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Editor's choice

Original Article

Eye for an eyespot: how iridescent plumage ocelli influence peacock mating success

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Each of the multicolored eyespots (ocelli) on the peacock's (*Pavo cristatus*) train is a complex structure with a purple-black center surrounded by concentric blue-green and bronze-gold regions. To investigate the influence of all 3 of these colors on male mating success, we used a physiological model of peafowl vision to quantify those colors as females would perceive them during male courtship displays. Males display at about 45° to the right of the sun's azimuth (on average) with the female directly in front, so we investigated how colors would be perceived when illuminated at 30°, 45°, and 60° to the right of a female observer. We studied 34 males displaying at leks in 3 feral populations and quantified their copulation success and the colors of their eyespots. Eyespot coloration explained half of the observed variation in peacock mating success, with the hue and iridescence of the blue-green patch being the most important color variables. When we experimentally masked ocelli on 9 males, their copulation success declined almost to 0, supporting the idea that the eyespots are a major focus of female attention and not a trait that is simply correlated with something else that influences female choice. Thus, our study shows that the blue-green eyespot color overwhelmingly influences peacock mating success. The influence of the other eyespot colors on male success is minimal at best, raising questions about their function.

Key words: **color pattern, iridescence, mate choice, peacock, plumage color, sexual selection.**

INTRODUCTION

Multicomponent courtship displays are ubiquitous in the animal kingdom (Bro-Jørgensen 2010), and some of the most striking involve color signals—the multiple body color patches of male Trinidadian guppies (e.g., Kemp et al. 2009) and the brightly colored plumage and bower decorations of male satin bowerbirds (Doucet and Montgomerie 2003; Savard et al. 2011) provide well-studied examples. Although a number of theories have been proposed to explain how multicomponent signals might evolve (e.g., Møller and Pomiankowski 1993; Bro-Jørgensen 2010), there has been little consensus on the function of signals that are composed of multiple color patches presented adjacent to one another during displays (e.g., Ferns and Hinsley 2004; Bortolotti et al. 2006).

The peacock's courtship display is a remarkably complex example of many colors presented simultaneously. Adult male peafowl have an elaborate train ornament that includes more than 150 feathers with an iridescent eye-like pattern near the feather tip, called an eyespot or ocellus (Figure 1; see Table 2 of Dakin and Montgomerie 2011). Each ocellus has several adjacent iridescent colors, including a dark purple-black center surrounded by 2 large concentric regions of blue-green and bronze-gold, as well as a few narrower outer bands of additional colors. All 3 of the main eyespot colors are produced by highly organized nanostructures of melanin rods connected by keratin within each barbule comprising the ocellus (Zi et al. 2003). The different eyespot colors are the result of variations in 2 parameters describing these crystal-like nanostructures—the lattice constant that defines the spacing between the melanin rods in the nanostructure and the total number of layers of rods (Zi et al. 2003).

These multicolored eyespot feathers have fascinated scientists for centuries. They were, for example, included in Isaac Newton's earliest studies of structural coloration in nature (Newton 1704). Moreover, their "trifling particulars of structure" evidently made Charles Darwin sick with worry (Darwin 1860) long before he proposed his theory of sexual selection to explain the evolution of ornamental traits by female preferences (Darwin 1871). In support of Darwin's idea that the beautiful eyespots are the product of sexual selection, Loyau et al. (2007) showed that both the brightness of the large blue-green portion of the eyespot and its iridescence were positively correlated with mating success in a feral peafowl population in France. In that study, Loyau et al. (2007) looked only at the blue-green color of the eyespot, possibly because it is the region with the greatest spectral purity (Figure 2) and thus is the most striking color to human eyes.

We designed the present study to quantify the 3 most prominent colors on the iridescent eyespots on courting males, to estimate how

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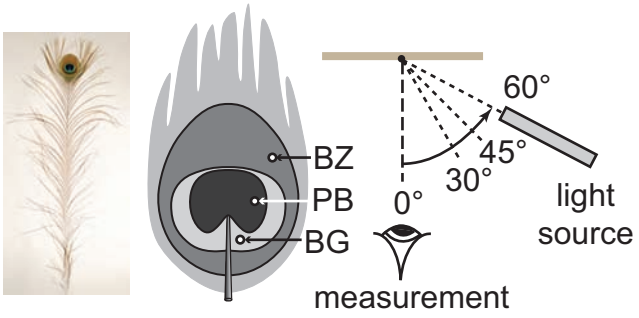

Figure 1
Directional reflectance spectrometry of a peacock eyespot feather using illumination angles of 30°, 45°, and 60° from the female's viewing position during courtship, with measurements taken at 0°. All feathers were measured on the right side when viewed from the front, as shown. The region of measurement for each of the purple-black (PB), bronze-gold (BZ), and blue-green (BG) color patches is marked with a dot.

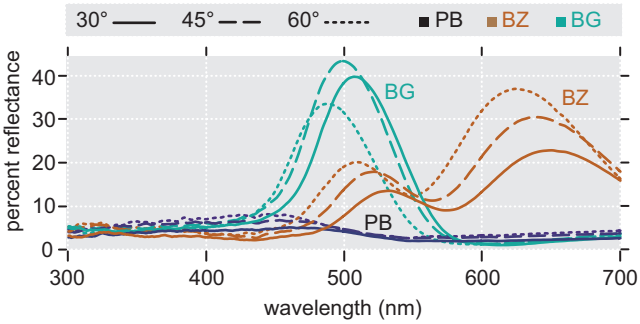

Figure 2
Typical reflectance spectra for peacock eyespot colors; curves are averages of measurements taken from a single feather from each of 10 males. Reflectance curves are shown for the PB, BG, and BZ patches at illumination angles of 30°, 45°, and 60° from the female's typical viewing position directly in front of the male during courtship.

females might perceive those colors, and to determine whether natural variation in those eyespot colors had any influence on male reproductive success. We have previously shown that peacocks display their erect trains so that the target female is directly in front and the train itself is oriented at about 45° to the right of the sun's azimuth, on average (Dakin and Montgomerie 2009). Therefore, we measured eyespot colors illuminated at 30°, 45°, and 60° to the right of the measurement probe set perpendicular to feather surface (Figure 1), so that our measurements would closely mimic the way these feathers would be displayed during courtship. We used visual modeling to estimate how peahens would see the eyespot colors illuminated at those 3 angles. On finding a correlation between male mating success and eyespot colors in our study populations, we conducted a manipulative experiment to further test whether these colors influenced female choice, rather than some other character simply correlated with the color traits we measured.

