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RESEARCH ARTICLE

A bare-part ornament is a stronger predictor of dominance than plumage ornamentation in the cooperatively breeding Australian Swamphen

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ABSTRACT
Many animals use coloration to signal dominance and fighting ability. In birds, plumage coloration is often linked to individual quality, but less research has investigated coloration in unfeathered traits (i.e. 'bare parts'), despite theoretical expectations that they might be more reliable signals. Here, we investigate the relationship between multiple ornaments and social dominance in a wild population of the cooperatively breeding Australian Swamphen (known locally as and hereafter referred to as Pūkeko; *Porphyrio melanotus melanotus*) to test the hypothesis that bare-part ornaments should be more strongly correlated with dominance than plumage coloration. We show that the size and color of the pūkeko's frontal shield (a bare-part ornament), as well as the brightness and chroma of the blue-UV breast plumage, are correlated with social dominance in adult birds. However, the correlation between frontal shield size and dominance was much higher than that between plumage color and dominance, and was also higher than most previously published correlations between plumage traits and dominance. Additionally, frontal shield size, but not breast coloration, was correlated with the size of the testes in male pūkekos, which may be because bare-part ornaments are more closely tied to an individual's current physiology than plumage ornaments. While correlative, our results demonstrate that bare-part and plumage traits could act as redundant ornaments, but with differing reliability, and suggest that future studies on bare-part ornaments will enhance our understanding of dominance signaling.

Keywords: color, feather, multiple ornamentation, pūkeko, aggression, badge of status, status signal, testes

Un ornement des parties nues est un prédicteur plus fort de la dominance que l'ornementation du plumage chez *Porphyrio melanotus melanotus*, une espèce à reproduction coopérative

RÉSUMÉ
Plusieurs animaux utilisent la coloration pour signaler la dominance et la capacité compétitive. Chez les oiseaux, la coloration du plumage est souvent liée à la qualité individuelle, mais peu de recherches ont étudié la coloration dans les traits non emplumés (i.e. « parties nues »), malgré les attentes théoriques qu'ils pourraient être des signaux plus fiables. Nous avons étudié la relation entre des ornements multiples et la dominance sociale chez une population sauvage de *Porphyrio melanotus melanotus*, une espèce à reproduction coopérative, afin de tester l'hypothèse que les ornements des parties nues devraient être plus fortement corrélés avec la dominance que la coloration du plumage. Nous montrons que la taille et la couleur de la plaque frontale de *P. melanotus melanotus* (un ornement des parties nues), ainsi que la luminosité et la saturation des couleurs du plumage bleu-UV de leur poitrine, sont corrélées avec la dominance sociale chez les oiseaux adultes. Cependant, la corrélation entre la taille de la plaque frontale et la dominance était plus élevée qu'entre la couleur du plumage et la dominance, et était également plus élevée que la plupart des corrélations antérieurement publiées entre les traits du plumage et la dominance. De plus, la taille de la plaque frontale, mais non la coloration de la poitrine, était corrélée avec la taille des testicules chez le mâle, ce qui peut être dû au fait que les ornements des parties nues sont plus étroitement liés à la physiologie actuelle d'un individu qu'aux ornements du plumage. Bien qu'ils soient corrélés, nos résultats démontrent que les parties nues et le plumage peuvent agir comme ornements redondants, mais avec une fiabilité différente, et ils suggèrent que les études futures sur les ornements des parties nues permettront d'améliorer notre compréhension de la signalisation de la dominance.

Mots-clés: couleur, plume, ornementation multiple, potentiel de maintien des ressources, agression, hiérarchie, insigne du statut, signal du statut, testicules

INTRODUCTION

Many animals use signals to communicate information about their quality to conspecifics. When signals convey information about fighting ability (also known as resource holding potential; Parker 1974), they can be used to form and maintain dominance relationships, and may therefore influence the distribution of resources among individuals (e.g., Rohwer 1975). Such signals are often referred to as 'status signals,' and are thought to be most beneficial for species that frequently interact with unfamiliar individuals (Rohwer 1982), or species for which the costs of having ambiguous dominance relationships are high (West-Eberhard 1983).

In birds, plumage coloration often has a signaling role (Dale 2006, Hill and McGraw 2006). While most research has focused on the role of coloration in mate attraction (Hill 2006), a large body of literature suggests that coloration is also used as a status signal (Senar 2006, Tibbetts and Safran 2009, Dey et al. 2015). In this context, numerous studies of model signal traits (e.g., the chest badge of the Harris's Sparrow [*Zonotrichia querula*]) have been invaluable toward determining the specific manner in which avian status signals function. However, many birds have complex patterns of coloration and researchers have become increasingly interested in exploring the relationships among multiple ornaments, as well as investigating the specific information conveyed by different types of coloration in a social context (Møller and Pomiankowski 1993, Chaine et al. 2011). Indeed, studying single ornamental traits may provide misleading results if receivers incorporate multiple ornaments into an integrated signal (Hegyi et al. 2015) or if they consider the congruence among multiple ornaments during assessment of a conspecific (Tibbetts and Izzo 2010). As a result, several recent studies have examined the relationship between different plumage ornaments within the same species (Chaine and Lyon 2008, Chaine et al. 2011, Laucht and Dale 2012, Mercadante and Hill 2014, Hegyi et al. 2015). In general, these studies have found that multiple ornaments may provide a varying amount of overlap in information content (Laucht and Dale 2012), with some sets of ornaments showing high covariation and functioning as a single signal, and other sets signaling different aspects of quality that are unrelated to one another.

