

The crest of the peafowl: a sexually dimorphic plumage ornament signals condition in both males and females

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Both male and female peafowl grow crests on top of their head – iridescent blue in males, dull iridescent green and brown in females – but the potential signal function of this plumage ornament is unknown. In this study, peafowl crests were measured in three feral populations, and morphological variation in this ornament was studied in relation to body condition (body mass in relation to tarsus length) and health (white blood cell concentration and ectoparasite load). Prior to the start of the breeding season, male crests are wider with greater pennaceous area, and are more likely to have all feathers grown out compared with female crests. Only crest length changed with measurement date, increasing over time; in males, crest measurements were not related to the extent of train feather development. Crest morphology is a potential signal of individual health and condition in both sexes, but in different ways. In females, the amount of crest plumage grown out to its full extent was related to body condition at the start of the breeding season, whereas in males, the size and pennaceous area of the ornament were related to ectoparasite load. Observations of within-sex agonistic behaviour suggest a possible role for the crest ornament in status signaling in males, because males that engage in more aggressive interactions tend to have wider crests. There was no evidence for a relation between crest morphology and agonistic behaviour in females.

Across bird species, crest plumage is often used for signaling and display. Female California quail *Callipepla californica* prefer males with elongated crest plumes (Calkins and Burley 2003), and there is evidence that crest ornaments are used for mutual mate choice in crested auklets *Aethia cristatella* (Jones and Hunter 1999) and European shags *Phalacrocorax aristotelis* (Daunt et al. 2003). Crest ornaments might also function as status signals in competition within the sexes. For example, larger crests signal social dominance in both male and female crested auklets (Jones and Hunter 1999), as well as in males of two quail species *C. gambelii* and *C. squamata* where experiments indicate that females do not choose mates based on crest ornamentation (Hagelin and Ligon 2001, Hagelin 2002).

The signal function of crest plumage can be mediated by features other than ornament size. For example, in blue tits *Cyanistes caeruleus* the colour of erectile crest plumage is involved in both mutual mate choice (Andersson et al. 1998, Hunt et al. 1999) and status signaling (Rémy et al. 2010). Northern cardinals *Cardinalis cardinalis* also have an erectile crest that is used in courtship displays and agonistic interactions, but crest size does not appear to be related to either mate choice (Jawor et al. 2003) or intrasexual aggressive behaviour (Jawor et al. 2004). Hagelin (2002) suggested that erectile crest plumes in quail might function as signals of intent during agonistic interactions.

Peacocks (genus *Pavo*) are known for their highly elaborate train feathers, displayed during courtship and

assessed by females during mate choice (Darwin 1871, Petrie et al. 1991, Petrie and Halliday 1994, Loyau et al. 2005a, 2007, Takahashi et al. 2008, Dakin and Montgomerie 2011). Both male and female peafowl also have a crest on top of the head (Kannan and James 1998; Fig. 1), but little is known about the function of this ornament. In the Indian peafowl *P. cristatus*, the crest is composed of 'spatula-tipped' (Kannan and James 1998) plumes characterized by a triangular pennaceous flag at the end of a wirelike rachis, similar to the racket plumes thought to have evolved independently in several other groups of birds (Bleiweiss 1987, Murphy 2007). The *P. cristatus* crest has about 20 of these spatula-tipped feathers (mean = 21.2, 95% CI = 20.15–2.25, n = 10 males, 10 females) arranged in a fan shape along the central axis of the top of the head (Fig. 1). This plumage is sexually dimorphic in colour: the barbules of crest feathers from adult males are brilliant iridescent blue, whereas in females these feathers are a mixture of brown and dull iridescent green (Kannan and James 1998, pers. obs.). Crest ornaments are also common in closely related species (*Afropavo*, *Argusianus*, *Rheinardia* and *Polyplectron*), including green peafowl *Pavo muticus*, the sister species to Indian peafowl (Kimball et al. 2001); green peafowl have a distinctive crest morphology with a narrow cluster of feathers that 'slant forward and are webbed to their base' (Kannan and James 1998).

The crest of *P. cristatus* is approximately 5 cm in length, so one might expect that it is fairly inexpensive to grow and maintain compared to the 150 cm long train of over 200 feathers (Petrie et al. 1996). This raises two questions: why does the peacock have a relatively small crest in addition to such an elaborate train, and why do both sexes have crests? One possibility is that this ornament has an adaptive function in females as well as males, either with respect to mutual mate choice or status signaling (Amundsen 2000). Alternatively, the female crest could be a byproduct of genetic correlation with males (Lande 1987), with the ornament having an adaptive function in males only.