METHODS

Field methods

We studied peafowl in 3 populations: 1) Assiniboine Park Zoo (APZ) in Winnipeg, Manitoba, Canada (April–May 2007), where about 60 peafowl ranged over 50 ha of pens and woodland; 2) Toronto Zoo (TZ) in Toronto, Ontario, Canada (April–June 2007), where about 30 peafowl ranged over 250 ha of pens and woodland; and 3) Los Angeles Arboretum (LAA) in Arcadia, CA, USA (February–April 2008–2010), where >100 peafowl lived in 50 ha of parklands and the surrounding residential areas. The LAA birds were free-living year-round, whereas the APZ and TZ populations were housed in large indoor pens during the coldest winter months (December–March). All 3 populations were wild-type birds that mated on leks, similar to free-living populations in the wild in the ancestral range of *Pavo cristatus* in India (Hillgarth 1984; Harikrishnan et al. 2010).

We caught birds prior to the start of the breeding season (April at APZ and TZ; January–March at LAA) and marked them with numbered leg bands. To measure colors, we removed 5 eyespots from the train of each captured adult male by cutting the rachis immediately below the eyespot on 5 of the longest eyespot feathers (i.e., the "major" eyespot feathers; see Dakin and Montgomerie 2011 for details of train feather morphology). For a separate study (Dakin and Montgomerie 2011), we also removed one of the shortest major eyespot feathers from each male in LAA ($n = 11$) in 2010, as well as 15–20 eyespots from the longest major eyespot feathers from 6 males at APZ and 1 male at TZ in 2007. We stored feathers in opaque paper envelopes prior to taking color measurements.

Several previous studies have shown that the number of eyespots displayed in the peacock's train can influence female mate choice (Petrie et al. 1991; Petrie and Halliday 1994; Loyau et al. 2005; Dakin and Montgomerie 2011) and that this relation can be independent of an effect of eyespot color (Loyau et al. 2007). For this reason, we counted the number of eyespots displayed by each male, so that we could account for eyespot number in our statistical analyses. To quantify the number of eyespots displayed in each male's train ornament during the breeding season, we digitally photographed displaying males after eyespots had been removed for analysis (see Dakin and Montgomerie 2011 for details).

Møller and Petrie (2002) indicated that the size of individual eyespots might be related to male immunocompetence. Based on this, one might predict that eyespot size could potentially influence mate choice, so we also measured the total area of each of the 5 eyespots removed from each male and calculated the average area for use in further analyses. Eyespot area was determined from digital images taken on a flatbed scanner (hp Scanjet 7400c) of each eyespot laid flat against a standard gray card background. We used Adobe Photoshop 10.0.1 (Adobe Systems 2008) to outline the outer edge of the large bronze region of each eyespot (see Supplementary Figure S1) and converted the area of this shape to square centimeters using a ruled scale on the gray card background.

Quantifying peacock mating success

We used slightly different methods each year to observe adult males attending leks and to record their copulation success (APZ: 14 males; TZ: 5 males; LAA 2008: 13 males; LAA 2009: 16 males; LAA 2010: 11 males). In 2007 (at APZ and TZ) and 2008 (at LAA), we conducted focal watches of all males visible at different lek sites (1–5 males per lek) for periods ranging from 0.5 to 2.5 h during peak lekking periods (07:00–12:00 and 16:00–18:00 local times; Petrie et al. 1991; Dakin R, unpublished data). We recorded the number of successful copulations obtained by each focal male (APZ: 34 copulations among 14 males, during 80 h of observation; TZ: 6 copulations among 5 males, 115 h; LAA 2008: 25 copulations among 13 males, 160 h). In 2010 (at LAA), we used the same methods, but performed focal watches of all males visible on 4 leks continuously (08:00–18:00 local time) for a 13-day period (15–27 March), recording all copulation attempts and successful

copulations (19 copulations among 11 males during 506 h of observation). In 2009 (at LAA), we tracked focal females (8 marked and 20 unmarked but individually identifiable) as they visited males on 6 leks during peak lekking periods, recording all copulations (23 copulations among 16 males) and courtship behaviors. We tracked females for periods of 54 min on average (95% confidence interval [CI] [47, 61], range 10–205, n = 132 observation periods on 28 females), for a total observation time of 121 h.

These observations provide accurate measures of a male's mating success relative to his competitors in any given year, but not necessarily between years because we varied our methods of observation. Thus, to compare males across the populations and years studied, we used the number of copulations obtained by each male standardized (mean = 0 and standard deviation = 1) within each population-year sample. In total, we recorded the mating success of 36 males (17 at LAA, 5 at TZ, and 14 at APZ). Birds at APZ and TZ were studied in only 1 year (2007) but individual males at LAA were studied in 1 (n = 6), 2 (n = 8), or 3 (n = 3) years, with eyespots being removed and measured from those males in each year that they were studied.

Measuring colors and iridescence

For each male, we selected for color measurement and analysis the eyespot with the most symmetrical purple-black patch of those collected in each year that he was observed. See Supplementary Figure S1 for further details on these symmetry measurements and our choice of feathers to measure.

We measured the iridescent colors of the 3 largest color patches (purple-black, blue-green, and bronze-gold) on the right side of every eyespot, as viewed from the front (Figure 1), and quantified these colors across the bird-visible spectrum (300–700 nm). To do this, we used a USB4000-UV-VIS spectrometer (Ocean Optics, Dunedin, FL) and took measurements at different angles of incident light by mounting illumination and measurement probes in a goniometer. We mounted collimating lenses onto the ends of 400-μm optical fibers for both illumination (560 mm from the feather surface) and measurement (470 mm from the feather) of a spot about 2 mm in diameter. The alignment of the 2 beams was confirmed by shining the beam from a laser pointer down the measurement fiber. We measured reflectance normal (90°) to the feather surface because peahens are positioned directly in front of males during their precopulatory train-rattling displays (Dakin and Montgomerie 2009). For illumination, we used an Ocean Optics DH-2000 Deuterium Tungsten Halogen light source (output 215–2000 nm), with the illumination probe set at angles 30°, 45°, and 60° to the right of the measurement probe (Figure 1), equivalent to a male displaying at 30°, 45°, and 60° to the right of the sun's azimuth, respectively. We chose those angles to span the normal range of illumination angles during a male's display (Dakin and Montgomerie 2009), not to determine which angle of illumination best predicted male success. All measurements were taken in a darkroom to eliminate any effects of ambient light.

