UV chroma than non-infested birds, indicating that birds with mange reflected a greater proportion of wavelengths in the UV range than non-diseased birds. The proximate mechanisms controlling the development of feather microstructure may be linked to relative hormone levels. FOLSTAD & KARTER (1992) proposed the immunocompetence handicap hypothesis (reviewed by ROBERTS et al. 2004), suggesting a proximate hormonal mechanism controlling and stimulating the development of ornamental traits linked to immune function. In particular, males which produce the highest levels of testosterone may experience reduced immune function and increased parasite susceptibility while still growing the highest quality ornaments. Correspondingly, ROBERTS et al. (2009) and PETERS et al. (2006) found that sexually mature, 1st-year male blue tits with experimentally increased testosterone levels, and juvenile male blue tits with naturally higher testosterone levels, respectively, grew feathers with more UV reflectance, potentially due to differences in preening behaviors. Perhaps male Steller's jays with higher levels of testosterone experienced reduced immune function and were more susceptible to mange, while still growing feathers with more UV reflectance. Similarly, experimental results suggested that UV plumage production in the red-backed fairy-wren (*Malurus melanocephalus*) was related to testosterone levels (LINDSAY et al. 2011). More research is needed to reveal possible links between plumage color, hormone production and disease susceptibility in this species.

Steller's jays in both treatment and control groups grew brighter feathers and taller crest stripes after their experimental treatments, although the relative change in both groups was similar. No significant changes in other variables were detected after experimental treatment. These results suggest there was no detectable effect of experimental treatment. Repeated treatments may have been necessary for substantive healing and permanent suppression of this chronic infestation (KAHN 2005; ULLAH et al. 2005). Furthermore, sampling more feathers from an individual may have increased the accuracy of our individual ornamental color production quantification, and increased sample sizes could have reduced the initial intrinsic differences in experimental groups.

Annual variation in birds' plumage may be attributed to other non-mutually exclusive mechanisms. Variation in energetic allotment for plumage development can be related to reproductive activities prior to the molt (e.g., nesting date, nest success, number of nesting attempts), environmental conditions during the molt (e.g., weather, food availability) (MCGRAW et al. 2002; OHLSSON et al. 2002), conditions and individual behavior after the molt (e.g., weather, food availability, preening behavior) (ÖRNBORG et al. 2002; DELHEY et al. 2006; SHAWKEY et al. 2007; GRIGGIO et al. 2010a; SURMACKI et al. 2011), and age-dependent production of color (SIEFFERMAN et al. 2005). As brightness (i.e., reflection of longer wavelengths) increases, the proportion of reflectance in the UV range (i.e., reflection of shorter wavelengths) decreases, possibly resulting in less colorful, UV-reflecting feathers (S. ANDERSSON & PRAGER 2006). For example, ÖRNBORG et al. (2002) found that structurally-based feather brightness increased and UV chroma decreased with increased feather wear in blue tits, and GRIGGIO et al. (2010a) found that time spent preening positively co-varied with UV reflectance in budgerigars (*Melopsittacus undulatus*). A preliminary analysis of our data indicated no effect of sampling date on any measure of plumage reflectance over our 90-day trapping period (all $P > 0.5$), although sampling feathers across an entire year may expose color changes due to wear in male Steller's jays.

Although the signaling role of plumage reflectance in Steller's jays is unknown, UV reflectance has been demonstrated to be an influential factor in assortative mating and intra-sexual competition in other species (S. ANDERSSON et al. 1998; HUNT et al. 1999; HILL 2006; SENAR 2006; GRIGGIO et al. 2010b). We propose that high-quality plumage may be the most durable, (i.e., highest structural integrity, feathers most resistant to wear), and preened the most, reducing the relative increase in brightness as the season progresses and maintaining higher UV reflectance. Mate selection in Steller's jays is thought to occur primarily in the few months preceding breeding, which is temporally farthest from molt (BROWN 1964; J.M. BLACK & P.O. GABRIEL unpub.), possibly allowing female birds to reliably assess potential mate quality and performance using variation in UV feather reflectance.

Similar to other recent studies addressing structural feather coloration, our result suggests potential condition- or feather growth rate-dependent production of structurally-based blue feather color. We also demonstrate, for the first time, that the occurrence of macro-parasite-caused disease was positively associated with higher UV reflectance. Understanding fitness consequences in relation to how the variation in sexual characteristics influences the behavior of mates, competitors, and predators will be informative. This knowledge will aid our understanding of the evolution and maintenance of sexual ornamentation in Steller's jays. Hormone production, immune function and genetic foundations of ornament development and plumage maintenance will also be productive avenues of research increasing our understanding of sexual selection.

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