In this study, I quantify sexual dimorphism in peafowl crest morphology, and consider the potential function of this ornament in both sexes. I test whether variation in the crest ornament might be an indicator of body condition (body mass controlling for tarsus length), or an indicator of health, based on hematological state and ectoparasite load. I also investigate the potential role of the crest ornament as a status signal by examining the relations between crest morphology and agonistic interactions within the sexes.

Material and methods

Field methods

This study was conducted in three feral peafowl populations: 1) Assiniboine Park Zoo (APZ) in Winnipeg, MB, Canada, where about 60 peafowl are free-ranging over 50 ha of pens and woodland; 2) Toronto Zoo (TZ) in Toronto, ON, Canada, where about 30 peafowl are free ranging over 250 ha of pens and woodland; and 3) Los Angeles Arboretum (LAA) in Arcadia, CA, USA, where >100 peafowl live in 50 ha of parklands and surrounding residential areas. The APZ and TZ populations are housed indoors during the coldest winter months (Dec–Mar), whereas birds in the LAA population are feral year-round. Birds in all three populations are lek-mating, as has been observed in the wild (Hillgarth 1984, Harikrishnan et al. 2010).

Birds were caught prior to the start of the breeding season for measurement (Apr 2007 at APZ and TZ; Jan–Mar in 2008, 2009 and 2010 at LAA) and marked for individual identification with a numbered leg band. The southern LAA population breeds from Mar–Apr whereas the more northern TZ and APZ populations breed from May–Jun. Thus, although capture dates span from Jan–Apr, all measurements were taken at similar times relative to the start of the annual breeding cycle in each population. At the time of capture, I measured body mass (± 0.01 kg) and tarsus length (± 1 mm); I also measured the length of the longest ‘fish-tail’ feather in the train (± 0.5 cm) on males as an index of the extent of feather development (Petrie et al. 1991, Loyau et al. 2005a). About 5–10 body feathers were plucked from each of the ulnar, breast and back regions and sealed in a paper envelope to assess ectoparasite load. A small sample of blood was taken by pricking the cutaneous ulnar vein with a 20 ga needle, then used to make blood smears on 2–4 separate glass slides to assess

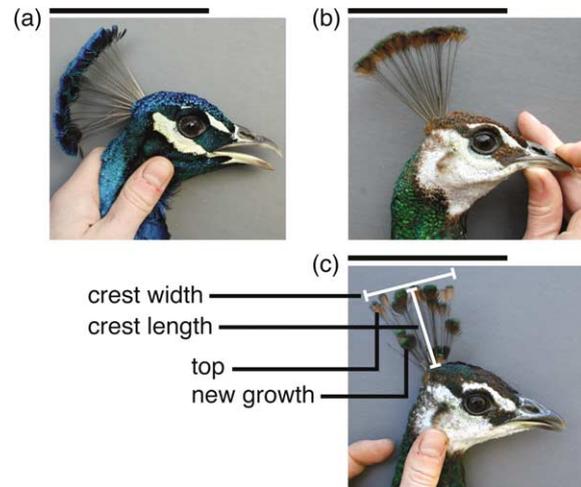


Figure 1. The fan-shaped crest ornament of (a) male and (b)–(c) female peafowl, showing measurements taken in this study. The birds in (b) and (c) illustrate the range of variation in new feather growth among females. Scale bars are 10 cm.

hematological health. For two females, the amount of obtained blood was not sufficient to make useable smears.

Measuring the crest ornament

To quantify crest morphology prior to the start of the breeding season, I measured the length and width of the ornament (as viewed from the side of the head) to the nearest 0.1 mm. Crest length was measured on the central crest feathers as the distance between the feather attachment and the tip, and crest width as the linear distance between the anterior and posterior extremes of the pennaceous region along the top of the crest (Fig. 1). Following this, I digitally photographed the left and right sides of each bird’s head and crest in profile (Fig. 1) using an 18% grey card with a ruler attached, positioned behind the bird’s head so that the eye on the opposite side was touching the card. I then removed a single posterior crest feather from each bird.