In contrast to plumage ornamentation, less research attention has been devoted to ornamentation in avian bare parts (e.g., legs, bills, and wattles). Like plumage, bare-part ornamentation is used in both mate choice (Omland 1996, Torres and Velando 2003) and rival assessment (Shawcross and Slater 1984, Ligon et al. 1990, Bright and Waas 2002, Murphy et al. 2009). However, bare-part traits are considered to be dynamic traits because they are able to change size or color over short time periods (i.e. hours or days; Faivre et al. 2003, Ardia et al. 2010), whereas change in plumage ornamentation is generally restricted to discrete molting periods. As a result, it has been suggested that bare-part traits may be better suited to signaling in aggressive contexts than plumage traits, as they may provide more accurate information about an individual's current condition and/or aggressive intent (Dey et al. 2015). Indeed, bare-part ornaments are correlated with social dominance in several species (e.g., Moss et al. 1979, Buchholz 1995, Emlen and Wrege 2004), yet few studies have directly compared plumage and bare-part ornamentation to evaluate the information content and reliability of these different signal modalities.

Androgens mediate dominance behavior in many animals (e.g., Joslyn 1973, Taves et al. 2009) and, since many ornaments are also androgen-dependent, these hormones are thought to be a key aspect of individual condition that is linked with social interactions and signal phenotype in vertebrates (Tibbetts 2014, Vitousek et al. 2014). In male birds, androgen levels are often correlated with the size of the testes, and there have been several studies demonstrating a relationship between the size of the testes and plumage ornamentation (e.g., Kimball and Ligon 1999, Merilä and Sheldon 1999). However, the correlation between these factors is typically low, perhaps because plumage ornamentation is determined by physiological conditions during molt, while the testes can change in size with environmental and social conditions. Most birds also have asymmetrical testes (Briskie and Montgomerie 2007, Calhim and Montgomerie 2015), and variation in testicular asymmetry has been argued to be related to individual condition, with higher-quality individuals having more asymmetrical testes (Møller 1994, Calhim and Birkhead 2009). Indeed, Møller (1994) demonstrated that testicular asymmetry was positively related to plumage ornamentation in Barn Swallows (*Hirundo rustica*) and House Sparrows (*Passer domesticus*). However, bare-part ornamentation may be more strongly correlated with testicular investment as many bare-part traits are androgen-dependent (Moss et al. 1979, Ligon et al. 1990, Eens et al. 2000, Ardia et al. 2010).

In this study, we compared bare-part and plumage-based ornamentation in the Australian Swamphen (*Porphyrio melanotus melanotus*; known locally and referred to hereafter as Pūkeko). In this cooperatively breeding bird, most individuals live in polygynandrous groups that defend a shared territory and cooperate to raise the group's offspring (Craig 1980). Pūkeko social structure shows considerable interpopulation variation (e.g., Jamieson 1997), but at our study site groups typically contain 5–15 individuals and had approximately equal sex ratios (C. Dey personal observation). Within social groups, Pūkeko form mixed-sex dominance hierarchies (Dey and Quinn 2014), which influence access to reproductive

opportunities (Craig 1980, Jamieson and Craig 1987) and nonsexual resources (Craig 1977). Additionally, when there are multiple breeding females in a group, they all lay in a single nest (Craig 1980). This phenomenon is known as 'joint laying,' and can lead to intragroup conflict because hatching success decreases with increasing total clutch size (Quinn et al. 2012, Dey et al. 2014b).

Like many other rails (e.g., Gullion 1951, Petrie 1988, Crowley and Magrath 2004), Pūkeko of both sexes have a fleshy frontal shield ornament that extends from the bill onto the crown. In Pūkeko, this ornament is shaped like a guitar pick, with the widest part of the shield located distally from the bill, and changes from black to bright red once birds reach sexual maturity. In other rails (e.g., American Coots [*Fulica Americana*]), the shield is highly vascularized, ranges from 2.0 mm to 3.5 mm thick, and is covered in a pigmented, keratinized callus layer (Gullion 1951); however, similar histological data is not available for Pūkeko. Regardless, previous studies have shown that the size of the Pūkeko's frontal shield is correlated with social dominance (Dey and Quinn 2014), and a recent experiment demonstrated that frontal shields are used as status signals (Dey et al. 2014a). Despite several studies on frontal shield size in Pūkeko, there have been no examinations of variation in frontal shield color. Furthermore, Pūkeko also have brilliant blue–violet ventral plumage that is displayed during aggressive interactions (C. Dey personal observation). Whether this ventral plumage has a signaling function is currently unknown. As a first step toward understanding multiple ornamentation in Pūkeko, we performed multivariate analyses of the relationships between ornament characteristics and key life history (i.e. sex, body size), environmental (season), and physiological traits (size and asymmetry of the testes). Additionally, we examined relationships between ornaments and measures of social dominance to test the general prediction that bare-part ornamentation should be more strongly correlated with dominance than plumage ornamentation. While our study was correlative, the breadth of our data allowed us to simultaneously consider, and control for, a variety of factors that may influence Pūkeko ornamentation, but which have often been neglected in other studies.

