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Dominant females have brighter ornamentation in a sexually dimorphic lekking species

Alexis D. Earl[1,2] | Richard K. Simpson[3] | Jessica L. Yorzinski[4]

[1]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas, USA

[2]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York, USA

[3]Department of Integrative Biology, University of Windsor, Windsor, Ontario, Canada

[4]Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, USA

Correspondence
Alexis D. Earl, Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York, 10027, USA.
Email: ade2102@columbia.edu

Abstract

Males often exhibit elaborate ornamentation that contributes to their fitness. Similarly, females can also exhibit elaborate ornamentation, but we have a relatively limited understanding of its function. Recent studies have demonstrated that female ornamentation can function in both intrasexual competition and male mate choice, but few studies have been conducted on lekking species. We therefore investigated the possibility that female ornamentation provides information about the dominance status of the bearer, which could mediate intrasexual competition. We examined this possibility using Indian peafowl (*Pavo cristatus*), a sexually dimorphic lekking species in which females exhibit elaborate ornamentation in the form of iridescent green neck plumage. We tested whether female ornamentation predicts dominance status using an information theoretic model averaging approach. We found that females with brighter ornamentation are more socially dominant than females with darker ornamentation. These results suggest that female ornamentation in this species provides social information about the dominance status of the bearer. This study provides insight into the evolution of conspicuous female traits by suggesting a potential role for female ornamentation in intrasexual competition in a lekking species.

KEYWORDS
female ornamentation, hierarchy, intrasexual competition, signaling, social behavior, social selection, structural coloration

1 | INTRODUCTION

The study of elaborate ornamentation maintained by sexual selection is fundamental to our understanding of evolution (Darwin, 1871). Historically, studies of conspicuous ornamentation have focused on male ornaments (Andersson, 1994). In contrast, elaborate female ornamentation had been considered non-adaptive, existing simply due to residual expression of genes associated with the traits of male conspecifics (Lande, 1980). Many studies have now challenged this argument by demonstrating that female ornamentation can be adaptive (Amundsen, 2000; Hare & Simmons, 2021; Jawor et al., 2004; LeBas, 2006; Tobias et al., 2012).

Recent work has found that female ornamentation can have a variety of functions, which include signaling fecundity or readiness to mate in order to influence male mate choice (Fitzpatrick & Servedio, 2018), and signaling infection status to potential social or sexual partners (Doutrelant et al., 2020). Female ornamentation can also mediate female intrasexual competition (LeBas, 2006; Tobias et al., 2012). For example, female ornamentation can mediate territorial disputes. In streak-backed orioles (*Icterus pustulatus*), females responded more aggressively to more colorful female intruders (Murphy, Hernández-Muciño, et al., 2009). Other studies have found that female ornamentation functions during competition for food (Murphy, Rosenthal, et al., 2009; Ziegelbecker et al., 2018)

and mating opportunities (Clutton-Brock, 2009). In female junglefowl (*Gallus gallus*), comb size is positively related to social status, which affects access to resources and reproductive success (Carleial et al., 2019).

Ornamentation may be particularly important during intrasexual competition when the ornament is condition-dependent and can therefore serve as an honest signal (Beck & Hopkins, 2019; Enbody et al., 2018; Jawor et al., 2004; Tibbetts, 2014). Female ornamentation that signals competitive ability can allow individuals to assess one another and determine the most likely outcome of a contest without engaging in a costly physical fight (Midamegbe et al., 2011; Santos et al., 2011). Similarly, female ornamentation that signals health and reproductive potential (Freeman-Gallant et al., 2014; Jawor et al., 2004) can attract the attention of mating partners, functioning in intersexual competition via male mate choice (Amundsen, 2000; Amundsen et al., 1997; Griggio et al., 2009; Torres & Velando, 2005). Females of species in which males invest in parental care (e.g., monogamy or cooperative breeding) are expected to engage in competition for access to males that can result in high reproductive skew among females (cooperative breeding) or only higher status females pairing with preferred males (monogamy), leading to selection on female competitive traits (Rubenstein & Lovette, 2009). Most studies to date on female ornamentation have focused on species with monogamous or cooperative breeding mating systems. However, female ornamentation also exists in species with other mating systems such as those that form leks, including Indian peafowl (*Pavo cristatus*; Dakin, 2011) and red junglefowl (Carleial et al., 2019).