Reflectance was taken relative to a white standard made of Teflon™ tape layered to be the same thickness as the eyespot feathers, to ensure that it could be mounted in our apparatus at the same distance as the feather surface from the reflectance and illumination probes. Dark standard readings were taken in a small black chamber that eliminated reflected light. We took the average of 10 scans at 100 ms integration time, with a boxcar smoothing function of 12 pixels, using SpectraSuite 2.0 software (Ocean Optics 2009). Every 15 min we recalibrated dark and white standard readings, to reduce the effects of instrument drift. We measured each of the 3 main eyespot color patches on every feather twice—remounting the samples in the apparatus between measurements—and used the average spectrum from the 2 measurements of each color patch for further analysis. We repeated this procedure for the 3 illumination angles (30°, 45°, and 60°), keeping the illumination probe locked in position while we measured all feathers at each illumination angle, to reduce measurement error.

Vision models

We used the measured reflectance spectra in conjunction with models of peacock vision to quantify how females might perceive the eyespot colors. There are different approaches to modeling avian vision that make different assumptions about the factors that affect what colors birds actually perceive (e.g., Endler and Mielke 2005; Stoddard and Prum 2008; Spottiswoode and Stevens 2010). Recognizing that there is no consensus about which type of vision modeling is most accurate, we analyzed our data using a tetrahedral color space model (Goldsmith 1990; Endler and Mielke 2005; Stoddard and Prum 2008) of avian vision, assuming constant illumination intensity across all bird-visible wavelengths (i.e., "idealized illumination" in Stoddard and Prum 2008).

We based the visual model on the peafowl retinal cone sensitivities reported in Hart (2002, Figure 7), each normalized to a total area of 1.0 under the spectral sensitivity curve in the bird-visible region (following Stoddard and Prum 2008). We converted each reflectance spectrum from a color patch to a locus defined by 3 spherical coordinates representing chroma (r) and hue (phi and theta) within the tetrahedral color space (Supplementary Figure S3). The values for hue (phi and theta) are both angles measured from the achromatic origin. Phi is the vertical angle (range from +90° to −90°), or hue latitude, and represents the UV-violet contribution to perceived color with more positive values indicating more UV perceived. Theta is the angular displacement (+180° to −180°) around a circle parallel to the base of the tetrahedron, or hue longitude, where perceived red-greens (e.g., bronze) are close to 0°, reds and purples are negative, greens and blues are positive, and blue-greens have high positive and negative angles. Following Stoddard and Prum (2008), we calculated achieved chroma, which is an estimate of the ratio of r to the maximum possible chroma along the hue vector (defined by phi and theta) for that locus.

Using this tetrahedral color space model, we calculated 3 sets of color variables to describe what a female would see when viewing the eyespot. First, we calculated the iridescence of each patch, as the Euclidean distance in tetrahedral avian color space ("color span" from Stoddard and Prum 2008, or "Δ_T" from Endler and Mielke 2005) between the color loci for the reflectance spectra of each patch at 30° versus 60°, 30° versus 45°, and 45° versus 60° illumination angles (Figure 1). These variables provide an estimate of the perceived difference in color when the feather is alternately illuminated at those pairs of angles. Our results (see below) suggested that the color span between 60° versus 30° was the best measure of iridescence for the blue-green patch, so we used that span as an index of iridescence for all 3 color patches.

Second, we calculated the chromatic contrasts between adjacent color patches (blue-green vs. purple-black; blue-green vs. bronze-gold) as the color spans (as defined above) between those patches at each illumination angle (30°, 45°, and 60°). Therefore, we assumed that each color is seen by the female in relation to the adjacent color patch and not against a background of vegetation as quantified by Loyau et al. (2007). Third, we determined both hue (phi

and theta) and achieved chroma of each patch at each angle of illumination (see Stoddard and Prum 2008 for details of calculations).

Thus, for each feather, we calculated 1) a measure of iridescence (a dynamic color variable) for each color patch, 2) 2 color contrasts at each illumination angle, and 3) 3 color variables (hue phi, hue theta, and achieved chroma) for each color patch at each illumination angle, for a total of 36 color variables.

Manipulating eyespot color

We tested whether eyespot color itself influenced male mating success in 2008 by covering the central purple-black and iridescent blue-green regions (but not the bronze-gold patch) of each eyespot in the trains of 9 males in the LAA population with a waterproof sticker (insignia repair tape, North Sails), cut in the appropriate shape (see Supplementary Figure S1). This adhesive-backed polyester material is light (about 127 g/m^2) and the total mass of material applied to each male was <11 g (estimated from 0.067 g per sticker, 150–170 stickers per male). We applied stickers to the front side of all eyespots on 9 males: black-colored stickers on 5 males and white-colored stickers on 4 males (Figure 3). Control males (n = 4) were handled similarly, but no stickers were applied. It should be noted that this treatment altered male appearance well beyond the normal range of variation among wild-type males (Figure 3) and may have affected other factors that we could not control.

We chose males for these 3 different treatments haphazardly by alternating treatment type as we caught birds, because we could not be certain of the total number of males we could catch before lekking began. The sticker material is waterproof with a long-lasting adhesive that males could not easily remove by preening, and nearly all stickers remained on the eyespots for the duration of the breeding season (>2 months), with treatment males displaying an average of only 4.3 eyespots (range 1–7) without stickers when we photographed them during the breeding season about a month after the stickers were applied.

To assess the effects of the stickers on mating success, we conducted focal watches of 1–4 males at a time at 7 different lek sites during peak lekking periods as described above. For each male, we recorded 1) the durations of attendance on the lek, train displays (i.e., train erect), and bouts of preening behavior and 2) the numbers of "train-rattling" bouts (see Dakin and Montgomerie 2009), copulation attempts ("hoot-dashes"; Petrie et al. 1991), and successful copulations.

As an additional measure of female interest, we quantified female visitation rate to each male in this experiment as the number of 5-min intervals where he had at least 1 female visitor present divided by the number of 5-min intervals that the male was observed on the lek. We defined a visitor as any female <5 m from the focal male when his train was erect, and not closer to any other adult male (see also Dakin and Montgomerie 2011).