I selected the single best photograph of each bird based on the clarity of the outline of pennaceous flags against the background, and used the ‘lasso’ tool in Adobe Photoshop 10.0.1 to outline the pennaceous flags and measure the area enclosed. This measurement was taken separately for: 1) the region along the top of the crest or ‘top area’, which includes the flags of feathers that have grown out to the maximum crest length at the time of capture, and 2) a ‘new growth area’ of any flags below and not contiguous with those at the top of the ornament (Fig. 1). A bird with all crest feathers grown out to roughly the same length at the time of capture would thus have a new growth area of 0 (Fig. 1a, b). Pixel areas were converted to cm^2 using the ‘ruler’ tool in Photoshop to measure 5.0 cm on the ruler in each photograph (mean = 97.5 pixels cm^{-1} , range = 52.7–136.6, $n = 144$).

Body condition and health

As a measure of body condition, I used body mass controlling for tarsus length, because individuals with greater mass for a

given skeletal size are thought to have greater energy reserves in the form of fats and other soft tissues (Green 2001). I also examined two measures of individual health describing hematological state and ectoparasite load.

To assess hematological state, I stained blood smears following Campbell (1995) and examined at least 10 fields per slide at $1000\times$ under oil immersion (mean no. fields per bird = 21.1, 95% CI = 20.5–21.9, $n = 142$), counting the total number of leucocytes (white blood cells) and erythrocytes (red blood cells) in each field. No blood parasites were seen in any of these blood smears, consistent with a previous study of peafowl in a zoo population (Hollamby et al. 2003). I determined white blood cell (WBC) concentration, a widely used measure hematological state in birds (Ots et al. 1998), by calculating the total number of leucocytes per 10 000 red blood cells (RBC) for each bird (mean no. RBC = 5980, 95% CI = 5738–6222; mean WBC per 10000 RBC = 165, 95% CI = 154–177, $n = 142$). Elevated leucocyte numbers are indicative of stress and inflammation (Ots et al. 1998), and the abundance of certain leucocyte types is correlated with measures of immunocompetence as well as sexual ornamentation in peacocks (Møller and Petrie 2002, Loyau et al. 2005b, Ros et al. 2009).

To quantify ectoparasite load, I examined body feathers 2–4 months after they were collected. Parasitic chewing lice (Insecta: Phthiraptera) are common in feral peafowl (Petrie et al. 1996, Stewart et al. 1996, Hollamby et al. 2003), and remained attached to the feather barbs, where they were counted under a dissecting microscope; other ectoparasites were not observed, neither on the feathers nor on the birds during handling. A direct energetic cost of feather lice has been demonstrated experimentally in birds (Booth et al. 1993), and increased infestation can result from poor health states (e.g. viral infections; Marzal et al. 2007) that might reduce the time and energy devoted to preening. As a measure of ectoparasite load, I divided the total number of lice and eggs by the total number of body feathers sampled from each bird (mean no. body feathers = 16.7, 95% CI = 15.9–17.6, $n = 144$). I combined the results from ulnar, breast and back feathers into one score for this analysis, since all body feathers from each bird were stored together in a single envelope. Previous research has shown that when estimating the abundance of chewing lice by visual inspection, incorporating multiple body regions gives a more accurate estimate than any single body region alone (Clayton and Drown 2001).

Behavioural observations

To determine the potential role of the crest ornament in competitive dominance interactions, I quantified agonistic behaviour that occurred on leks during the breeding season. In the APZ and TZ populations (May and Jun 2007), as well as in the LAA population (Mar–Apr 2008), leks were observed during peak lekking periods of 07:00–12:00 and 16:00–18:00 local times (Petrie et al. 1991, pers. obs.). A total of 80 h of observations were conducted on 8 focal leks in the APZ population, 115 h on 5 leks in TZ, and 160 h on 7 leks in LAA in 2008. I also quantified agonistic interactions at LAA in 2010, using continuous observations

on 4 leks from 8:00 to 18:00 local times, over a 13-day period (15–27 Mar, total observation time 506 h).

During these observations, all ‘displacements’ between two individuals of the same sex were recorded (Petrie et al. 1992). Displacements included aggressive chases, and were defined as any interaction where one individual moved rapidly and directly towards another and the second individual moved away from the approaching bird. Such behaviour is common in both male and female peafowl (Petrie et al. 1991, 1992, pers. obs.). All displacement events recorded on leks involved males defending their display courts from other males, or females interacting with other females while visiting leks. Although females also act aggressively towards juvenile males on leks, I have not seen adult males targeting females with aggression in this context.