In lek mating systems, males provide no parental care or resources to females; thus, males theoretically gain fitness benefits by mating with as many females as possible. As a result, females in lekking species are expected to have complete choice over mating partners, with high reproductive skew among males and low reproductive skew among females (Andersson, 1994). However, contrary to classic sexual selection theory, there is evidence that mating opportunities for females in lekking species may be limited by intrasexual competition for the most preferred males' genes (Bro-Jørgensen, 2002; Hannon et al., 1982; Karvonen et al., 2000; Petrie et al., 1992; Rosvall, 2011; Saether et al., 2001) and by male mate choice (Saether et al., 2001; Werner & Lotem, 2003).

Female ornamentation has rarely been investigated in lekking species (but see Dakin, 2011; Trail, 1990), and little is known about why females of some lekking species are highly ornamented (e.g., Indian peafowl) while others are less so (e.g., redcapped manakins, *Ceratopipra mentalis*). Dakin (2011) found that Indian peahen crest morphology predicted body condition, but not female–female agonistic behavior; therefore, the crest may signal health and condition but not dominance status. Another study found that highly ornamented females in a monomorphic lekking species (capuchinbirds, *Perissocephalus tricolor*) engaged in aggressive intrasexual competition, while less ornamented females in a dimorphic lekking species (Guianan cock-of-the-rock,

Rupicola rupicola) did not, suggesting that female ornamentation in lekking birds evolved due to competition among females (Trail, 1990).

Sexual differences in ornamentation are traditionally thought to depict the intensity of sexual selection on males and females; highly dimorphic species are thought to experience sexual selection on males only, while monomorphic species experience sexual selection on both sexes (Doutrelant et al., 2020). However, female ornamentation may be under strong sexual selection even in highly dimorphic species. Female sex-specific ornamentation is likely more relevant to selection on female traits, even when the female's ornament is less conspicuous than the ornamentation of male conspecifics. Particularly, when females are responsible for parental care, as is the case in lekking species, conspicuousness can be more costly for females than males, so ornament elaboration for the sexes may differ (Doutrelant et al., 2020). More research is needed in order to better understand the function of female-specific ornamentation in lekking species.

Our goal was to investigate a possible function of female ornamentation—mediating intraspecific competition by signaling dominance status—in a lekking species, using Indian peafowl as our model system. Indian peafowl are a lekking species in which females compete with one another (Petrie et al., 1992) and exhibit sex-specific elaborate ornamentation consisting of structurally colored green neck feathers (Figure 1). Prior studies have suggested a functional role for structural coloration as a signal for condition in males and females of many species because the production and maintenance of the feather nanoparticles responsible for structural coloration is condition-dependent (Doucet, 2002; Hill et al., 2005; Keyser & Hill, 1999; McGraw et al., 2002; Siefferman & Hill, 2005; White, 2020). We tested whether variation in female ornamentation is related to female dominance. We predicted that dominant females would have ornamentation that is brighter or more colorful than subordinates.