We attempted to distribute focal watches equally among the different lek sites. The mean total time that each male was in view was 12.0 h (95% CI [9.6, 14.4], range 6.1–18.9, n = 13 males), with the variation in total time observed due to natural variation in male attendance and not because of a biased distribution of observation periods. To account for different males being observed for different periods, we calculated male-specific rates of train-rattling bouts, copulation attempts, and successful copulations per hour. As a measure of display rate, we divided the total time males spent with their trains erect by the total time they were observed on the lek; male preening rate was calculated the same way. We used rates of train-rattling bouts, female visitation, copulation attempts, and successful copulations as measures of male mating success (Dakin and Montgomerie 2011). Because the presence of a female usually caused males to raise their trains, display rate and female visitation rate are highly correlated (r = 0.64, P = 0.02, n = 13 males). Thus, we defined a male's tendency to display independent of female visitation as his "residual display rate," calculated as the residuals of male display rate regressed on female visitation rate.

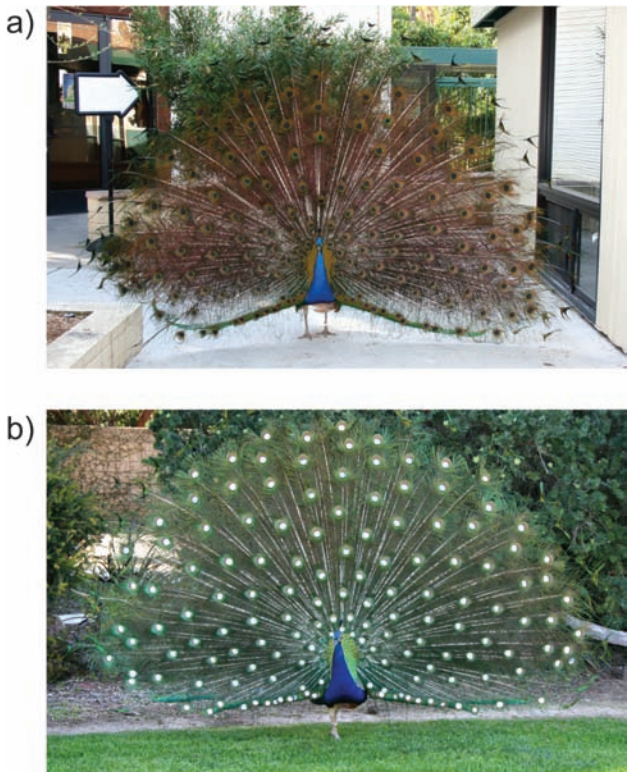

Figure 3
Experimental manipulation of peacock eyespot colors. Experimental males had either (a) black or (b) white stickers masking the purple-black and blue-green patches on all of the eyespot feathers in their train ornament.

Because the number of males in each treatment for this experiment was necessarily small, due to the limited number of males that could be observed in any given year, we use effect sizes to assess the biological importance of differences between experimental treatments and the control.

Ethical note

All methods used in this study were approved by the Queen's University Animal Care Committee (Animal Utilization Protocols Montgomerie-2005-044-Or and Montgomerie-2009-006-Or) and the animal care committees of the APZ, TZ, and LAA. The handling procedures and manipulations of eyespot colors did not result in injury to any animals.

Analyzing data

We used JMP 10.0.1 and R 2.15.2 (R Development Core Team 2012) for all statistical analyses. Several variables describing male mating success (standardized copulation number in the pooled population-year sample, and both copulation rate and copulation attempt rate in the color manipulation experiment) were zero-inflated so we used fourth-root transformations to normalize

residuals (Quinn and Keough 2002). For the color manipulation experiment, we used parametric Dunnett's tests to compare experimental treatments (males with black or white stickers) to the control (males with no stickers).

We checked the distribution of each tetrahedral color space variable to ensure that it was unimodal and normally distributed. Because theta is measured as the angle around a circle, we wanted to ensure that the distributions of this variable did not include 180° as that would result in a bimodal pattern. Only the theta values from the blue-green patch were clustered around ±180° so we added 360° to negative values to normalize those distributions.

To assess collinearity between predictor color variables, correlations between color variables were calculated by resampling because several males were measured in different years. To do this, we chose 1 value per male at each of 1000 iterations and calculated the mean of r and P over all iterations. Preliminary analysis of the correlations among color variables revealed that 2 males we studied at APZ were significant outliers (see Supplementary Figure S4). Neither of these males obtained any copulations, so to ensure that they would not bias our results, we removed them from further analyses that we report here. Including these males in the analyses resulted in the same general conclusions, in most cases resulting in stronger relations than the ones we report.

To explore whether our measurements of the eyespot colors might explain variation in male mating success, we constructed general linear mixed models to predict (fourth-root transformed) standardized copulation number in our pooled population-year sample, assigning male identity as a random variable because some males at LAA were studied in more than 1 year. We used an information-theoretic framework (Burnham et al. 2011) for model building, which has the virtue of revealing different models that are all reasonable fits to the data and thus avoids the problem of eliminating potentially important variables as a result of collinearity. Because there were often many potential predictor variables in a given analysis, and because some of these variables were highly correlated with one another, we took an exploratory approach to model building (Zuur et al. 2009). First, we built a model from the blue-green iridescence predictors as iridescence of this patch has previously been shown to correlate with male mating success in this species (Loyau et al. 2007). Second, we built a model using only the color contrast variables. Third, we built separate models for each color patch using the hue (phi and theta) and achieved chroma from the tetrahedral color space model for that patch. Finally, we built a global model to predict male copulation success using the predictors included in the best model from each set. We included the number of eyespots displayed on a male's train as a predictor in all models. Although the number of eyespots does not appear to influence male copulation success across the normal range of variation in our study populations, some males in our sample had >20 eyespot feathers removed experimentally, enough to reduce their mating success (Dakin and Montgomerie 2011).

Models in each set with delta corrected Akaike information criterion (ΔAICc) ≤2 were considered to be equally likely "top models," given the data (Burnham et al. 2011). We report the averaged model from the top models in each set (see Supplementary Material for a summary of all of the top models) and a coefficient of determination (pseudo-R^2, based on the likelihood ratio test) that represents the proportion of variance in the response that is explained by the predictors in each model. We report an adjusted-pseudo-R^2 scaled to the maximum possible R^2 for each model (Nagelkerke 1991) to allow comparison among models. We used the lme function in the R package nlme (v3.1-103) and the dredge function in MuMIn (v1.7.7) to compare and evaluate models in each set, to do model averaging, and to calculate the adjusted-pseudo-R^2 values.

