THE FUNCTION AND MECHANISMS OF FEMALE ORNAMENTATION

IN A LEKKING BIRD

A Thesis

by

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ABSTRACT

The study of male ornamentation has been fundamental to advancing the understanding of sexual selection, yet we are only now beginning to examine elaborate ornamentation of females. Although female ornamentation was once thought to be non-adaptive, recent studies have provided evidence demonstrating that female ornamentation functions in both intrasexual competition and male mate choice; however, few studies have examined the role of female ornamentation in lekking species. I investigated the function and mechanisms of female ornamentation in Indian peafowl (*Pavo cristatus*), a lekking species in which females exhibit an elaborate ornament (iridescent green neck plumage). I quantified the brightness, chroma, and hue of neck plumage from 24 captive peahens. I tested whether female ornamentation correlates with dominance order within the female social hierarchy. I also tested whether female dominance affects courtship behavior. Finally, I tested whether the steroid hormones, estradiol and corticosterone, are predictive of variation in female ornamentation and dominance. I found that more dominant females have brighter ornaments, but there was no evidence of a relationship between dominance and either chroma or hue. Additionally, dominant females copulated more, and prevented subordinate females from interacting with displaying males. Our data did not reveal a significant relationship for estradiol or corticosterone with ornamentation or social status. This study provides insight into the evolution and function of conspicuous female traits by suggesting a role for female ornamentation in intrasexual competition in a lekking species.

ACKNOWLEDGEMENTS

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INTRODUCTION

Evolutionary biologists have investigated the ultimate function of elaborate male ornamentation since Charles Darwin presented the concept of sexual selection in the 1800s (Darwin, 1871). In contrast, the function of elaborate female ornamentation had been considered nonadaptive, existing simply due to residual expression of genes associated with the traits of male conspecifics (Lande, 1980). Many recent studies have challenged this argument by suggesting that female ornamentation is adaptive (Jawor, Gray, Beall, & Breitwisch, 2004; LeBas, 2006; Tobias, Montgomerie, & Lyon, 2012).

Recent work has found that female ornamentation functions in intrasexual competition (LeBas, 2006; Tobias et al., 2012). For example, female ornamentation can mediate territorial encounters. In streak-backed orioles (*Icterus pustulatus pustulatus*), females responded more aggressively to female intruders that were more versus less colorful (Murphy, Hernández-Muciño, Osorio-Beristain, Montgomerie, & Omland, 2009). Other studies have found that female ornamentation functions during competition for food (Murphy, Rosenthal, Montgomerie, & Tarvin, 2009; Ziegelbecker, Richter, & Sefc, 2018) and mating opportunities (Clutton-Brock, 2009). Ornamentation is often condition dependent and thus can act as an honest signal (Doutrelant et al., 2008; Henderson, Heidinger, Evans, & Arnold, 2013; Jawor et al., 2004; Remeš & Matysioková, 2013; Siefferman & Hill, 2005; Weiss, 2006). Female ornamentation that signals fighting ability can allow individuals to evaluate one another and determine the most likely outcome of a contest without engaging in a costly physical fight (Midamegbe, Grégoire, Perret, & Doutrelant, 2011; Santos, Scheck, & Nakagawa, 2011). Similarly, female ornamentation that signals health and reproductive potential can attract the

attention of potential mating partners (Freeman-Gallant, Schneider, Taff, Dunn, & Whittingham, 2014; Jawor et al., 2004; Midamegbe et al., 2011). Female ornamentation also functions in intersexual competition via male mate choice (Amundsen, 2000; Amundsen, Forsgren, & Hansen, 1997; Griggio, Devigili, Hoi, & Pilastro, 2009; Torres & Velando, 2005). Most studies on female ornamentation have focused on species with monogamous or cooperative-breeding mating systems, but female ornamentation also exists in species with other mating systems, particularly those that form leks.

While females in lekking species theoretically have complete choice over mating partners, some studies suggest that their mating opportunities are limited by intrasexual aggression (Bro-Jørgensen, 2002; Hannon, Sopuck, & Zwickel, 1982; Karvonen, Rintamäki, & Alatalo, 2000; Petrie, Hall, Halliday, Budgey, & Pierpoint, 1992; Saether, Fiske, & Kalas, 2001) and male mate choice (Saether et al., 2001; Werner & Lotem, 2003). Female ornamentation has rarely been investigated in lekking species (but see Trail, 1990 & Dakin, 2011) and little is known about why females of some lekking species are highly ornamented while others are less so. Dakin (2011) found that Indian peahen (*Pavo cristatus*) crest morphology predicted body-condition at the start of the breeding season, but not female-female agonistic behavior, suggesting that the crest functions to signal health and condition but not dominance status (Dakin, 2011). A comparative study on differences in female ornamentation between two lekking species (Trail, 1990) found that highly ornamented females in the monomorphic species engaged in intense intrasexual aggression while less ornamented females in the dimorphic species did not; this study concluded that female ornamentation in lekking birds likely evolved due to competition among females (Trail, 1990). These studies suggest that female

ornamentation in lekking species is functional but our understanding of this topic is still limited.