2 | METHODS

2.1 | Animals and facilities

We conducted this study in College Station, Brazos County, TX (30°37'40.717"N 96°20'3.864"W) on a population of captive Indian peafowl (24 peahens and 12 peacocks) during the 2018 breeding season (March–May). The birds were originally captured as adults (exact age unknown) from feral populations in Florida and California between 2009 and 2012. The birds have lived as a single flock in an outdoor enclosure (18.3 m × 24.4 m × 2.1 m) but were occasionally separated for other studies (e.g., Yorzinski, 2019). Individuals had a metal band on one leg and a plastic band on the other leg, both with unique identification codes which allowed us to record individual-level behavioral observations. Individuals were given food and water ad libitum.
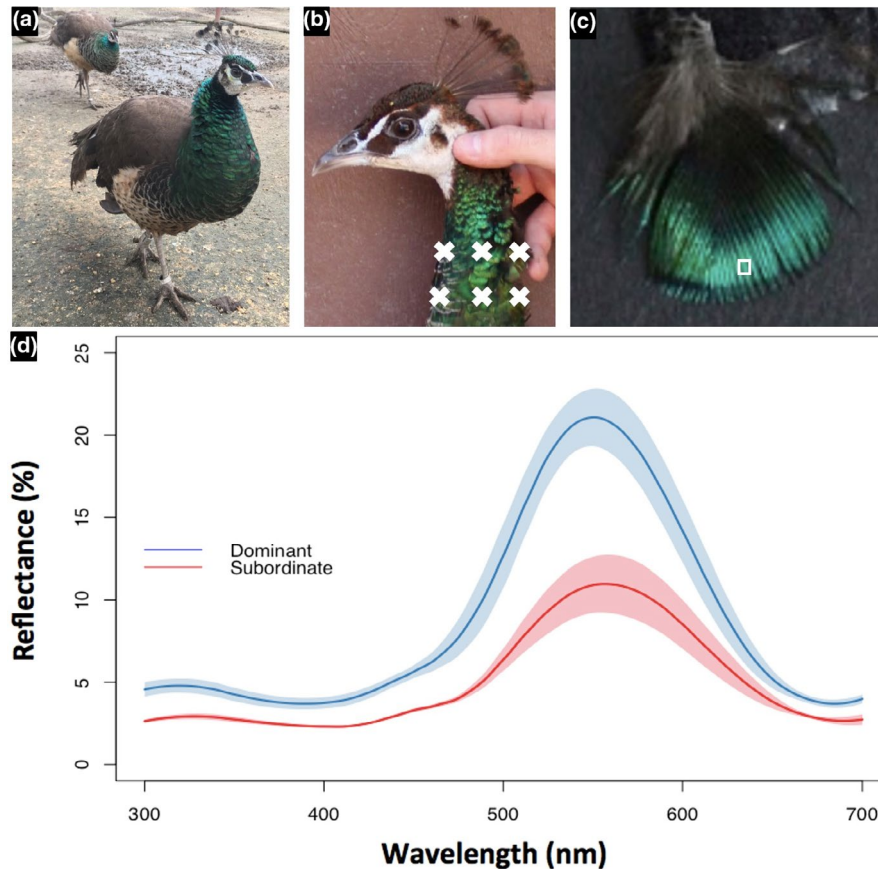
FIGURE 1 (a) Two peahens from our study population showing their neck feathers, which range in color from white to brown to gray to buffy (light) to iridescent green. (b) We collected a total of 24 feathers from the neck ornamentation of each of 24 peahens. Of these 24 feathers, six were collected from each neck region (ventral, dorsal, right/left lateral) with three feathers from an area close to the head (eight centimeters down the neck from the crown of the peahen's head) and the other three feathers from an area slightly farther from the head (13 centimeters down the neck from the crown of the peahen's head). White "X"s on the peahen's neck indicate the locations where we collected feathers. (c) A representative feather from a peahen's neck. The white box indicates the spot on the feather where measurements were collected from. (d) Reflectance curves demonstrating the physical properties of the feather reflectance (i.e., brightness, hue, chroma; see Methods) for one of our most dominant peahens and one of our least dominant peahens. Although these curves show very little difference (<50 nm) in hue, and no large difference in chroma (shape of peak), the dominant individual clearly has a higher reflectance across the entire spectra indicating higher brightness (area under the curve) than the subordinate individual