METHODS

This study was conducted at the Tawharanui Open Sanctuary (36°22′S, 174°49′E) on the North Island of New Zealand. At this site, Pūkeko live in permanent, mixed-sex social groups of 5–15 individuals that defend an all-purpose territory. Further details on Pūkeko social organization and reproductive ecology are published elsewhere (Jamieson et al. 1994, Jamieson 1997, Dey et al. 2012, Quinn et al. 2012). From 2008 to 2013, we captured adult Pūkeko during 5 sampling

TABLE 1. Sampling periods and the number of captured Australian Swamphen, or Pūkeko (*Porphyrio melanotus melanotus*), used in this study.

Sampling period	Start	End	Number of birds
1	October, 2008	February, 2009	44
2	August, 2010	November, 2010	137
3	January, 2012	April, 2012	116
4	April, 2013	June, 2013	50
5	October, 2013	November, 2013	14
6	May, 2014	June, 2014	108 [a]
All			469

[a] Birds were collected postmortem following a partial cull of the study population.

periods (see Table 1) using trapping procedures that are described elsewhere (Quinn et al. 2012). At the time of first capture, each individual was fitted with a numbered metal band and a unique combination of 4 colored plastic bands to enable us to identify individuals through time. We collected several morphological measurements, including frontal shield width, which is highly correlated with the overall area of the frontal shield ornament ($R^2 = 0.87$, $n = 50$). We sexed birds by measurement (Craig et al. 1980) and collected breast plumage and frontal shield coloration data (see below).

In May and June of 2014, 108 previously banded individuals were collected postmortem immediately after a partial cull of the population (performed by the landowner under New Zealand Department of Conservation Wildlife Authority Permit #38671-FAU). We measured the frontal shield width and breast plumage coloration of these birds. In addition, for the 60 male birds in the sample, the right and left testis were separated and weighed to the nearest 0.01 g with a digital scale.

In total, measurements from 469 captures of 272 individuals were considered in this study (Table 1). Not all types of data were collected during each capture (see below) and therefore sample sizes varied among analyses.

Frontal Shield Coloration
During sampling periods 2–4 (Table 1), we took standardized digital photographs of Pūkeko frontal shields to quantify shield coloration. For each captured individual, we took 3 photographs using a Fujifilm Finepix S700 camera (Fujifilm, Tokyo, Japan). To standardize photography conditions, the photographs were taken indoors, from a set distance (50 cm), and were illuminated primarily by the camera's flash. The subject was oriented such that the transverse plane of the frontal shield was held parallel to the lens of the camera (i.e. the full surface area of the frontal shield was visible), and the same individual (C. Dey) held the bird in all photographs. To control for variation between pictures, we also included a red color standard within each picture.

TABLE 2. Principal component loadings of Pūkeko frontal shield coloration measured in red–green–blue (RGB) color space.

Loading	PC1	PC2
Red	−0.40	0.91
Green	−0.64	−0.36
Blue	−0.66	−0.21
Proportion of variance	0.72	0.26

Frontal shield coloration was quantified using the colorZapper package (Valcu and Dale 2014) in R (R Core Team 2015). For each photograph, we selected a polygon that encompassed the typical color of the individual's frontal shield and avoided any areas of glare caused by the camera's flash. The colorZapper package then calculated the mean intensity of red (R), green (G), and blue (B) coloration (on a scale of 0 to 255) for 400 randomly chosen pixels within the polygon. Although this method does not consider UV reflectance, spectrophotometry has shown that Pūkeko frontal shields do not have substantial reflectance in the UV range (see electronic supplementary material in Dey et al. 2014a). RGB values were then used in a principal component (PC) analysis (Table 2), with PC1 being related to total reflectance (R^2 (R + G + B) = 0.95) and PC2 being a measure of redness. Preliminary analysis suggested that measured shield brightness was highly variable among photos (intraclass correlation coefficient (ICC) measured from 7 individuals captured on 2 separate occasions within a 1 week period = 0.38) and was not related to behavioral or life history variables; thus, we only considered PC2 for all further analyses (ICC = 0.60). Although measurement repeatability of PC2 was high, PC2 values were also correlated with the measured 'value' (part of the hue–saturation–value [HSV] color space) of the red color standard ($R^2 = 0.26$, $n = 130$), suggesting that some PC2 variation among individuals was attributable to variation in photographic conditions. As a result, we ran a regression of PC2 against the 'value' of the red color standard, and used the residuals as our shield color score in subsequent analyses.

Breast Plumage Coloration

To quantify Pūkeko breast coloration, we collected 8–10 semiplume feathers from the breast of each adult captured during sampling periods 1, 2, 3, 4, and 6 (Table 1). Feathers were cut from the center of the breast, directly over the sternal keel, and were stored in plastic bags for later analysis. Although we did not directly test whether this method produced similar results to measuring plumage coloration on live birds, similar methods performed on Eurasian Great Tits (*Parus major*), which have much smaller feathers than Pūkeko, showed that measurements taken from 10–15 feathers produced similar results to directly measuring live birds (Quesada and Senar 2006).