Furthermore, we know little about the physiological mechanisms influencing ornamentation in females. Behavioral and morphological traits that covary are often linked by shared physiological mechanisms, producing an integrated phenotype (Barron, Webster, & Schwabl, 2015; Cain & Ketterson, 2012). In males, the integrated phenotype including aggressive behavior and conspicuous ornamentation is often linked by the male primary steroid hormone, testosterone (Collis & Gerald, 1992; Kimball, 2006; Zuk, Johnson, Thornhill, & Ligon, 1990). In females, there is evidence that estradiol, the primary female sex steroid hormone, correlates with intrasexual aggression (Pärn, Lindström, Sandell, & Amundsen, 2008; Rubenstein & Wikelski, 2005; Woodley & Moore, 1999a, 1999b) and female ornamentation (Calisi & Hews, 2007). For example, in female spiny lizards (*Sceloporus pyrocephalus*), ornamental color of the gular region, which is extended during female intrasexual aggressive interactions, is correlated with estradiol (Calisi & Hews, 2007). Corticosterone, a glucocorticoid that elevates in response to stress, also impacts female ornamentation in some species. This may be because higher corticosterone can interfere with feather protein deposition (Romero, Strochlic, & Wingfield, 2005) and increase metabolism (Jimeno, Hau, & Verhulst, 2018; Loiseau, Fellous, Haussy, Chastel, & Sorci, 2008). As an example, baseline corticosterone levels in female blue tits were negatively correlated with their structural color signal from crown feathers (Henderson et al., 2013). While some studies have uncovered mechanisms underlying female ornamentation, we still have much to learn, especially in lekking species.

I therefore investigated whether female ornamentation in a lekking species is functional, and if so, whether hormonal mechanisms link the ornament with the function. Indian peafowl (*Pavo cristatus*) are an ideal lekking species in which to examine female ornamentation because they are a sexually dimorphic species in which females exhibit neck ornamentation consisting of structurally-colored feathers. Many studies have suggested a functional role for structural coloration as a signal for condition because the production of nanoparticles that creates this coloration is condition dependent (Doucet, 2002; Hill, Doucet, & Buchholz, 2005; Keyser & Hill, 1999; McGraw, Mackillop, & Dale, 2002). There is also evidence that peahens compete with each other for mating partners (Petrie et al., 1992). I tested whether feather ornamentation reflects dominance status. I predicted that dominant females would have ornamentation that is brighter or more colorful (higher values of chroma and hue). In addition, I examined whether hormones underlie variation in female ornamentation. I predicted that females with brighter or more colorful plumage would have higher levels of estradiol and lower levels of corticosterone during the breeding season. Lastly, I tested whether the dominance status of females influenced courtship behavior. I predicted that dominant females would guard displaying males and have more mating opportunities than subordinate females.

MATERIALS AND METHODS

Animals and Facilities

This study was conducted in College Station, Brazos County, TX (30° 37' 40.717" N 96° 20' 3.864" W) on a population of captive peafowl (*Pavo cristatus*; 24 peahens and 12 peacocks) during the breeding season. The birds were originally captured from feral populations in Florida and California between 2009 and 2012. They were housed in an outdoor enclosure (18.3 x 24.5 m). Individuals had a metal band on one leg and a plastic band on the other leg. Individuals were given food and water ad libitum.

Dominance Hierarchy

I determined the dominance hierarchy of all peahens within our study population in March 2018 based on wins and losses in physical contests surrounding a limited amount of a preferred food (Royal Wing® Total Care™ - Nut & Fruit Blend). I scored dyadic interactions between individuals using an ethogram of known peahen dominance behaviors (Yorzinski, 2014), which included displacing (dominant walks or runs toward subordinate and subordinate moves away), pecking (dominant's beak quickly comes into contact with subordinate), and hopping (dominant jumps on top of subordinate and subordinate moves away). I recorded interactions between each dyad until one individual won at least three more times than the other individual. After the initial 60 hours of observation, dyads that did not meet the above criteria were separated from the group and observed until one of the individuals won at least three times more than the other. I then determined the dominance hierarchy using David's score (David, 1987; Yorzinski, 2014), which calculates a dominance value that accounts for nonlinear relationships.

Hormone Collection & Measurement

I collected blood (0.5 mL) from all peahens (n = 24) between 8 AM and 10 AM on April 18, 2018. To minimize disturbance to the flock, I lured a peahen using food into a separate room (6.2 m x 6.3 m) of the enclosure that was not visible to other flock members. I collected a blood sample from the brachial wing vein (25 gauge needle attached to a 1 mL syringe) within three minutes of when she walked into the separate room. I then released her into another isolated room (18.3 m x 6.2 m) within the enclosure that was separate from the flock. I repeated this process for each peahen. After I collected blood samples from all individuals, I centrifuged the samples, separated the plasma from the red blood cells, and stored all samples in a freezer at -20° C. Samples were then shipped on dry ice to Indiana University for processing.

Baseline circulating levels of estradiol (E2) and corticosterone (CORT) in peahens were determined using 50 μL and 10 μL of plasma, respectively. After a diethyl-ether extraction, hormones were assayed using ELISA kits (E2: #ADI-900-176, Enzo Life Sciences, Ann Arbor, MI, USA; CORT: #501320, Cayman Chemical, Ann Arbor, MI, USA). Parallelism and extraction efficiency were validated for both assays using a pool of peahen plasma. Peahen plasma collected during the breeding season had high fat content (even after the extraction) and this prevented initial parallelism validation of the assay. Therefore pooled samples were centrifuged at 5000 rcf for 15 minutes and then plasma was siphoned off the top of the fat using a 100 μL Hamilton syringe prior to the extractions. This method enabled proper validation of the assay and therefore this method was used on all samples. Samples were randomized across two plates for each assay.

Coefficients of variance were as follows: E2: n = 2 plates, intra-plate variability = 10.2% and 5.5%, inter-plate variability = 18%; CORT: n = 2 plates, intra-plate variability = 1.7% and 0.8%, inter-plate variability = 1.2%.

Feather Collection & Measurement

I collected 24 feathers from the neck ornamentation (iridescent green feathers on the neck) of each peahen on a single day (May 1, 2018). In particular, I collected six feathers from each of four ornamentation regions: ventral, dorsal, left lateral and right lateral of the neck. From each of the four ornamentation regions, I sampled three of the six feathers from an area closer to the head (eight centimeters down the neck from the crown of the peahen's head) and the other three feathers from an area farther from the head (13 centimeters down the neck from the crown of the peahen's head). The feathers were removed by cutting the rachis below the barbs. Feathers were stored indoors at room temperature (20° C) in labeled opaque envelopes and then mounted on matte black card stock.