2.2 | Dominance status

We determined the dominance hierarchy of all peahens within our study population in March 2018 based on wins and losses in physical contests surrounding food. Using ad libitum behavioral sampling and an ethogram of known peahen dominance behaviors, we scored dyadic interactions between individuals who were interacting freely in the flock (Yorzinski, 2014). The dominance behaviors 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). To encourage social interactions among the birds, we provided them with a limited amount of preferred food (Royal Wing® Total Care™—Nut & Fruit Blend). We placed the preferred food in discrete piles and replenished it whenever half of it was eaten. We recorded interactions between each dyad until one individual won at least three more times than the

other individual. After an initial 60 h of observation of the full flock (with all individuals having access to all areas of the enclosure), dyads that did not interact with one another often enough in the group to meet the above criteria ($n < 3$) were separated from the flock and observed in a separate room of the enclosure (6.2 m × 6.3 m × 2.1 m). It is possible that the dominance relationships between females when they were within the full flock were different compared to when they were separated. However, we compared the dominance relationships between a subset of female dyads ($n = 8$; 16 different individuals) when they were within the full flock compared to when they were separated and found that the dominance relationships were always the same.

Overall, we observed 2131 dyadic interactions (mean: 7.1 ± 0.3 SE number of interactions between each dyad; range: 3–44). The large number of these observations indicated that dominance relationships during the study period were likely well-resolved. We determined the dominance hierarchy using David's score (David, 1987;

Yorzinski, 2014), which calculates a dominance value that accounts for nonlinear relationships. More specifically:

$$\text{David's Score} = w + w_2 - l - l_2,$$

where w is the sum of the proportion of wins by the subject, w_2 is the sum of the weighted proportion of wins of the individuals against whom the subject has won, l represents the sum of the proportion of losses by the subject, and l_2 represents the sum of the weighted proportion of losses of the individuals against whom the subject has lost. We used a De Vries correction to calculate normalized David's scores and account for variation in number of interactions between dyads (De Vries, 1998; De Vries et al., 2006).

2.3 | Feather collection & measurement

We collected 24 ornamental iridescent green feathers from the neck of each peahen on a single day (May 1, 2018). In particular, we collected six feathers from the ventral region of the neck and six feathers from the dorsal region, the left lateral, and the right lateral region of the neck. From each of the four regions, we sampled three of the six feathers from an area just below the head and the other three feathers from an area 5 cm directly below the first sampled area (Figure 1a,b). We removed the feathers by cutting the rachis below the barbs. We weighed each peahen immediately before feather collection (ZIEIS Veterinary Pet Scale; 5 g accuracy).

We stored the feathers indoors at room temperature (20°C) in opaque envelopes and then mounted them on matte black card stock. We quantified individual variation in feather reflectance using UV–Vis spectrometry. Specifically, we quantified color reflectance of all feathers (Figure 1c) across the avian-visible spectrum (300–700 nm) using a Maya2000-pro spectrometer (Ocean Optics, Inc.) and a DH2000-DUV light source (output 190–2500 nm; Ocean Optics, Inc.). We quantified reflectance of single mounted feathers rather than grouped feathers, as recommended for iridescent feathers, to minimize potential for error (Meadows et al., 2011). The spectrometer illumination and collection probes were mounted using a stand with three protractors to adjust the angle of the sample, illumination, and observation into biologically relevant positions (Meadows et al., 2011), mimicking how peafowl would be viewing these plumage ornaments (Dakin & Montgomerie, 2013). We attached collimating lenses onto the ends of 600 μm 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. Following prior work in peacocks, we set the illumination probe at 60° to the right of the horizon and both the stage and collection probe at 90° (Dakin & Montgomerie, 2013). While prior work in peacocks also measured feather reflectance (although for eyespot feathers) with the illumination probe at 30° and 45° (Dakin & Montgomerie, 2013), the reflectance of the female neck ornamental feathers at 30° and 45° was low and it was

therefore not possible for us to accurately measure reflectance at those angles (due to background spectral noise). We measured reflectance relative to a calibrated white (99%) reflectance standard (Spectralon WS-1-SL diffuse reflectance standard; Labsphere, Inc.). The mounted feathers were stacked on cards to be measured at the same distance from the probes as the reference standard. We took dark standard readings by removing the collection probe and capping the spectrometer. We recalibrated the dark reflectance standard every 15 min (Dakin & Montgomerie, 2013), and the white reflectance standard was placed on the stand between each new feather measurement to minimize instrumental drift. We collected reflectance data using the OceanView software (Ocean Optics, Inc.; integration time: 90–120 ms). All measurements were taken in a darkroom to minimize ambient light.