All predictor variables were standardized before analysis so that the partial regression coefficients could be used to assess the relative strength of each predictor. The relative importance of each predictor is also determined during model averaging as the sum of the Akaike weights (up to a maximum of 1.0) from all of the top models in which that predictor appears.

RESULTS

Number and size of eyespots

The males we studied had from 127 to 162 eyespots (mean = 148, 95% CI [145, 151], n = 48 samples from 34 males). The eyespots we removed ranged in size from 8.3 to 14.9 cm^2 (mean area = 11.1 cm^2, 95% CI [10.7, 11.6]). Neither the number (beta = 0.02, $F_{1,38.3}$ = 1.2, P = 0.27) nor the average size (beta = −0.07, $F_{1,37.8}$ = 0.5, P = 0.48) of the eyespots a male displayed had a significant effect on copulation success, in a model that included both as predictors (with male identity as a random effect to control for repeated measures of the same male; n = 48 samples from 34 males). However, because all 16 of the males in our study displaying fewer than 140 eyespots obtained no copulations (as expected, see Dakin and Montgomerie 2011), we included eyespot number as a potential predictor in all subsequent models. Eyespot number alone explained only 2% of the variation in male copulation success in our entire sample (r = 0.15, P = 0.41, calculated by resampling, n = 48 samples from 34 males).

Eyespot colors

Figure 2 shows typical reflectance spectra for each of the 3 large color patches in the eyespot at illumination angles of 30°, 45°, and 60° relative to the female viewer (see also Figure 1). Correlations among blue-green iridescence variables are all significant, both positive and negative. Correlations among the 6 color contrast variables are all positive and almost all are significant. Correlations among the tetrahedral color space variables, achieved r, phi, and theta, are both positive and negative, with about two-thirds of the pairwise correlations being statistically significant. This level of collinearity can make regression parameters unreliable but should not unduly influence the predictive power of the resulting model (Quinn and Keough 2002, p. 127). Because of this collinearity, however, we are cautious about interpreting the relative importance of specific color variables in predicting male copulation success (see Discussion).

Iridescence and mating success

For the blue-green patch, the only measure of iridescence included in the top models was the difference in colors illuminated at 60° versus 30° (i.e., iridescence 60°/30°; Table 1). This is not surprising because this measure of iridescence represents the largest difference in reflected colors, compared with iridescences 60°/45° and 45°/30°, which are both also positively and significantly correlated with iridescence 60°/30° (r > 0.48, P < 0.01, n = 48 samples from 34 males). Note, however, that iridescence 60°/45° is negatively, and not significantly, correlated with iridescence 45°/30° in the blue-green patch (r = −0.28, P = 0.17, n = 48 samples from 34 males). Based on these results, we used only iridescence 60°/30° in subsequent analyses of iridescence for all 3 color patches.

Table 1

Models to predict male copulation success from each set of color variables and all of these variables combined (see text for details of model building)

Model set	Predictors in model	Standardized coefficient [95% CI]	Relative importance	R^2
Blue-green iridescence	**Number of eyespots**	0.22 [−0.12, 0.56]	0.52	0.19 (**0.19**)
	Blue-green iridescence 60°/30°	0.37 [0.07, 0.67]	1.0	
Iridescence at 60°/30° of all color patches	**Number of eyespots**	0.22 [−0.11, 0.55]	0.55	0.19 (**0.19**)
	Blue-green iridescence 60°/30°	0.38 [0.08, 0.68]	1.0	
	Bronze-gold iridescence 60°/30°	−0.22 [−0.52, 0.08]	0.50	
Color contrasts	**Blue-green × bronze-gold at 60°**	0.27 [−0.11, 0.64]	0.51	0.05 (**0.10**)
	Blue-green × bronze-gold at 30°	0.20 [−0.13, 0.54]	0.16	
	Blue-green × bronze-gold at 45°	0.19 [−0.15, 0.53]	0.14	
	Blue-green × purple-black at 60°	−0.13 [−0.57, 0.32]	0.11	
	Number of eyespots	0.11 [−0.23, 0.45]	0.11	
Purple-black patch	Achieved chroma at 30°	−0.25 [−0.64, 0.14]	0.59	0.07 (**0.0**)
	Phi at 30°	−0.29 [−0.67, 0.09]	0.29	
	Number of eyespots	0.16 [−0.19, 0.52]	0.36	
Blue-green patch	**Number of eyespots**	0.22 [−0.08, 0.51]	0.67	0.54 (**0.51**)
	Theta at 60°	2.95 [1.73, 4.16]	1.0	
	Theta at 45°	−0.45 [−1.40, 0.50]	0.15	
	Theta at 30°	−2.50 [−3.92, −1.07]	1.0	
	Phi at 60°	−2.05 [−3.23, −0.87]	1.0	
	Phi at 45°	−0.48 [−1.25, 0.30]	0.33	
	Phi at 30°	1.91 [0.54, 3.27]	1.0	
Bronze-gold patch	Number of eyespots	0.21 [−0.13, 0.54]	0.27	0.03 (**0.11**)
	Achieved chroma at 45°	0.25 [−0.08, 0.58]	0.66	
	Achieved chroma at 30°	0.17 [−0.12, 0.46]	0.29	
	Theta at 45°	−0.17 [−0.53, 0.18]	0.14	
	Theta at 30°	−0.19 [−0.53, 0.15]	0.12	
	Phi at 60°	0.19 [−0.15, 0.54]	0.11	
	Phi at 45°	0.15 [−0.18, 0.47]	0.07	
	Phi at 30°	0.21 [−0.12, 0.54]	0.24	
All variables	**Number of eyespots**	0.22 [−0.07, 0.51]	0.69	0.49 (**0.51**)
	Bronze-gold achieved chroma at 45°	0.13 [−0.14, 0.40]	0.22	
	Blue-green theta at 60°	2.79 [1.64, 3.94]	1.0	
	Blue-green theta at 30°	−2.51 [−3.89, −1.12]	1.0	
	Blue-green phi at 60°	−1.94 [−3.11, −0.77]	1.0	
	Blue-green phi at 30°	1.74 [0.50, 2.98]	1.0	

For each set, the average of the top models is presented, with the variables included in the best model in each set highlighted in bold. The R^2 values given are adjusted likelihood-ratio-based pseudo-R^2 values, a measure of the proportion of variation in male copulation success explained by each model. These R^2 values are shown for the averaged model and the best model (bold) in each model set. See Supplementary Table S1 for a summary of the top models (ΔAICc ≤ 2) in each set.