We collected UV–Vis reflectance values by stacking the feathers atop a black card and taking spectral readings from the distal, pennaceous portion of the feather, which is the only part of the feather that contains the blue–violet coloration. We used an Ocean Optics (Dunedin, Florida, USA) USB2000 spectrophotometer with a PX-2 pulsed xenon light source to collect reflectance for wavelengths between 300 and 700 nm (integration time: 100 ms; 5 readings averaged per recording; boxcar 3). At the end of the combined reflection probe and light source, there was a nonreflective black pointer cut at a 45° angle. Two readings were taken from each feather stack (one from each side of the rachis, with the probe held parallel to the feather barbs). Then, we used the spectrograms to calculate mean brightness and chroma for each reading (mean brightness = average reflectance between 300 and 700 nm; chroma = [maximum reflectance − minimum reflectance]/mean brightness; Montgomerie 2006). We averaged the values from each side of the rachis to produce one value for chroma and brightness for each sample. Although plumage hue (i.e. peak wavelength) is a common color measurement that has been linked to quality in a number of studies, our measurement of hue had low repeatability (ICC = 0.01), which may have been due in part to overall low intraspecific variability and/or iridescence in Pūkeko breast plumage. As a result, here we consider only breast plumage chroma and mean brightness, which were highly repeatable for samples measured on 2 separate occasions (ICC = 0.73 and 0.63, respectively; $n = 10$).

Dominance Observations

To determine the relationship between ornamentation and social dominance, in January and February, 2012, we performed behavioral observations of 11 social groups in which all adult group members were distinguishable by band combinations. Details of the observation methodology are published elsewhere (Dey and Quinn 2014, Dey et al. 2014a). Briefly, we performed 10 30-min behavioral observations of each social group and recorded all dominance interactions (i.e. subordinate postures, displacements, pecks, kicks, and charges; Craig 1977) that occurred among group members (average number of interactions during 5 hr of observation = 85, range = 5–241). All interactions were pooled and used to calculate David's dominance score (David 1987) for each individual in each of the 11 social groups. This method is appropriate for dominance ranking when not all pairs of individuals interact (David 1987), and incorporates information about both the number of opponents that are dominated, as well as the rank of those opponents. Blinded observations (e.g., of individual ID or ornamentation) were not possible, as we were observing focal animals in the field. However, observers did not have access to morphometric or

TABLE 3. Results of linear mixed modeling for Pūkeko shield ornamentation. For categorical predictor variables, the level of the variable that corresponds with the effect is indicated in brackets (e.g., Sex [male] is the effect for the difference between 'male' and the reference level).

Response	n	Predictor	β	95% CL	P
Dominance score	98	Shield width	10.63	7.79, 13.39	<0.001
	49	Shield color	8.45	1.87, 15.00	0.02
Mass	449	Shield width	0.13	0.11, 0.15	<0.001
		Sex [male]	0.11	0.10, 0.14	<0.001
		Season [nonbreeding]	−0.01	−0.03, 0.01	0.47
	130	Shield color	0.01	0.03, 0.04	0.68
		Sex [male]	0.23	0.19, 0.26	<0.001
		Season [nonbreeding]	−0.02	−0.05, 0.02	0.34

colorimetric data for the observed birds, and variation in ornamentation was virtually indistinguishable from the distance at which observations were performed.

Statistical Analysis

Statistical analysis was performed with R statistical software (R Core Team 2015), using the lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2015), and MuMIn (Bartoń 2015) packages. The goals of our analyses were: (1) to determine whether each type of ornamentation (shield size, shield color, breast plumage brightness, and breast plumage chroma) was correlated with social dominance, and whether each ornament was correlated with dominance after controlling for potentially important confounding variables, (2) to determine which type of ornamentation was the best predictor of dominance, and (3) to test whether male ornamentation was related to gonadal investment. In all analyses, we scaled continuous predictor variables by 2× their standard deviation to make the regression coefficients comparable with binary predictor variables (Gelman 2008).

First, we ran 4 separate linear mixed effects (LME) models to test for a relationship between ornamentation and David's dominance score. In each model, the dominance score was included as the response variable, and the ornamentation score was included as a fixed effect. When multiple ornamentation scores were available for an individual, we used the measurements taken in closest temporal proximity to the behavioral observations. In each model, we also included social group ID as a random intercept to account for shared variance among individuals living in the same social group. Including this random effect improved model fit for all 4 models.

Although the models described above were a direct test of the relationships between dominance and ornamentation, the sample size for some models was small because not all types of ornamentation were measured for each individual (see Tables 3 and 4) and direct dominance observations were only performed on a subset of individuals. As a result, we ran a second set of models using body mass as a proxy for dominance, which allowed us to use a much larger number of samples and to control for important life history variables that could have influenced the relationship between dominance and ornamentation. In Pūkeko, body mass is strongly correlated with dominance score (marginal $R^2 = 0.50$; Nakagawa and Schielzeth 2013). We used log-transformed body mass as the response variable in our models, and included ornamentation score, sex, and season (a binary score of whether or not measurements were taken during the peak breeding season of August–November; Dey and Jamieson 2013) as fixed effects. In each model, year and bird ID were included as random intercepts to account for shared variance among individuals captured in the same year and for repeated measures of individuals. Importantly, body mass is not intrinsically linked to frontal shield size (or any

TABLE 4. Results of linear mixed modeling for Pūkeko breast plumage coloration. For categorical predictor variables, the level of the variable that corresponds with the effect is indicated in brackets (e.g. Sex [male] is the effect for the difference between 'male' and the reference level).