We analyzed the reflectance data using avian visual models for peafowl tetrachromatic vision (tetrahedral color space within the R package "Pavo"; Maia et al., 2013) to assess color through the eyes of the peafowl (Stoddard & Prum, 2008). Our visual model used the peafowl chromatic visual sensitivity system (V-vis), the achromatic receptor stimulation for the double cone sensitivity of *Gallus gallus* (a close relative of the peafowl), and illumination set to "ideal" (homogenous illumination across all bird sensitive wavelengths; Stoddard & Prum, 2008), following prior work on this species (Dakin & Montgomerie, 2013). Using this avian visual model, we quantified four standard avian tetrachromatic color space variables per feather: brightness, chroma, hue phi (hereafter "hue UV") and hue theta (hereafter "hue VIS"; Stoddard & Prum, 2008).

2.4 | Statistical analysis

We used an information theoretic model averaging approach (Burnham & Anderson, 2004) to examine the relationship between color space variables and female dominance status. We used R version 4.0.2 (2020-06-22) for all statistical tests (R Core Team, 2020). We built a global generalized linear model (base "stats" package, the packages "lme4" and "lmerTest"; Bates et al., 2015; Kuznetsova et al., 2017) with dominance status of peahens (as calculated using normalized David's score; $n = 24$) as the response variable. The fixed effects included were mean brightness, mean VIS hue, mean ventral UV hue, mean dorsal & lateral UV hue, and mean chroma. We pooled the color variables across regions of the neck due to many moderate to high correlations between regions ($r > 0.4$, $p < .04$) with the exception of UV hue in the ventral region of the neck which was not correlated to UV hue in the dorsal or lateral regions of the neck so it was included separately (Table 1). We also included peahen body mass as a fixed effect because mass is often associated with dominance, and in another population of peahens the best models of dominance included mass as a (nonsignificant) fixed effect (Dakin, 2011). We calculated the Akaike weights from all nested models with up to two fixed effects and took the sum of the Akaike weights of evidence for each fixed effect's inclusion in the model to calculate

TABLE 1 Correlations across regions of the peahen neck ornamentation for color space variables demonstrated with correlation coefficients and *p*-values in parentheses (R base "stats" package in the *cor.test* function).

	Dorsal	Ventral	Lateral	
Brightness	–	0.44 (*p* = .03)	–	Dorsal
	–	–	0.45 (*p* = .03)	Ventral
	0.67 (*p* < .01)	–	–	Lateral
Chroma	–	0.5 (*p* = .01)	–	Dorsal
	–	–	0.64 (*p* < .01)	Ventral
	0.6 (*p* < .01)	–	–	Lateral
Hue VIS	–	0.47 (*p* = .02)	–	Dorsal
	–	–	0.67 (*p* < .01)	Ventral
	0.5 (*p* = .01)	–	–	Lateral
Hue UV	–	**0.12 (*p* = .59)**	–	Dorsal
	–	–	**0.26 (*p* = .22)**	Ventral
	0.58 (*p* < .01)	–	–	Lateral

Note: Feathers from all regions of the neck sampled were moderately to highly correlated (*r* > 0.4, *p* < .04) for each color space variable except for hue UV, for which the ventral feathers were not correlated (in bold) with the dorsal or lateral feathers.

each variables' relative importance (RI) in explaining the variation in the response variable (dominance status) using the R package *MuMIn* (Barton, 2016). We limited component models to a maximum of two fixed effects per model, due to greater than two fixed effects being inappropriate for our sample size (*n* = 24 individual peahens) (Table 2). Variables with high RI values (e.g., >0.7) indicate variables that occur in the models with the highest Akaike weights, the highest number of models, or both. Because evaluating RI values alone can be misleading (Galipaud et al., 2014; Simpson & McGraw, 2018), we calculated average beta estimates and confidence intervals only for fixed effects from models within two ΔAICc of the top model (estimates and intervals calculated based on the full model average, not the conditional average, in the *model.avg* function; Barton, 2016). The fixed effects from the models within 2 ΔAICc of the top model that were included in model averaging had VIF <2 (R package: "car"), demonstrating a minimal effect of possible collinearity between variables. We confirmed the model assumptions of normality by evaluating the residuals plotted in qq-normal plots. We only interpreted fixed effects that had a 95% confidence interval around their beta estimate that did not include zero.