Individual variation in feather reflectance was quantified using UV-VIS spectrometry. I quantified variation in ornamentation reflectance of all feathers across the avian-visible spectrum (300–700 nm) using the Maya2000-pro *spectrometer (Ocean Optics, Inc., Largo, FL, USA). The* illumination probe and light collection probe were mounted using a stand with three protractors to adjust angle of the light source, collection probe and the table (Meadows, Morehouse, Rutowski, Douglas, & McGraw, 2011). I attached collimating lenses onto the ends of 600 μm premium fiber, solarization-resistant, 1 m optical fibers for both illumination (probe placed at 37 mm from the feather surface)

and collection (probe placed at 50 mm from the feather) of a spot approximately 2 mm in diameter. The alignment of the two beams was confirmed by shining a light down the measurement fiber. For illumination, I used a DH2000-DUV light source (output 190 – 2500 nm; *Ocean Optics, Inc.)*, with the illumination probe set at 60° to the right of the measurement probe. Previous work in peacocks measured feather reflectance at 30°, 45°, and 60° (Dakin & Montgomerie, 2013); because the reflectance of the female neck ornamentation feathers at 30° and 45° was low, it was not possible for us to accurately measure reflectance at those angles. The stage and collection probe remained at 90° for all measurements. Feathers were mounted on the stage at the height that achieved maximum alignment for the illumination angle. I measured reflectance relative to a certified reflectance standard (Spectralon WS-1-SL diffuse reflectance standard; Labsphere, Inc., North Sutton, NH, USA). The mounted feathers were stacked on cards to be measured at the same distance from the probes as the reference standard. I took dark standard readings by removing the collection probe and capping the spectrometer. I recalibrated the dark reflectance standard every 15 minutes (Dakin & Montgomerie, 2013) and the white reflectance standard was placed on the stand between each new feather measurement to minimize instrumental drift. OceanView software *(Ocean Optics, Inc.;* integration time: 90-120 ms*)* was used to process the reflectance data. All measurements were taken in a darkroom to minimize ambient light.

I then exported the reflectance data from the OceanView software and converted the percent reflectance measurements to color space variables using a model of peafowl tetrachromatic vision (tetrahedral color space within the R package "Pavo") to account for peafowl-specific visual sensitivities (Maia, Eliason, Bitton, Doucet, & Shawkey,

2013; Stoddard & Prum, 2008). This model used the peafowl chromatic visual sensitivity system, the achromatic receptor stimulation for the double cone sensitivity of *Gallus gallus* (which is most similar to peafowl compared with the other options), and illumination set to "ideal" (homogenous illumination across all bird sensitive wavelengths; Stoddard & Prum, 2008). Previous work on peacock feather iridescence used this same model (Dakin & Montgomerie, 2013). This model converted the percent reflectance measurements for each feather output by OceanView to calculate one achromatic color space variable (brightness), and three chromatic color space variables (chroma, hue UV, and hue VIS). Hue UV and hue VIS include hue in the 300-380 nm and 380-700 nm part of the spectrum, respectively.

Courtship Trials & Measurement

      I examined the impact of the female dominance hierarchy on courtship interactions during the breeding season (May 2018) between 7:00 and 12:00. Males and females were separated for one week prior to the start of these trials. The females were housed within one room of the enclosure (18.3 m x 6.2 m) while the males were separated within another room of the enclosure (18.3 m x 18.3 m); the females and males could hear but not see each other. Trials were conducted in another room of the enclosure (6.2 m x 6.3 m) that was visually isolated from the rest of the flock. This testing room had cameras (Swann SWPRO 535CAM security cameras; Swann Security Systems, Santa Fe Springs, CA, USA) in each corner of the room; the videos from the cameras were synchronized using a DVR (4-channel HD DVR; Night Owl Security Products LLC, Naples, FL, USA). The experimenter (ADE) remained outside this testing room but

monitored the trials through a camcorder (DCR-SR40; Sony Corp, Tokyo, Japan) that was directed inside the room.

For each trial, two randomly selected females and one randomly selected male were placed in the testing room and allowed to freely interact. After one hour, the birds were returned to their respective rooms. Each female participated in two trials (but were never paired with the same individuals) and these two trials were separated by at least eight days. One trial from two of the females was excluded from the analyses because the relationship between those females and their randomly selected female partners was ambiguous; in all other trials, the dominance relationship between the female dyads was clear (and the same as what was observed previously in March).

I analyzed the videos of all trials (QuickTime Player 10.4; Apple Inc., Cupertino, CA, USA) and recorded the number of successful copulations as well as the number of attempted copulations (male performed the hoot-dash display but the female avoided; Petrie 1992) for each female. I also recorded female-female aggression via dominance displays within 1.5 meter of the male based on the previously described dominance ethogram (Yorzinski, 2014).

Statistical Analysis

R version 3.5.1 (2018-07-02) was used for all statistical tests. I used generalized linear models (packages "stats" and "lme4") to test whether the color space variables predicted dominance status in peahens. The dependent variable was David's score; the independent variables were the mean values of brightness, chroma, hue UV, and hue VIS

for all 24 feathers from each peahen as well as peahen mass. I reran this model with only predictor variables that had p-values less than 0.10.

I also tested whether the color space variables varied by ornamentation region (ventral, dorsal, or lateral) using linear mixed-effects models (packages "lme4" and "emmeans") with individual bird identity as the random effect. Because I found that color space varied by ornamentation region (see Results), I performed a follow-up analysis to determine whether the color space of specific ornamentation regions (ventral, dorsal, or lateral) reflected dominance status. I pooled measurements from the left and right lateral ornamentation because I found that they were similar (paired t-test: brightness $t = 0.394$, $DF = 46$, $P = 0.695$; chroma $t = 0.957$, $DF = 46$, $P = 0.344$; hue UV $t = 0.832$, $DF = 46$, $P = 0.410$; hue VIS $t = 1.960$, $DF = 46$, $P = 0.056$).