Iridescence 60°/30° of both the blue-green and bronze-gold patches were included in the top models (Table 1) in the iridescence set, controlling for the number of eyespots, and the averaged model explained 19% of the variation in male copulation success. Interestingly, the iridescence of the bronze-gold patch is a negative predictor in this model, suggesting that females prefer males with less iridescence in the bronze-gold patch. The iridescences of these 2 patches are not significantly correlated ($r = 0.16$, $P = 0.38$, $n = 48$ samples from 34 males).

Color contrasts and mating success

The averaged model contained 4 color contrast variables but explained only 5% of the variation in male copulation success (Table 1). Only the contrast between the blue-green and bronze-gold patches illuminated at 60° was included in the best model in this set (Supplementary Table S1) and had by far the highest relative importance in the averaged model (Table 1). All 4 color contrast variables were highly correlated with one another ($r > 0.74$, $P < 0.0001$, $n = 48$ samples from 34 males).

Different eyespot patch colors and mating success

All of the top models based on tetrahedral color space variables for the blue-green patch included 1) hue (theta) with the patch illuminated at both 30° and 60° and 2) hue (phi) with the patch illuminated at 60° (Table 1 and Supplementary Table S1). The averaged model also included eyespot number (Table 1), and the best model explained 51% of the variation in male copulation success.

The best model for the purple-black patch was the null model (Supplementary Table S1), but some of the top models for this color patch also included eyespot number, as well as hue (phi) and achieved chroma with the patch illuminated at 30°, and these are all included in the averaged model (Table 1).

The best model for the bronze-gold patch included only achieved chroma with the patch illuminated at 45° and explained 11% of the variation in male success. Some top models for this patch included one or more of the other bronze-gold color variables (Supplementary Table S1) but all of these had low relative importance in the averaged model (Table 1).

For the blue-green and bronze-gold patches, hue (theta) values for feathers illuminated at 60° and 30° were highly correlated with iridescence of those patches at 60°/30° ($R^2 > 0.95$ in each case). Thus, the iridescence of these 2 patches can be described as the difference in hue captured by the LW, MW, and SW cones and not the UV cones. Because of the strong relation between iridescence and hues (theta) of feathers illuminated at 30° and 60°, we did not include iridescence measures as predictors when constructing the global model below.

Global model of male mating success

To assess the combined influence of iridescence, contrasts, and color variables on male mating success, we constructed a model using all of the variables in the best models for color contrasts and tetrahedral color space variables from each patch as potential predictors (see Supplementary Table S1). As noted above, we chose to include tetrahedral color space variables for hue (theta) at 60° and 30°, rather than iridescence variables, as these were highly correlated. The top models from this analysis (AICc ≤ 2) included all of the variables in the best models from the other model sets, except the hue (theta) of the bronze-gold patch illuminated at 30° (Table 1). The best model in this "all variables" set included only color variables from the blue-green patch and the number of eyespots and explains 51% of the variation in male success (Table 1).

Thus, males had higher copulation success if they had 1) more eyespots with 2) more iridescence in the blue-green patch (i.e., greater difference in theta for this patch when illuminated at 30° vs. 60°), 3) a blue-green hue more toward the blue part of the spectrum (negative phi) when illuminated at 60°, while more toward the UV (positive phi) when illuminated at 30°, and 4) a more saturated bronze-gold patch (higher achieved chroma) illuminated at 45° (see "all variables" model set in Table 1). Note that the distribution of data in Figure 4 shows that the relations between copulation success and the color predictors in the averaged model (Table 1) are very similar among our 3 study populations, with no obvious outliers. Note also that the effect of eyespot number on male mating success is mainly due to the fact that we removed >20 eyespots from the trains of several males, as there was no relation between copulation success (fourth-root transformed and standardized, see Methods) and the number of eyespots among the 29 males that did not have >20 eyespots removed (beta = 0.004, $F_{1,36.5} = 0.02$, $P = 0.89$, with male identity as a random effect to control for repeated measures of the same male; $n = 43$ samples from 29 males).

Color manipulation experiment

The train length (Figure 5a) and number of eyespots displayed (Figure 5b) did not differ significantly between males with ($n = 5$ with black, 4 with white) and without ($n = 4$) stickers masking the large purple-black and blue-green patches on their eyespots (Dunnett's tests, $P > 0.36$ for all comparisons). In addition, the males with stickers did not differ significantly from control males for any of the 36 color variables we measured from their eyespot feathers (Dunnett's tests, $P > 0.10$ for all comparisons; see Supplementary Table S2 for comparisons of color variables that predict male mating success). Thus, there is no evidence to suggest that the stickers were placed on males that would have been predicted (from these variables) to have lower mating success, on average.

The application of stickers to the males' eyespots had no appreciable effect on their attendance on the lek (Figure 5c) or the amount of time they spent preening (Figure 5d). Although we frequently observed males attempting to remove stickers, the stickers did not appear to influence the amount of time they devoted to either preening or lek attendance (Dunnett's tests, $P > 0.59$ for all comparisons).

The color manipulation resulted in a decrease in male display rate, but this may have been due to a difference in female visitation, because female visitation rates (Figure 5e) were significantly lower for white-stickered ($P = 0.04$) but not for black-stickered males ($P = 0.19$). The average female visitation rate for males without stickers was nearly 4 times that of white-stickered males. The difference between control and experimental males in residual display rate (i.e., display rate controlling for female visitation rate) was not significant (Dunnett's tests, $P > 0.07$; Figure 5f).