3 | RESULTS

Only feather brightness, ventral hue UV, and peahen mass were included in models that were less than 2 ΔAICc of the top model (Table 2). Feather brightness best explained the variation in peahen dominance status (RI = 1; Table 3), with dominant females having brighter neck ornamentation than subordinate females (Figure 1d and 2), and the 95% confidence interval of the beta estimate for feather brightness did not overlap zero (Table 3). Dominance status was not strongly related to ventral hue UV or peahen mass (i.e., model estimate 95% CI overlapped with zero). The full set of component models used for model averaging is provided in Table 2.

4 | DISCUSSION

We found feather brightness to be the best predictor of peahen dominance and that dominant peahens have brighter neck ornamentation than subordinate peahens. Our results provide evidence linking the brightness of female-specific structural ornamentation with dominance status in a lekking species. Therefore, it is possible that peahen neck coloration can be used as a signal of social dominance, though future experimental work is needed to confirm this. Signals of social dominance (or "badges of status") evolve when they improve the fitness of the signaler by mediating competition for resources that are critical for reproductive success—including food, territory, and mates (Tobias et al., 2012). When a conflict of interest is resolved by the opponents evaluating one another using badges of status, individuals can avoid risk of injury, as well as risk of lost time and energy, that they could incur from physical confrontation (Murphy, Hernández-Muciño, et al., 2009).

Social selection, selection arising from social and competitive interactions (which includes sexual selection as a nested subset; Tobias et al., 2012), shapes the evolution of social dominance signals (Lyon & Montgomerie, 2012; West-Eberhard, 1979, 1983). Non-sexual social selection may be responsible for the elaboration of this female trait, because females with brighter ornamentation are more dominant in aggressive interactions surrounding food (we calculated dominance status based on interactions during food competition; see Methods). It is also possible that selection acts on this trait in other contexts—including competitions for mating opportunities via sexual selection (Lyon & Montgomerie, 2012). Previous work in a feral population of peafowl found that dominant females solicited courtship from males more often than subordinate females did and that there were more aggressive interactions among females in front of preferred males (Petrie et al., 1992). Petrie et al. (1992) suggested that dominant peahens monopolize preferred males by repeatedly engaging them in courtship interactions. Even though females in lekking species can theoretically mate with any males they select, intrasexual selection

TABLE 2 The component model set used to test predictors of dominance status of peahens in the female dominance hierarchy (as measured using normalized David's score; see Methods)