Response	n	Predictor	β	95% CL	P
Dominance score	33	Brightness	9.94	7.82, 12.71	0.01
	33	Chroma	15.47	5.92, 25.00	0.003
Mass	226	Brightness	0.03	0.00, 0.05	0.03
		Sex [male]	0.19	0.17, 0.22	<0.001
		Season [nonbreeding]	−0.08	−0.14, −0.03	0.009
	226	Chroma	0.03	0.00, 0.05	0.21
		Sex [male]	0.19	0.17, 0.22	<0.001
		Season [nonbreeding]	−0.10	−0.15, −0.05	0.005

other ornamentation) in Pūkeko; experimental studies have shown that changes in shield size occur without changes in body mass (Dey et al. 2014a), and that shield size is significantly correlated with dominance even after controlling for body mass (Dey et al. 2014a). While we did not have age data for most individuals in this study (and therefore could not include age in our models), individuals who were recaptured in different sampling periods did not show changes in average ornamentation score between captures (C. Dey personal observation), suggesting that there is no consistent increase or decrease in ornamentation with age after Pūkeko reach adulthood.

Because different ornaments were measured on different individuals, we could not perform statistical analyses that included all ornaments in the same model. Instead, we used meta-analytic techniques to determine which ornament best predicted social dominance. To perform this analysis, we ran a series of LME models, and calculated correlation coefficients (r) from t-statistics using methods outlined in Nakagawa and Cuthill (2007). In the first 4 models, dominance score was used as the response variable, with shield size, shield color, breast chroma, or breast brightness the sole fixed effect in each of the 4 models. In these models, social group ID was again included as a random intercept. We also ran 4 additional models using log-transformed body mass, a strong proxy for social dominance, as the response variable. These models had much larger sample sizes than those that used observed dominance scores, and therefore allowed for more confidence in the fitted relationship between ornamentation and dominance. In these 4 models, the 4 ornamentation scores (described above) were again used as sole fixed effects (1 in each model). We also included year and bird ID as random intercepts to account for shared variance among observations from the same year and repeated measures of some individuals. To analyze significant differences among types of ornamentation, we bootstrapped 95% confidence intervals for regression coefficients using the parametric bootstrap function boot-Mer in the lme4 package (Bates et al. 2015). We considered 2 ornaments to have significantly different correlations with dominance if their confidence intervals did not overlap, which is a conservative test for rejection of the null hypothesis at α = 0.05 (Schenker and Gentleman 2001).

To analyze the relationship between ornamentation and testicular investment, we ran a set of linear models (LM) using measurements from males that were collected immediately following a cull in 2014 (sampling period 6). Importantly, the birds used for this analysis were sampled outside the breeding season, and therefore interindividual variation in the size of the testes was unlikely to have been due to variation in reproductive condition, but instead was likely reflective of differences in individual
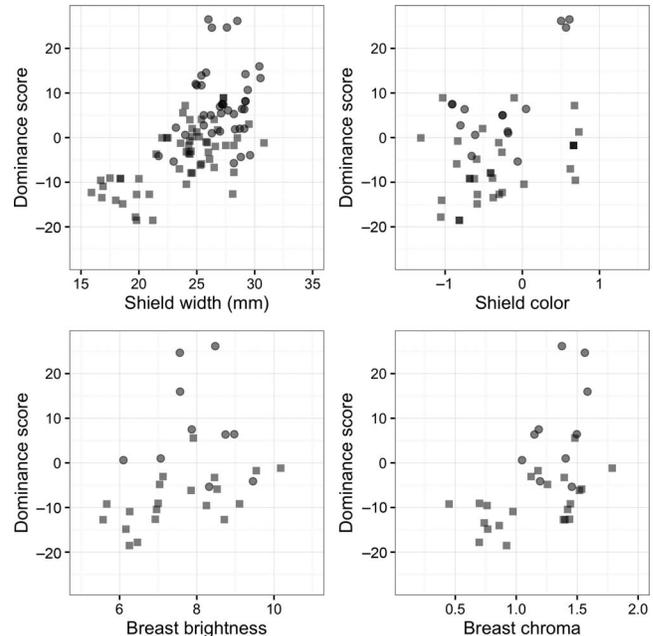

FIGURE 1. The relationship between social dominance and 4 aspects of ornamentation in the Australian Swamphen, or Pūkeko (*Porphyrio melanotus melanotus*). Samples from male birds are shown with circles, while samples from female birds are shown with squares. Dark gray shading is created by overlapping data points. Dominance score was determined from direct observations of Pūkeko social groups and calculated using the method of David (1987). All aspects of ornamentation had a significant relationship with dominance in linear mixed-effects models (see Tables 3 and 4). Figure created using ggplot2 (Wickham 2009).

quality (e.g., androgen levels). In these models, we again used ornamentation as the response variable, and used the size of the testes [log(right testis mass + left testis mass)] and asymmetry of the testes [log(left testis mass/ right testis mass)] as the predictor variables. Shield color was not measured for these birds, so the analysis was performed on frontal shield size and breast plumage coloration only.