The distribution of displacement events among individuals was highly right-skewed, with 48/71 females and 12/38 males never seen engaging in these interactions (males: mean no. interactions = 5.7, 95% CI = 2.8–8.6, $n = 38$; females: mean = 1.0, 95% CI = 0.5–1.6, $n = 71$), in spite of the fact that all of the studied males were adults with regular display court territories on the leks (i.e. none were floaters). The birds that did not engage in these agonistic interactions on the leks were not a random sample, however. Among birds observed in at least one interaction, the total number of interactions was highly correlated with the number of interactions where that bird was the aggressor (Pearson correlations, male: $r = 0.97$, $p < 0.0001$, $n = 25$; female: $r = 0.93$, $p < 0.0001$, $n = 22$), but not with the number of interactions where it was the target (male: $r = 0.29$, $p = 0.16$, $n = 25$; female: $r = 0.07$, $p = 0.76$, $n = 22$), excluding a single outlier for each sex that was targeted exceptionally frequently (38/40 interactions for the male as target; 9/10 for the female). This pattern indicates that the birds not seen engaging in these interactions were mainly subordinate individuals that avoided direct competition. To summarize these data, I assigned birds to the following three categories that correspond to increasing dominance status: 0 = birds that did not engage in any agonistic interactions ($n = 12$ males, 48 females), 1 = birds that were the target at least half of the time ($n = 9$ males, 11 females) and 2 = birds that were the aggressor in agonistic interactions more than half of the time ($n = 17$ males, 12 females).

Data analysis

Analyses were performed using JMP 9.0.0 and R 2.13.0 (R Development Core Team 2011). In the LAA population where some birds were measured and observed in multiple years, I analyzed males in the first year they were captured. Only 2 LAA females were captured in more than one year (2009 and 2010 for both), and because focal observations on leks were not conducted in 2009, I analyzed data from these females in 2010. I also excluded one adult male from APZ who was missing all crest feathers. Total sample sizes for measured birds were: APZ, $n = 13$ males, 34 females; TZ, $n = 6$ males, 15 females; LAA, $n = 30$ males, 46 females.

I used general linear models to test for sex differences in crest morphology controlling for the effects of study population and measurement date. Most males (31/49) had no new growth though some had substantial new growth; in contrast, only a few (15/95) females had no new growth. Thus, I analyzed new growth area as a categorical variable (presence/absence of new pennaceous growth) using a generalized linear model with a quasibinomial distribution of errors (to correct for overdispersion) and logit link function, because the raw data were not normally distributed and no transformation could be found to correct this.

To test whether crest morphology is related to feather development in males, I examined the relation between train length and male crest measurements in general linear models controlling for population and measurement date, as train length increases with date in these populations (Dakin and Montgomerie 2011). As above, I used a generalized linear model with a quasibinomial distribution to model the presence or absence of new growth area in relation to train development.

The exact age of birds was not known. However, because some males were captured in more than one year at LAA, I used linear mixed models with male identity as a random variable to test for an effect of increasing age on male crest measurements ($n=44$ measurements of 16 males). This was not examined in females because only 2 were captured in more than one year.

To investigate the potential signal content of the crest ornament, I examined general linear models of body condition, WBC concentration and ectoparasite load using the four crest measurements and study population as potential predictors. As an index of body condition, I analyzed body mass controlling for average tarsus length. I applied a 4th root transformation to WBC concentration and a square root transformation to both ectoparasite load and new growth area of female crests to normalize model residuals involving these zero-inflated variables (Quinn and Keough 2002); new growth area in males was analyzed as a categorical variable as described above. To control for collinearity and the problem of multiple comparisons, I used AICc (Akaike's Information Criterion corrected for small sample sizes) to select the best model from the set of all possible models. I also examined models with $\Delta\text{AICc} \leq 2$ in each set, as these 'top models' are also considered to be plausible, given the data (Burnham et al. 2011); these are reported in Appendix 1.

To investigate the role of the crest ornament in within-sex agonistic behaviour, dominance category was treated as an ordinal response and analyzed using logistic regression models with cumulative response probabilities fit by maximum likelihood (lrm function in the R package Design ver.2.3-0). I followed the same model selection procedure described above, using the four crest measurements and study population as predictors. A previous study of peafowl reported that a male's ability to maintain a lek territory is related to his tarsus length (Loyau et al. 2005a). For this reason, and because one might also predict that dominant birds would tend to be larger or in better body condition, I also included body mass and tarsus length as potential predictors. Coefficients for the dependent variables in these models are tested with the Wald χ^2 statistic. I also report Nagelkerke's R^2 which gives a measure of the improvement

of the fitted model over the null model, to a maximum of 1; this pseudo R^2 does not indicate the percent of the variance explained by the model.