Component model	df	Log likelihood	ΔAICc	Akaike weight
Dominance ~ Feather Brightness + Feather UV Hue (ventral)	4	−70.06	0.00	0.37
Dominance ~ Feather Brightness + Peahen Mass	4	−70.41	0.68	0.26
Dominance ~ Peahen Mass	3	−73.10	3.15	0.08
Dominance ~ Feather Brightness	3	−73.6	4.16	0.05
Dominance ~ Feather Brightness + Feather UV Hue (dorsal & lateral)	4	−72.32	4.52	0.04
Dominance ~ Feather Brightness + Feather VIS Hue	4	−72.49	4.84	0.03
Dominance ~ Feather Chroma + Peahen Mass	4	−72.71	5.28	0.03
Dominance ~ Feather VIS Hue + Peahen Mass	4	−72.82	5.51	0.02
Dominance ~ 1 (Null)	2	−75.74	5.82	0.02
Dominance ~ Feather UV Hue (ventral) + Peahen Mass	4	−73.04	5.95	0.02
Dominance ~ Feather UV Hue (dorsal & lateral) + Peahen Mass	4	−73.05	5.98	0.02
Dominance ~ Feather Chroma + Feather Brightness	4	−73.18	6.23	0.02
Dominance ~ Feather Chroma	3	−75.25	7.46	0.01
Dominance ~ Feather UV Hue (dorsal & lateral)	3	−75.34	7.64	0.01
Dominance ~ Feather UV Hue (ventral)	3	−75.58	8.12	0.01
Dominance ~ Feather Chroma + Feather UV Hue (ventral)	4	−74.26	8.39	0.01
Dominance ~ Feather VIS Hue	3	−75.73	8.43	0.01
Dominance ~ Feather Chroma + Feather UV Hue (dorsal & lateral)	4	−74.37	8.61	0.00
Dominance ~ Feather Chroma + Feather VIS Hue	4	−75.05	9.98	0.00
Dominance ~ Feather VIS Hue + Feather UV Hue (ventral)	4	−75.06	9.99	0.00
Dominance ~ Feather UV Hue (dorsal & lateral) + Feather UV Hue (ventral)	4	−75.25	10.37	0.00
Dominance ~ Feather VIS Hue + Feather UV Hue (dorsal & lateral)	4	−75.26	10.38	0.00

Note: Models include combinations of avian color space variables from female feathers (i.e., brightness, hue UV, hue VIS, and chroma), and peahen mass. Feather measurements from all regions of the neck sampled (dorsal, lateral, and ventral) were pooled for each color space variable because they were correlated, except for hue UV of the ventral feathers which was kept separate because it was not correlated with hue UV of the lateral or dorsal feathers (lateral and dorsal feather hue UV were correlated with each other; Table 1). Models were limited to a maximum of two fixed effects per model, which is the maximum number appropriate for our sample size (*n* = 24 individual peahens). All models within two ΔAICc of the top model were included for our final model parameter estimation.

among females can limit mating opportunities (Petrie et al., 1992). Further study is needed to determine whether intrasexual competition is mediated by peahen ornamentation in sexual contexts. Future studies could also test whether female ornamentation reflects fitness because dominant peahens—in addition to monopolizing preferred males (Petrie et al., 1992)—may be able to monopolize food and other resources that influence reproductive success.

Peahen neck ornamentation consists of structurally colored feathers that are iridescent green. Structural coloration can serve as an honest signal of condition (Grindstaff et al., 2012; Keyser & Hill, 2000; McGraw et al., 2002; White, 2020). Across many different species, bright structural coloration is associated with better health and condition in both males (Doucet, 2002; Doucet & Montgomerie, 2003) and females (Siefferman & Hill, 2005). While no previous work has investigated structural coloration in peahens, structurally colored ornamentation in peacocks signals health and immune function (Loyau et al., 2005) and peahens prefer to mate with peacocks with brighter and more iridescent ornamentation (Dakin & Montgomerie, 2013; Loyau et al., 2007). It is therefore possible that peahen feather

ornamentation also reflects health and condition and that males prefer brighter ornamented females. Future studies could test these hypotheses, for example, by manipulating peahen neck plumage coloration. In addition, bright ornaments may be particularly effective signals because they contrast with the environment and are more conspicuous than duller ornaments (Endler, 1990; McNaught & Owens, 2002).

Chromatic color space variables were not related to dominance status in peahens. Neither chroma nor hue were strong predictors of dominance status. Brightness, often of achromatic plumage patches, predicts dominance status in many other species and may be a particularly important color space variable for competitive interactions. For example, in male black-capped chickadees, only the brightness of white patch plumage is related to dominance (Doucet et al., 2005). In Eurasian magpies (after-hatch-year), brightness of the iridescent green ornamented tail feathers was the only predictor for whether females were territorial or not (Nam et al., 2016). In tree swallows, coloration (hue and chroma) of the iridescent blue/green dorsal feathers has been identified as a sexually selected signal and is

TABLE 3 Results from our information theoretic model averaging analyses, which only includes models within two ΔAICc of the top model, testing how peahen ornamental feather color space variables relate to peahen dominance status (determined using normalized David's score; see Methods)