RESULTS

Ornamentation and Social Dominance
All types of ornamentation considered in this study (shield size, shield color, breast chroma, and breast brightness) showed a significant positive relationship with social dominance (Tables 3 and 4, Figures 1 and 2). Additionally, frontal shield size and breast plumage brightness were significantly related to body mass, a proxy for social dominance (Tables 3 and 4), even after controlling for sex and season. As expected, males had greater body mass than females. Additionally, Pūkeko were slightly less heavy in the nonbreeding season in some models.
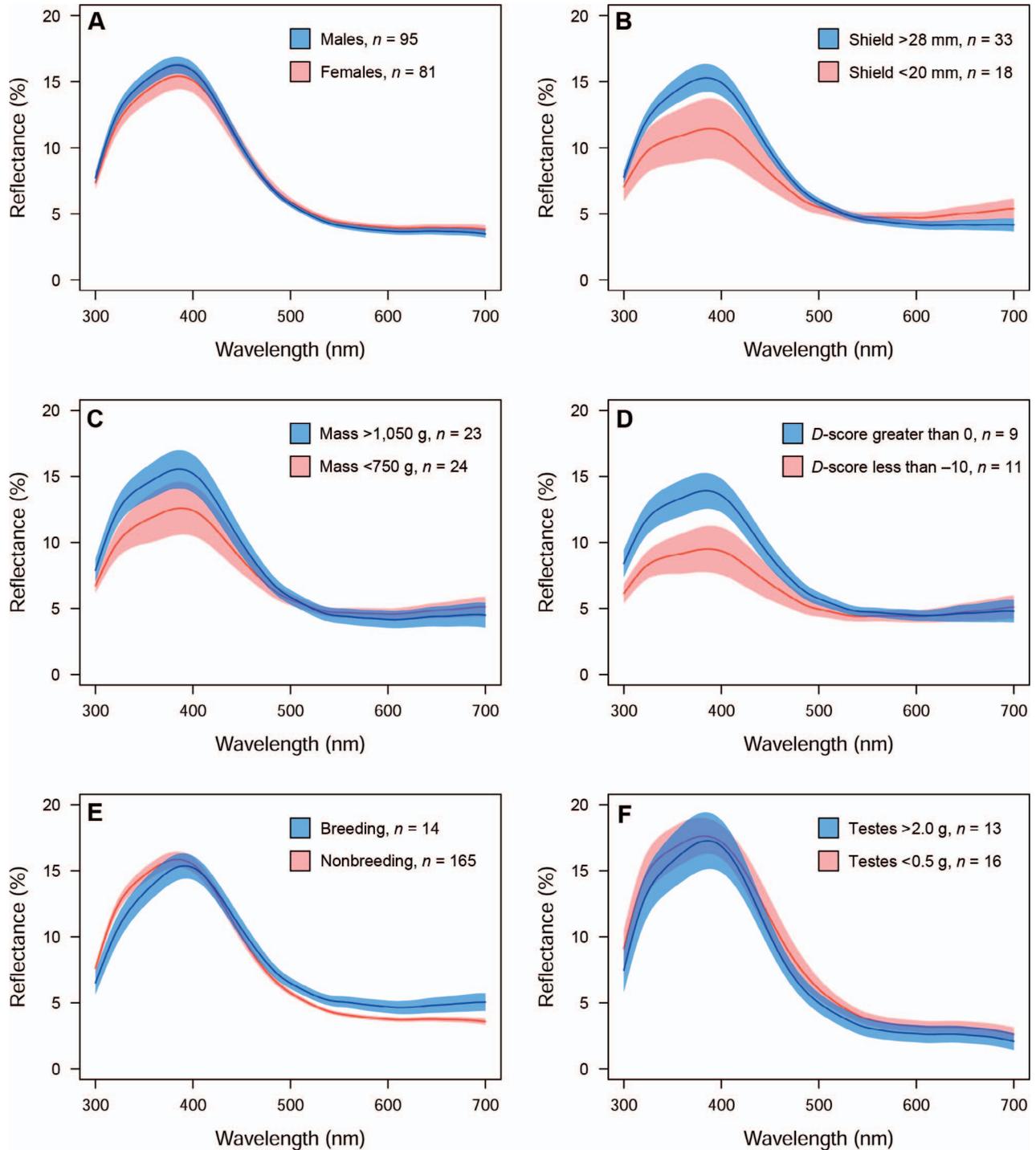
FIGURE 2. Reflectance spectra for Pūkeko breast plumage. Shown are the 95% confidence intervals of the mean reflectance for Pūkeko in relation to various morphological, behavioral, and life history variables: (**A**) sex, (**B**) shield width, (**C**) body mass, (**D**) dominance score, (**E**) season, and (**F**) testes mass. For plotting purposes only, continuous predictor variables are shown as binary factors based on whether they were above or below thresholds shown in the panels. See Table 4 for results of statistical analysis.
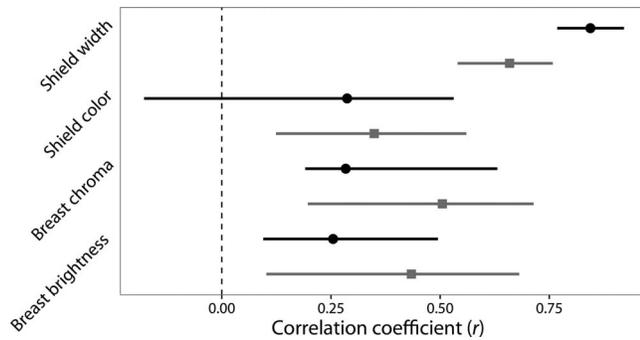
FIGURE 3. Correlation between ornamentation and social dominance in Pūkeko. Shown are the estimated correlation coefficients (with 95% confidence intervals) for the relationship between each ornament and either the directly observed dominance score (gray squares), or an indirect measure of dominance, body mass (black circles). Figure created using ggplot2 (Wickham 2009).