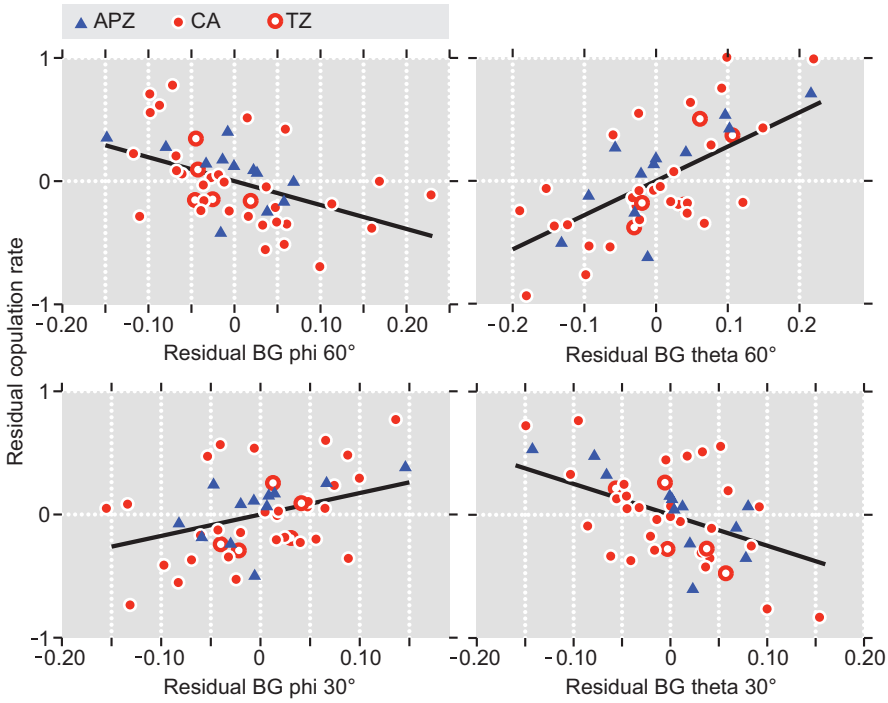

Figure 4
Partial regression plots showing effects of different eyespot colors on peacock copulation success. These graphs show the residual copulation rate from the best "all variables" regression (Table 1) plotted against residuals of latitudinal (phi) and longitudinal (theta) components of hue of the BG patch illuminated at 30° and 60°, controlling for the number of eyespots. Symbols indicate populations from which the data were collected.

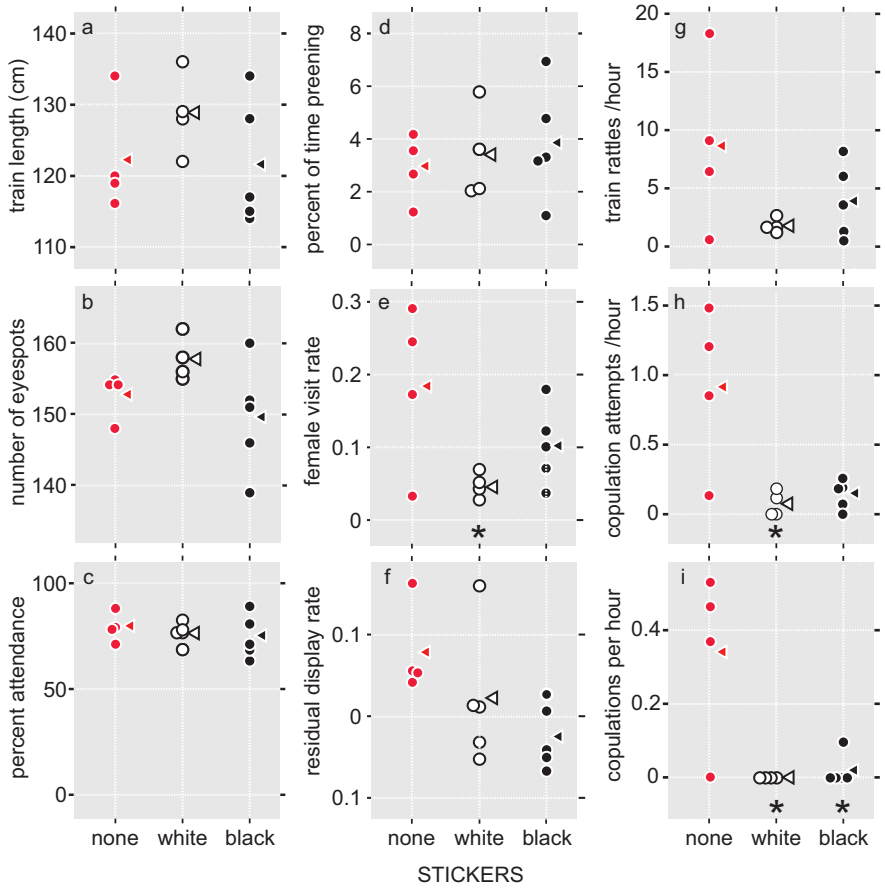

Figure 5
Comparison of (a, b) morphologies and (c–i) behaviors of males with white (n = 4), black (n = 3), and no (n = 4) stickers applied to all of their eyespots. Triangles indicate mean values; asterisks at the bottom of each pane indicate that the treatment is significantly different from the control (none) by Dunnett's test.

The application of stickers to eyespots also resulted in a decrease in the rate of train-rattling bouts (Figure 5g), and the average rate of males without stickers was nearly 3 times that of males with stickers, though this effect was not significant for either white-stickered (Dunnett's tests, P = 0.10) or black-stickered males (P = 0.25). The rate of train-rattling bouts may be an indication of male attractiveness to females, as train-rattling displays always precede copulation attempts (Dakin and Montgomerie 2009).

Copulation attempt rates (Figure 5h) were substantially lower for stickered males, with the average attempt rate for males without stickers being more than 8 times that of males with stickers. This difference was significant for white-stickered (Dunnett's test, P = 0.03) but not black-stickered males (P = 0.11). Most important, males with eyespot colors hidden by stickers had a significant reduction in copulation rates relative to males with natural eyespot colors (Dunnett's tests, P = 0.04 for black stickers, P = 0.02 for white; Figure 5i), with all 4 white-stickered males and 4 of the 5 black-stickered males achieving no copulations at all (and only 1 of 4 males without stickers failing to copulate). The average copulation rate of males without stickers was more than 3.5 times that of the lone black-stickered male who obtained a copulation.

The large effect sizes in comparisons between males with and without stickers indicate that females were less interested in visiting, being courted by, and copulating with males whose natural eyespot colors were not visible (see Supplementary Table S2).

DISCUSSION

A large proportion of the variation in peacock mating success in the populations we studied can be explained by the plumage colors of the males' eyespots illuminated at angles typical of those during male courtship displays. Indeed, controlling for the potentially slight effect of eyespot number—primarily due to the experimental removal of >20 eyespots from some males—the colors alone accounted for about half of the variation in peacock copulation success in our study populations. To the best of our knowledge, this is one of the largest effects of an ornamental trait on reproductive success that has been documented in birds. Given that our estimate of copulation success is based on sampling a relatively small proportion of the time that each male spent courting, it is quite likely that some of the unexplained variation is due to sampling error. Thus, as supported by the results of our manipulative experiment, we conclude that peacock eyespot colors have a major influence on male mating success, and probably on male fitness as well, because paternity can be predicted from mating success in other birds with similar mating systems (e.g., Reynolds et al. 2007).