I used generalized linear models (packages "stats" and "lme4") to investigate whether E2 and CORT predicted dominance status. David's score was the dependent variable and the independent variables were E2, CORT, the interaction between E2 and CORT, and peahen mass. I ran additional analyses to examine the relationship between hormones and the color space variables. I ran separate models in which each color space variable was the response variable and hormones (E2, CORT, and their interaction) were the explanatory variables; I also included peahen mass as a fixed effect.

To determine whether dominant females limit subordinate females' mating opportunities, I ran generalized linear mixed models with a Poisson distribution (package "lme4"). The dependent variable was the number of copulations and the independent variable was the dominance status (David's score) of the females. I included the individual male as the random effect and trial number (whether it was the first or second

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trial of a given female) as a fixed effect. I reran this model a second time but used the

number of attempted copulations as the dependent variable. Lastly, I evaluated whether

female dominance status during food competition (David's score) is related to female

aggressive behavior during courtship (number of aggressive behaviors between females

in the courtship trials).

RESULTS

Feather ornamentation

Dominant females had brighter ornamentation than subordinates (t = 2.609, DF = 18, P = 0.018; Table 1). Chroma (t = -0.723, DF = 18, P = 0.479), hue UV (t = 0.189, DF = 18, P = 0.852), and hue VIS (t = -1.439, DF = 18, P = 0.167) did not predict dominance status. Dominant individuals tended to weigh less than subordinates (t = -1.821, DF = 18, P = 0.085). The results were similar when I reran this analysis using only variables with p-values less than 0.10 (Table 2).

The color space of feathers varied by ornamentation region: dorsal and lateral ornaments were significantly brighter than ventral ornaments (dorsal vs. ventral: t = 5.100, DF = 46, P < 0.0001; lateral vs. ventral: t = -4.982, DF = 46, P < 0.0001). Dorsal and lateral ornaments exhibited similar brightness (t = 0.117, DF = 46, P = 0.992; Table 3). The brightness of the dorsal ornament (t = 2.539, DF = 18, P = 0.021) but not the ventral ornament (t = 1.308, DF = 18, P = 0.207) predicted dominance status: dominant individuals had brighter dorsal ornaments than subordinates. There was a trend for dominant individuals to also exhibit brighter lateral ornaments than subordinates (t = 2.026, DF = 18, P = 0.058). Although there were differences among ornamentation regions in brightness, chroma and hue (Table 3), only brightness was related to dominance status. The results were similar when I reran this analysis using only variables with p-values less than 0.10 (Table 1; Table 2).

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Table 1: Results of generalized linear model testing whether the brightness, chroma and hue of female ornaments predicts dominance status while controlling for peahen mass. Asterisks indicate significant differences.

Ornamentation Region	Fixed Effects	Estimate	Std. Error	t-value	P
All	Brightness	5179.225	1984.827	2.609	0.018*
All	Chroma	-468.099	647.529	-0.723	0.479
All	Hue UV	18.003	95.316	0.189	0.852
All	Hue VIS	-664.028	461.581	-1.439	0.167
All	Mass	-0.172	0.094	-1.821	0.085
Dorsal	Brightness	5281.979	2080.595	2.539	0.021*
Dorsal	Chroma	-409.469	606.933	-0.675	0.509
Dorsal	Hue UV	-95.696	67.888	-1.410	0.176
Dorsal	Hue VIS	-212.627	236.512	-0.899	0.381
Dorsal	Mass	-0.103	0.095	-1.085	0.292
Lateral	Brightness	3205.272	1582.088	2.026	0.058
Lateral	Chroma	-520.212	580.655	-0.896	0.382
Lateral	Hue UV	-2.261	79.156	-0.029	0.978
Lateral	Hue VIS	117.838	482.409	0.244	0.810
Lateral	Mass	-0.252	0.109	-2.319	0.032*
Ventral	Brightness	3327.558	2543.214	1.308	0.207
Ventral	Chroma	-475.922	630.556	-0.755	0.460
Ventral	Hue UV	84.078	94.015	0.894	0.383
Ventral	Hue VIS	-277.357	240.998	-1.151	0.265
Ventral	Mass	-0.269	0.104	-2.577	0.019*

Table 2: Results of generalized linear model testing whether variation in color space predicts dominance status while controlling for peahen mass. This model includes only predictor variables with p<0.10 in the original model (Table 1). Asterisks indicate significant differences.

Ornamentation Region	Fixed Effects	Estimate	Std. Error	t-value	P
All	Brightness	2906.718	1265.844	2.296	0.032*
All	Mass	-0.213	0.084	-2.528	0.019*
Dorsal	Brightness	2359.709	1057.211	2.232	0.037*
Dorsal	Mass	-0.185	0.086	-2.160	0.042*
Lateral	Brightness	2082.615	1026.484	2.029	0.055
Lateral	Mass	-0.219	0.086	-2.543	0.019*
Ventral	Brightness	1800.606	1464.641	1.229	0.233
Ventral	Mass	-0.227	0.092	-2.474	0.022*

Table 3: Results from linear mixed effects models using contrasts to determine pairwise differences of ornamentation regions. Asterisks indicate significant differences.