Which Ornament Best Predicts Dominance?

Frontal shield width had the highest correlation with social dominance (Figure 3) when considering both direct ($r = 0.65$, 95% CL = 0.54, 0.76) and indirect dominance measures ($r = 0.84$, 95% CL = 0.77, 0.92). However, confidence intervals for the relationships between direct dominance scores and ornamentation were broad and therefore the confidence intervals among all ornaments overlapped (Figure 3). Using body mass, an indirect measure of social dominance with a much larger sample size, the confidence interval for shield width did not overlap with that of other ornaments (Figure 3), and this correlation was therefore significantly greater than for other forms of ornamentation.

Ornamentation and Testicular Investment

Consistent with most other birds, testicular asymmetry in Pūkeko was strongly left-biased (paired t-test, $n = 60$: mean difference in log(mass) = 0.27, 95% CL = 0.21, 0.32, $P < 0.001$). While the mass of the testes strongly predicted frontal shield size in male Pūkeko (LM, $n = 60$: estimate = 2.91, 95% CL = 2.00, 3.82, $P < 0.001$; Figure 4), there was no relationship between testicular asymmetry and shield size (estimate = 0.10, 95% CL = −0.81, 1.00, $P = 0.83$). Breast plumage chroma showed a weak and nonsignificant relationship with the mass of the testes (LM, $n = 60$: estimate = 0.16, 95% CL = −0.01, 0.33, $P = 0.05$) and was not predicted by testicular asymmetry (estimate = −0.03, 95% CL = −0.19, 0.13, $P = 0.72$). Additionally, neither testes mass nor asymmetry was related to breast plumage brightness (LM, $n = 60$: size estimate = −0.56, 95% CL = −1.40, 0.28, $P = 0.19$; asymmetry estimate = −0.17, 95% CL = −1.00, 0.67, $P = 0.69$).

DISCUSSION

In this study, we have shown that frontal shield size and color, as well as breast plumage brightness and chroma, are significantly related to social dominance in the Pūkeko. However, breast plumage coloration and frontal shield coloration are weak predictors of dominance, especially after controlling for confounding variables. In contrast, frontal shield size is strongly related to dominance, and is also correlated with the size of the testes. These results are consistent with previous studies, which have suggested that frontal shield size is the primary status signal used by this species (Craig 1977, Dey et al. 2012, 2014a, Dey and Quinn 2014), but also suggest that breast plumage and frontal shield coloration may provide some additional information about individual dominance status.

Interestingly, the correlations between frontal shield size and both indices of dominance used in this study were higher than the average correlation between plumage
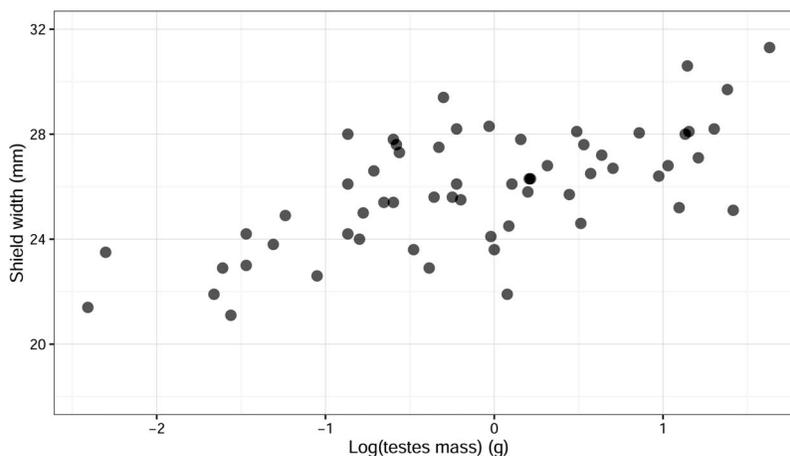
FIGURE 4. Frontal shield size is positively related to the size of the testes in Pūkeko. Shown is the relationship between frontal shield width and the size of the testes [log(left testis length + right testis length)] for 60 male Pūkeko. Figure created using ggplot2 (Wickham 2009).

ornaments and dominance presented in a recent meta-analysis ($r = 0.359$; table 2 in Santos et al. 2011). While Santos et al. (2011) showed that the relationship between plumage ornamentation and dominance is dependent on various factors (e.g., type of coloration, study design), 89% of the effect sizes considered in their meta-analysis were smaller than the correlation between shield size (a bare-part ornament) and dominance found in the current study. Conversely, the correlation between Pūkeko breast plumage coloration and dominance is consistent with the average correlation between structural plumage traits and dominance (Santos et al. 2011). This comparison generally supports the hypothesis that bare-part ornaments are more reliable predictors of dominance status than are plumage ornaments (Dey et al. 2015, this study), and suggests that an increased focus on bare-part signaling could generate new insights into the field of animal communication.