Our findings, therefore, confirm and extend the results of a previous study of feral peafowl in France (Loyau et al. 2007), in which

male mating success was correlated with measures of brightness and iridescence taken from the blue-green region of the eyespot. Loyau et al. (2007) do not explain why they measured only the blue-green color on the eyespot, but their choice was a good one, as we have shown that the other colors have little or no apparent influence on female choice (Table 1). In their study, iridescence of the blue-green patch—measured as the maximal change in chromatic contrast against a constant background with changing angle of reflectance—explained about 25% of the variation in male copulation success (data extracted from their Figure 4), as did the brightness of that patch. Our measures of color and iridescence explained approximately twice as much of the variation in male success. This may be because we used somewhat different measures of iridescence, or because we had a larger sample of males and observations, or because our measurements more accurately represented male color variation, because our apparatus was designed to minimize inconsistencies in the position and distance of iridescent samples relative to the measurement probes. Loyau et al. (2007) did not find a significant effect of the number of eyespots in the male's train once they controlled for eyespot color, but this is not surprising in a population in which most males display close to the maximum number of eyespots (see also Dakin and Montgomerie 2011).

The results of our color manipulation experiment suggest that the black and white sticker treatments may have had differing effects: white-stickered males were visited by females less often than were control males, whereas black-stickered males were visited at about the same rate as control males (Figure 5e). As well, no white-stickered males copulated at all during our observations, whereas 1 black-stickered male was seen copulating once. One possible reason for this difference may be that females rejected the white-stickered males at a greater distance, before actually visiting them on the leks, based on their unusual appearance. To human observers at least, the white-stickered eyespots were easier to notice at a distance (Figure 3), whereas black-stickered males were indistinguishable from normal males at long range. Thus, females may have only noticed the altered colors of black-stickered males after close inspection, during lek visits. However, because of the small sample sizes involved, and because we could not control for other potential effects of the sticker treatment beyond the change in coloration (e.g., the stickers may have altered the acoustic components of the males' train-rattling displays), these findings should be considered preliminary and interpreted with caution. Nevertheless, we feel that the results of this experiment provide convincing evidence that eyespot colors influence male mating success directly and that the patterns we describe are not simply the result of females preferring some other trait correlated with those colors.

Our findings have several general implications. First, there has been considerable interest in the function of iridescent signals, especially in the context of sexual selection (reviewed in Doucet and Meadows 2009), but few studies have reported strong relations between natural variation in these signals and reproductive success (but see Kemp 2007; Loyau et al. 2007; see also Kemp et al. 2009; Savard et al. 2011), perhaps because these colors can be difficult to measure accurately (Meadows et al. 2011). Here, we found that male mating success could be predicted by iridescent plumage colors illuminated at typical light angles for male courtship displays (Dakin and Montgomerie 2009). We suggest that a better understanding of the selective pressures shaping iridescent color signals in other animals can be achieved by considering viewing geometry and receiver perception when measuring these signals.

Second, our findings have implications for the evolution of multiple ornaments. Since the first theoretical papers on this topic (e.g., Møller and Pomiankowski 1993; Pomiankowski and Iwasa 1993; Johnstone 1996), there have been numerous studies of multicomponent and multimodal displays and traits (reviewed in Bro-Jørgensen 2010). The peacock's multicolored eyespots present an interesting case, in that the different eyespot colors are all produced by similar nanostructural mechanisms and—most likely—similar developmental processes. In this study, we found that variation among males in the blue-green color strongly predicted male mating success, but there was very little evidence of sexual selection by female choice acting on variation among males in the other 2 color patches (Table 1). Specifically, our analyses suggest that although the saturation and iridescence of the bronze-gold patch might have a small effect, variation among males in the purple-black color is apparently not related to male mating success.

Why does the eyespot contain 3 color patches if 2 of them do not influence male mating success? One possibility is that the purple-black and bronze-gold patches are incidental byproducts of the production of the blue-green patch during feather development. Another possibility is that those 2 patches are the ghosts of sexual selection past, no longer having much influence on female choice. It is also possible that the bronze and purple-black colors enhance the appearance of the blue-green patch, or that they serve as reference colors to facilitate the assessment of the blue-green patch, without selection acting on current variation in those colors. Further experiments that mask or alter each eyespot colors separately could help address these questions, along with research examining the genetic and developmental mechanisms responsible for these structural colors. Such studies could potentially contribute to fundamental questions in the evolution of multicomponent signals as well as our understanding of the nature of courtship displays (Montgomerie and Doucet 2007).

Our study also builds on the findings of Loyau et al. (2007) to suggest that peahens in separate feral populations on different continents use similar criteria when evaluating potential mates. An increasing body of evidence demonstrates that female mate preferences are often quite variable, even within a single population over time (e.g., Chaine and Lyon 2008; see also Jennions and Petrie 1997). The between-population consistency reported here suggests that peahens may have at least some universal preferences for the iridescent eyespot colors.

Although our study provides strong support for female choice based on male eyespot coloration, many questions remain. Why do train-rattling peacocks orient relative to the sun when displaying to females, and how does this behavior affect female perception of the males' displays? Is the 45° illumination angle more informative for females than other angles? How does the movement of feathers during the train-rattling display affect how females see and respond to those colors? It should be noted that the measurement geometries used in the present study do not capture everything that goes on during peacock courtship displays, including the ability of males to turn relative to the female and to adjust the vertical tilt of the train ornament, or the fact that there may be iridescent effects that involve multiple feathers over the large, hemispherical train.

Furthermore, what is the effect of altering particular color patch attributes—rather than masking entire patches of color—on female choice? The black and white stickers we used here altered male appearance well beyond the natural range of variation. So far, no method has been developed to mimic or alter iridescent plumage colors in birds, analogous to the experimental alteration of pigment-based colors (e.g., Hill 1991). In a letter to J.J. Weir, Darwin pondered that "It wd be a fine trial to cut off the eyes of the tail-feathers

of male-peacocks, but who wd sacrifice the beauty of their bird for which reason to please a mere naturalist!" (Darwin 1868). There is clearly much untapped potential for the peacock to tell us more about sexual selection.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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