Color Space Variable	Contrast	Estimate	Std. Error	t-value	DF	P
Brightness	dorsal-ventral	0.023	0.005	5.100	46	<.0001*
Brightness	dorsal-lateral	0.001	0.005	0.117	46	0.992
Brightness	ventral-lateral	-0.023	0.005	-4.982	46	<.0001*
Chroma	dorsal-ventral	0.034	0.014	2.415	46	0.051
Chroma	dorsal-lateral	-0.009	0.014	-0.659	46	0.788
Chroma	ventral-lateral	-0.043	0.014	-3.074	46	0.010*
Hue UV	dorsal-ventral	-0.512	0.095	-5.383	46	<.0001*
Hue UV	dorsal-lateral	-0.221	0.095	-2.326	46	0.062
Hue UV	ventral-lateral	0.291	0.095	3.057	46	0.010*
Hue VIS	dorsal-ventral	-0.173	0.032	-5.477	46	<.0001*
Hue VIS	dorsal-lateral	-0.098	0.032	-3.085	46	0.010*
Hue VIS	ventral-lateral	0.076	0.032	2.392	46	0.054
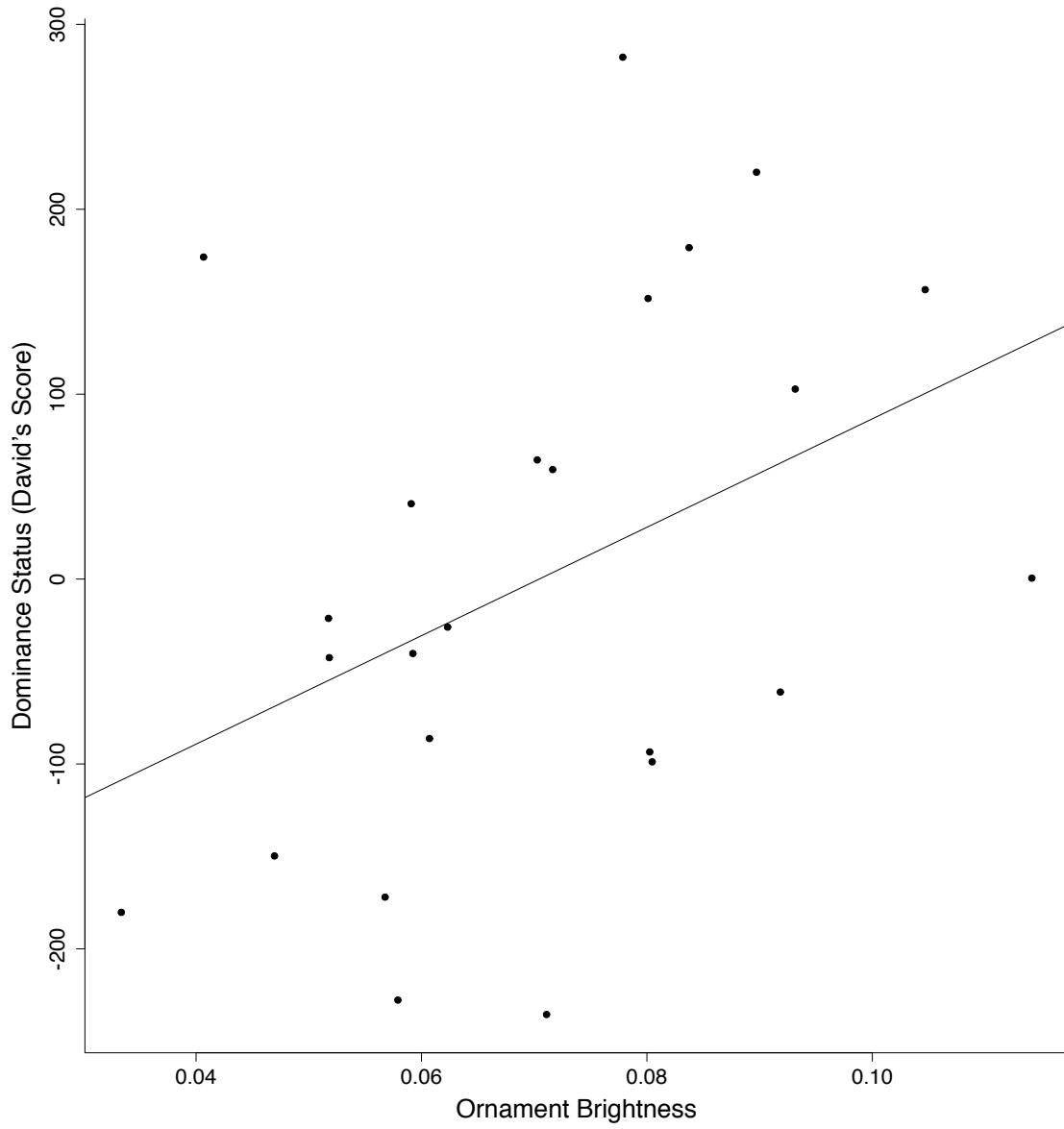
Figure 1: Relationship between ornament brightness (all regions) and dominance status.

Hormones

      I did not find significant relationships between E2, CORT, or their interaction and dominance status (E2: t = 0.060, DF = 19, P = 0.953; CORT: t = 0.229, DF = 19, P = 0.821; E2*CORT: t = -0.094, DF = 19, P = 0.926; Table 4; Figure 2; Figure 3). None of the color space variables had a relationship with either hormone (Table 5; Figure 4; Figure 5).

Table 4: Generalized linear model assessing the relationship between dominance status and hormones (E2 and CORT) while controlling for peahen mass.

Fixed Effects	Estimate	Std. Error	t-value	P
E2	74.930	1247.973	0.060	0.953
CORT	75.125	327.432	0.229	0.821
E2*CORT	-67.502	719.975	-0.094	0.926
Mass	-0.187	0.118	-1.585	0.129

Table 5: The results of four generalized linear models, each assessing the relationship between one of the four color space variables (brightness, chroma, hue UV, and hue VIS) and E2 and CORT while controlling for peahen mass.