Although bare-part and plumage traits are both known to have signaling roles in birds, there are few avian species for which both of these types of ornamentation have been studied concurrently, and as such their relative importance remains unclear. Of the studies that have simultaneously considered both bare-part and plumage ornamentation, many have shown support for the 'redundant messages' hypothesis (Møller and Pomiankowski 1993) by demonstrating that both signal modalities are correlated with aspects of quality (e.g., Jawor et al. 2004, Laucht and Dale 2012), with success in mate-choice competitions (e.g., Johnson et al. 1993, Jawor et al. 2003) or in dominance interactions (Mateos and Carranza 1997, Ramos-Fernández et al. 2004). However, other studies have demonstrated that one ornament type is more important for signaling; for example, a meta-analysis of the well-studied Red Junglefowl (*Gallus gallus*) showed that comb characteristics, but not plumage ornamentation, were the subject of mate choice (Parker and Ligon 2003). Similarly, bill color, but not plumage ornamentation, was related to pairing success in Mallards (*Anas platyrhynchos*; Omland 1996). Because these studies have provided equivocal results, a synthetic, quantitative analysis (e.g., a meta-analysis) comparing the strength of the relationships between bare-part and plumage ornaments with the qualities that they might signal (i.e. dominance, attractiveness) would be valuable for the study of avian communication, and could help to guide future research.

In our study, we found a strong relationship between the size of the testes and frontal shield size in male Pūkeko. This finding is consistent with the results of studies of other species, which have demonstrated links between frontal shield characteristics and aspects of individual quality (Fenoglio et al. 2002, Alvarez et al. 2005). The size of the testes is correlated with circulating testosterone levels in many birds (Garamszegi et al. 2005), and therefore our results are consistent with a relationship between androgens and frontal shield size in Pūkeko. Importantly, our measurements of testicular size were taken outside the breeding season, suggesting that dominant Pūkeko maintain relatively high levels of circulating androgens throughout the year. Although we were not able to directly or indirectly measure androgens in females, it is likely that female shield size is also androgen-dependent. Baseline testosterone levels are correlated with bill color in female American Goldfinches (*Spinus tristis*; Pham et al. 2014), and Common Moorhen (*Gallinula chloropus*) females increase frontal shield size in response to testosterone implants (Eens et al. 2000), demonstrating that androgens are a key mediator of ornament expression in both sexes.

While Pūkeko have significant testicular asymmetry, we found no relationship between this asymmetry and any aspect of ornamentation. Our results are consistent with 3 other studies that failed to find a relationship between testicular asymmetry and aspects of quality in birds (Birkhead et al. 1998, Kimball et al. 1997, Merilä and Sheldon 1999). Additionally, an experiment by Birkhead et al. (1998) showed that increased testicular asymmetry was associated with poor, rather than good, body condition in Zebra Finches (*Taeniopygia guttata*). Indeed, the available evidence suggests that a positive relationship between testicular asymmetry and quality is not general across birds, and we have a poor understanding of the factors contributing to intra- and interspecific variation in testicular asymmetry (Calhim and Montgomerie 2015).

Bare-part ornaments have the potential to be highly informative signals because of their ability to respond rapidly to changes in individual physiology (e.g., Faivre et al. 2003, Ardia et al. 2010), which can be driven by changes in social or environmental conditions. Indeed, a recent experiment demonstrated that Pūkeko frontal shields can decrease in size within a 7-day period in response to increased aggressive challenges from group-mates (Dey et al. 2014a), which may provide a mechanism that tightly links signal expression to an individual's dominance rank. Many bare-part ornaments respond rapidly to changes in androgen levels (Allee et al. 1939, Eens et al. 2000, Ardia et al. 2010), which influence, and are influenced by, social interactions (Hirschenhauser and Oliveira 2006). As a result, androgen hormones may provide a general mechanism by which social interactions can indirectly influence signal phenotypes.

While Pūkeko are known to respond to experimental manipulations of frontal shield size, further study is required to determine whether they perceive and respond to natural variation in shield or breast plumage color. Interestingly, breast plumage coloration was found

to reflect UV light (Figure 2), which is thought to be a 'special' signaling channel for birds because it cannot be perceived by mammalian predators (Hausmann et al. 2003). Although rails do not possess the UV-sensitive cones found in most passerines (Ödeen and Håstad 2013), they can still perceive shorter wavelength light than humans because avian corneas and lenses are transparent to UV-A light (Cuthill 2006). As a result, Pūkeko may represent an interesting model for studies that compare UV (breast plumage) and non-UV (frontal shield) coloration.

In cooperatively breeding animals, dominance relationships can have a strong influence on the allocation of reproduction and individual fitness (Hauber and Lacey 2005, Nonacs and Hager 2011). Although dominance hierarchies could be maintained by individual recognition, many cooperatively breeding species also use morphological traits to signal and maintain dominance relationships (e.g., Tibbetts and Izzo 2010, Rat et al. 2015). In this study, we demonstrated that frontal shield size and color, as well as breast plumage color, were correlated with social dominance in the Pūkeko. However, frontal shield size was more informative across a range of analyses, demonstrating that different ornament types (e.g., bare-part vs. plumage traits) may provide differing amounts of information on individual quality (Møller and Pomiankowski 1993). These results therefore contribute to our understanding of multiple ornamentation in animals, and suggest that an increased focus on bare-part ornamentation in birds may advance the study of animal communication.

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