Response	Predictors	Estimate	95% CI	RI
Dominance Status (David's score)	Feather Brightness	177.61	**19.58 to 335.64**	1.00
	Ventral Feather UV Hue	−12.47	−36.64 to 11.70	0.58
	Peahen Mass	0.00	−0.01 to 0.01	0.42

Note: The model beta estimates (i.e., slope) and 95% confidence intervals (CI) for each fixed effect are calculated based on the full model average. Confidence intervals that do not overlap with zero are in bold. Fixed effects are ordered based on relative importance (RI) which measures the summed Akaike weight for each fixed effect across the included models. The coefficient of determination for the global model (package "rsq") is $R^2 = 0.61$. Details on each component model are provided in Table 2.
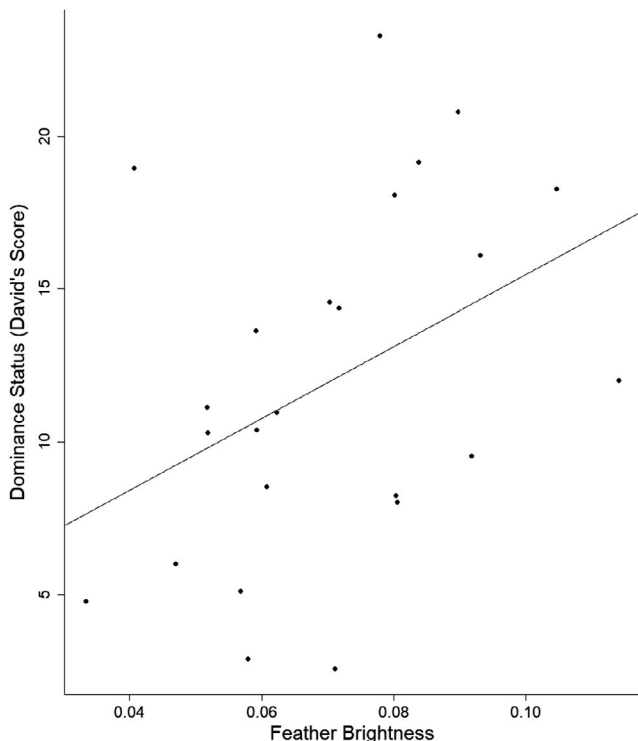
FIGURE 2 Brightness of ornamental neck feathers predicts female dominance status. Each data point represents an individual peahen ($n = 24$ peahens), with her mean feather brightness (x-axis) plotted against her dominance (y-axis) as calculated using David's score normalized with a De Vries correction (see Methods). The feather brightness value is the mean brightness of all feathers collected from the neck ornament of a given peahen ($n = 24$ feathers per peahen). The regression line represents the linear model of the relationship between mean brightness and dominance status

related to age and some immune measures (Taff et al., 2019). On the other hand, evidence suggests that tree swallow plumage brightness signals resilience to stress and frequency of social interactions (Taff et al., 2019), is a signal specifically accessed between females, and influences female–female agonistic interactions (Berzins & Dawson, 2016). In the white-shouldered fairywren, ornamented females are brighter and lower in chroma than unornamented females, and ornamented females have lower chroma than ornamented males, but no difference in brightness from ornamented males (Enbody et al.,

2017). Thus, plumage brightness may be markedly relevant for female intrasexual competition; however, more studies are needed to evaluate the relative contribution of each signal component within and across taxa.

Our results show that female ornaments in peafowl provide information about the bearer, suggesting a possible signal function, thus adding to a growing body of evidence that female ornaments—in a wide range of taxa—are potentially adaptive. In particular, females of lekking species may invest in female-specific traits that signal dominance in female–female competition. Future studies should experimentally manipulate peahen feather brightness in order to evaluate its effect on social status and reproductive success.

ORCID

Alexis D. Earl https://orcid.org/0000-0001-9758-6121
Richard K. Simpson http://orcid.org/0000-0002-1319-8197
Jessica L. Yorzinski https://orcid.org/0000-0002-4193-6695

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