Color Space Variable	Fixed Effects	Estimate	Std. Error	t-value	DF	P-value
Brightness	E2	0.213	0.186	1.142	19	0.268
Brightness	CORT	0.063	0.049	1.284	19	0.215
Brightness	E2*CORT	-0.126	0.108	-1.170	19	0.257
Brightness	Mass	0.000	0.000	0.773	19	0.449
Chroma	E2	0.602	0.635	0.948	19	0.355
Chroma	CORT	0.187	0.167	1.123	19	0.276
Chroma	E2*CORT	-0.388	0.367	-1.058	19	0.303
Chroma	Mass	0.000	0.000	0.222	19	0.827
Hue UV	E2	-1.161	3.527	-0.329	19	0.746
Hue UV	CORT	-0.082	0.925	-0.089	19	0.930
Hue UV	E2*CORT	0.619	2.035	0.304	19	0.764
Hue UV	Mass	0.000	0.000	1.078	19	0.294
Hue VIS	E2	0.102	0.700	0.146	19	0.886
Hue VIS	CORT	-0.045	0.184	-0.243	19	0.811
Hue VIS	E2*CORT	0.100	0.404	0.248	19	0.807
Hue VIS	Mass	0.000	0.000	1.579	19	0.131

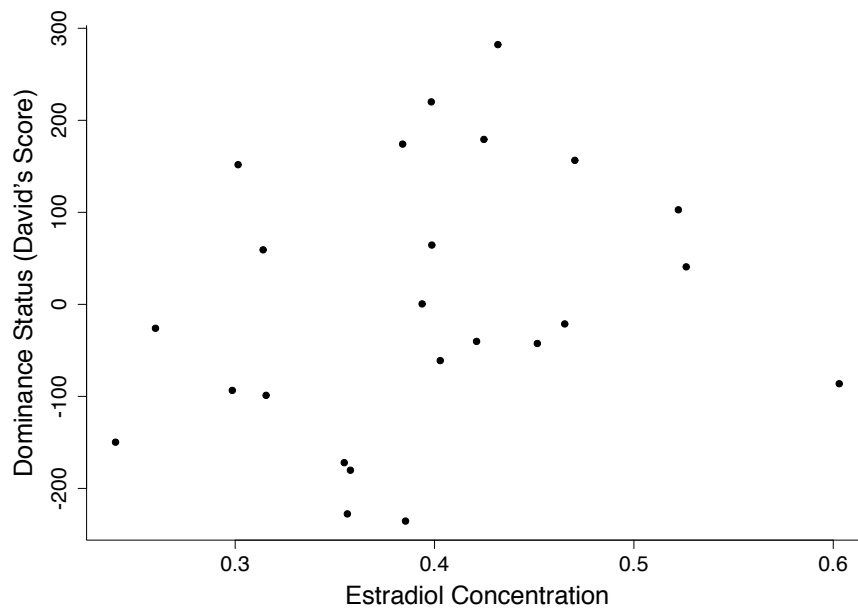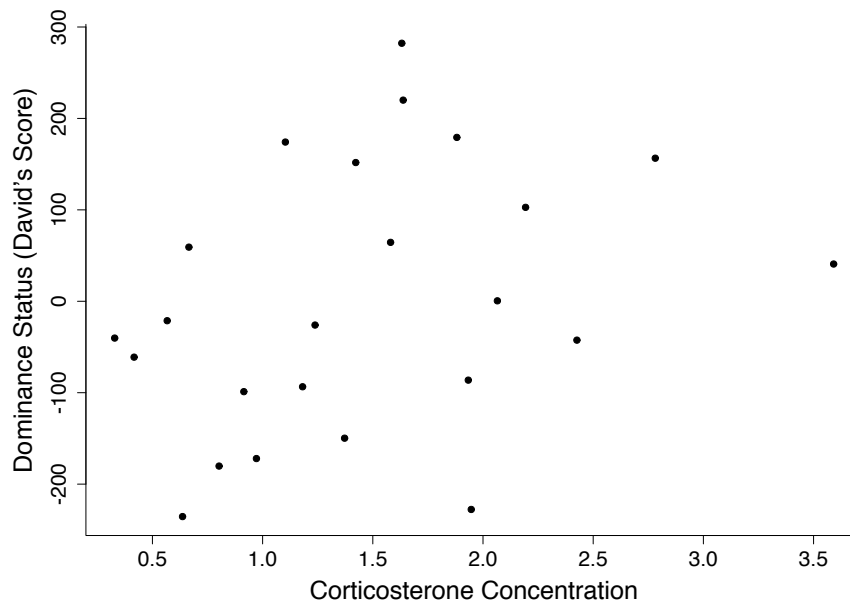**Figure 2:** Relationship between estradiol levels and dominance status

Figure 3: Relationship between corticostrone levels and dominance status
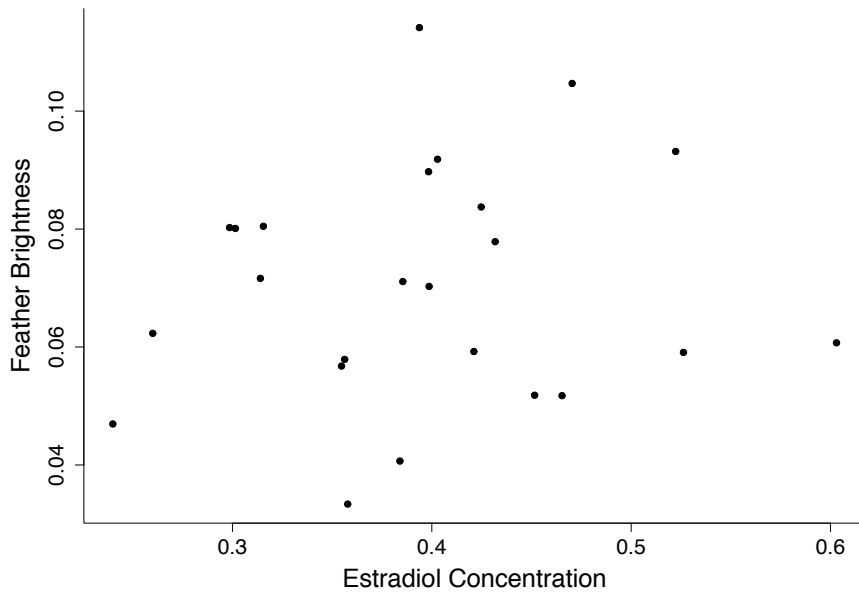
Figure 4: Relationship between estradiol levels and ornament brightness (all regions)
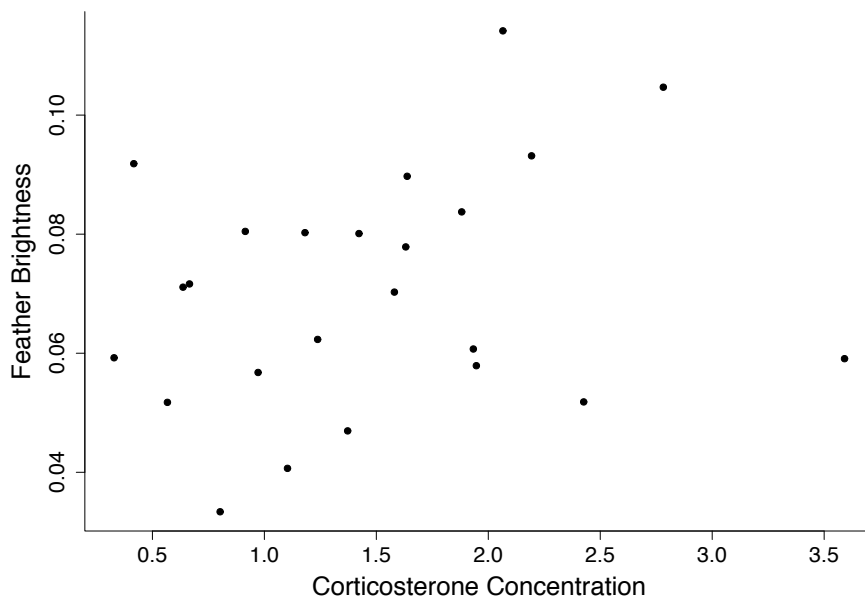
Figure 5: Relationship between corticosterone levels and ornament brightness (all regions)

Courtship Trials

Dominant females copulated with males more often than subordinate females did ($z = 2.447$, DF = 26, P = 0.014; Table 6). In addition, dominant females received more copulation attempts ($z = 2.685$, DF = 26, P = 0.007; Table 6). Finally, aggression among females (number of aggressive displays in front of displaying males) was highly correlated with dominance status (determined from feeding trials; see 'Dominance hierarchy' above; $z = 9.823$, DF = 26, P < 0.001; Figure 2).

Table 6: Generalized linear mixed effects models assessing dominance score (controlling for trial number) as a predictor of number of copulations and attempted copulations. Asterisks indicate significant differences.

Response Variable	Fixed Effects	Estimate	Std. Error	z-value	P
Copulations	Dominance	0.002	0.001	2.447	0.014*
	Trial Number	-0.032	0.256	-0.124	0.901
Attempted Copulations	Dominance	0.003	0.001	2.685	0.007*
	Trial Number	0.333	0.311	1.073	0.283

Figure 6: The relationship between David's score and female aggression during courtship.

DISCUSSION AND CONCLUSIONS

To our knowledge, this study provides the first evidence that female ornamentation functions in intrasexual competition within lekking species. Peahens have ornamentation consisting of structurally-colored feathers around their necks. I 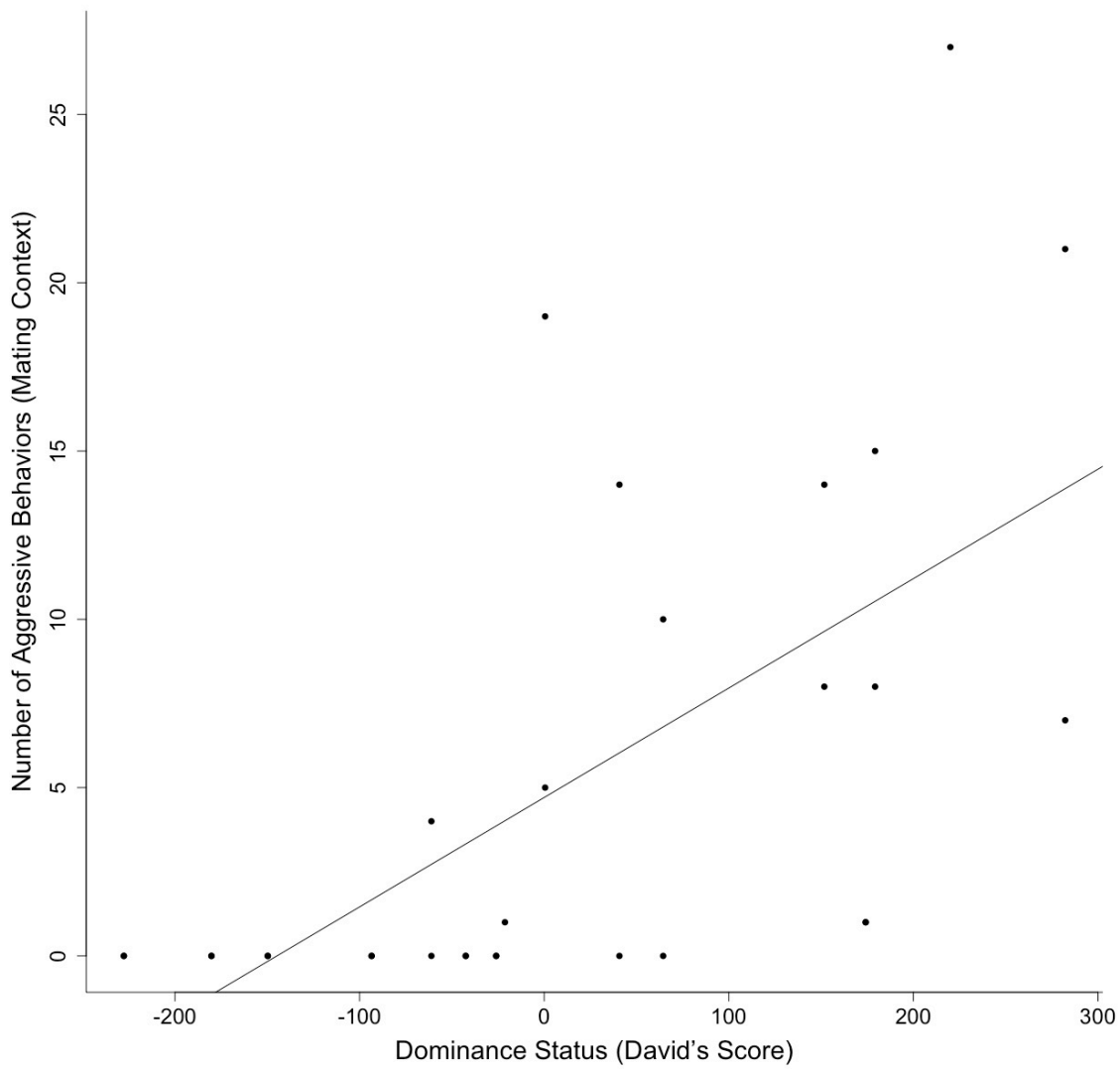found that dominant peahens had brighter ornaments than subordinate peahens. This is consistent with a study on peacocks, which found that males with brighter feathers had higher mating success (Loyau et al., 2007). In other avian species, brightness of structural coloration has been associated with male (Doucet, 2002; Doucet & Montgomerie, 2003; Keyser & Hill, 2000) and female (Siefferman & Hill, 2005) health and condition. Similar to the Loyau (2007) findings that brightness was the only color space variable associated with peacock mating success, I found brightness (and not chroma or hue) to be the only color space variable predictive of peahen dominance.

The brightness of peahen ornamentation varied within the ornament. The ornamentation was brighter in the dorsal and lateral feathers compared to the ventral feathers. Dorsal neck feathers are targeted by conspecifics in both competitive and mating contexts. During aggressive intrasexual interactions, females often peck or pull the dorsal neck feathers of their rivals. In a mating context, peacocks grasp peahens' dorsal neck feathers in their bills during copulation. During these competitive and mating contexts, the females' ornamentations may become damaged by abrasion (Surmacki, Liu, Mercadante, & Hill, 2011). Given that dominant females exhibited brighter ornaments than subordinate females, it is possible that dominant individuals' feathers are more resistant to abrasion (Fitzpatrick, 1998) but further studies would be needed to test this possibility. The impact of abrasion on feather brightness is worth exploring further because feather brightness may signal dominance, which affects competition for food and mating opportunities.

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I found that dominant peahens (determined in a feeding context) performed more dominance behaviors in front of displaying males. In addition, dominant females copulated more frequently than subordinate peahens and received more copulation attempts from males. Copulation attempts occurred when females rejected the male's courtship by moving out of the way of the male's hoot-dash display. These findings expand upon a previous study on a feral population of peafowl, which found that males court dominant females more than subordinate females (Petrie et al., 1992). This study suggested that peahens compete for access to males even after previous copulations, and mate with the same preferred male more than once (Petrie et al., 1992). This may be the result of an interaction between physiology and behavior where the combination of long-term sperm storage and copulating with multiple males results in sperm competition in which mating again with a preferred male increases the odds that he will sire the offspring (Kokko & Jennions, 2008). This conflicts with traditional sexual selection theory, as it applies to mate choice in lekking systems, which assumes that males compete for access to as many females as possible and females choose their preferred male. In this scenario, all females have equal opportunity to copulate with preferred males, resulting in high reproductive skew among males but not females. Female reproductive skew is often described as driven by competition for food and nest sites or "non-sexual social selection" (Tobias et al., 2012). However, in peahens both social selection (e.g., during competition for food) and sexual selection (e.g., during competition for mates) may drive elaboration of ornamentation (Tobias et al., 2012).

I did not find underlying hormonal mechanisms linking peahen ornamentation and dominance status. Dominance was unrelated to circulating baseline E2 or CORT concentrations. Similarly, feather brightness was also unrelated to circulating baseline E2 or CORT

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concentrations. Although circulating E2 or CORT do not predict dominance or ornament brightness, differences in tissue sensitivity rather than circulating levels of hormones might better explain the link between ornamentation and dominance status (Creel, 2001; Rosvall, Reichard, Ferguson, Danielle, & Ketterson, 2012). Since CORT is typically upregulated under stressful conditions, feather brightness may only be related to CORT levels when food is limited (Breuner & Berk, 2019). Given that our peahens had unlimited access to feed, CORT effects may have been limited. Furthermore, feather CORT is more often repeatable than circulating blood CORT levels (Taff, Schoenle, & Vitousek, 2018) and may be a better predictor of stress levels than circulating blood CORT. Future studies could consider other hormonal mechanisms that might regulate female aggression and ornamentation, such as testosterone (T) and progesterone (P). Both T and P have been correlated with aggression and dominance in both sexes in many other species (Carré et al., 2017; Enbody, Boersma, Schwabl, & Karubian, 2018; O'Connell, Ding, & Hofmann, 2013; Pikus, Guindre-Parker, & Rubenstein, 2018).

In conclusion, this study suggests that the brightness of a structural ornament signals female dominance status in a lekking species. This ornamentation is likely a sexually selected trait because brighter ornamented, dominant females win more competitions for both food and mating opportunities. Future studies should experimentally manipulate peahen feather brightness in order to evaluate the effect on social status in addition to mating behavior and reproductive success. Our results add to the growing body of evidence for functional female ornamentation in a wide range of taxa. These data suggest that lekking females can have ornamentation which functions in intrasexual competition, and spans contexts from competition for food to competition for mating opportunities.

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