Two birds were outliers for crest measurements: a female with new growth area of 8.54 cm^2 , which was >6 times the median of all other females (median = 1.33, mean = 1.65, range = 0–4.96 cm^2 , $n=94$) and a male with crest width of only 2.3 cm, which was $<1/3$ the median of all other males (median = 7.91, mean = 7.77, range = 4.66–10.00 cm, $n=48$), so I excluded these two from analyses involving those variables.

Results

Sexual dimorphism in crest morphology

Male and female peafowl crests differ significantly in morphology when controlling for the effects of population and measurement date (Table 1). Male crests are significantly wider with a greater pennaceous area at the top, but there was no appreciable difference between the sexes in length of the crest feathers. Females are significantly more likely than males to have new growth just prior to the start of the breeding season, and thus their crests appear to be more irregular (Fig. 1). There were significant differences between study populations in all crest measurements except width (Table 1). Only crest length changed significantly with measurement date, increasing over time when controlling for population (Table 1).

Correlations between various measures of crest morphology are summarized in Table 2. Crests with greater top area tend to be wider and have less new growth. Females with wider crests also have significantly less new growth, but there was no relation between width and new growth area in males. Among females, crest length is positively correlated with crest width as well as top area, and negatively correlated with new growth area. Crest length is not significantly related to any other crest measurements in males.

Male feather development and age

There was no relation between male train length and crest length when controlling for population and measurement date (effect of train length: $F_{1,44}=0.15$, $p=0.70$), nor was there any relation between train length and crest width (train length: $F_{1,43}=1.13$, $p=0.29$), top area (train length: $F_{1,44}=0.71$, $p=0.41$), or the presence of new growth (train length: $F_{1,44}=0.66$, $p=0.42$) controlling for population and measurement date. Male crest morphology is therefore independent of the extent of train feather development.

Among LAA males captured in more than one year, crest length did not change significantly with year when controlling for measurement date (effect of year: $F_{1,26}=0.23$, $p=0.63$, $n=44$ measurements of 16 birds). Similarly, there was no consistent change in male crest width (year: $F_{1,26}=0.96$, $p=0.34$), top area (year: $F_{1,26}=0.36$, $p=0.56$), or new growth area (year: $F_{1,26}=0.28$, $p=0.60$) between years, controlling for measurement date. Thus, there was no evidence that crest morphology changed with age in males.

Table 1. Sexual dimorphism in peafowl crest morphology. Means for each sex are given along with models incorporating sex, date, and population; significant effects are highlighted in bold. Sample sizes differ where outliers were excluded from models (see text). Crest new growth area was modeled as a categorical variable (present or not) using a generalized linear model with a quasibinomial distribution of errors.

	n	Mean \pm 95% CI	Effect	β	SE	F	p	DF
Length (cm)			Sex (M)	-0.05	0.06	0.72	0.40	1,139
			Date	0.01	0.005	7.70	0.006	1,139
			Pop			5.13	0.007	2,139
Males	49	5.68 \pm 0.13	Pop (LAA)	0.74	0.23			
Females	95	5.69 \pm 0.06	Pop (TZ)	-0.11	0.01			
Width (cm)			Sex (M)	1.10	0.22	25.77	<0.0001	1,138
			Date	-0.01	0.02	0.54	0.46	1,138
			Pop			1.62	0.20	2,138
Males	48	7.77 \pm 0.34	Pop (LAA)	-0.24	0.82			
Females	95	6.62 \pm 0.26	Pop (TZ)	-0.56	0.34			
Top area (cm ²)			Sex (M)	3.53	0.36	98.63	<0.0001	1,139
			Date	0.04	0.03	2.19	0.14	1,139
			Pop			7.28	0.001	2,139
Males	49	10.32 \pm 0.83	Pop (LAA)	4.68	1.36			
Females	95	6.40 \pm 0.41	Pop (TZ)	0.43	0.56			
New growth area (cm ²)			Sex (M)	-2.44	0.44	31.15	<0.0001	1,139
			Date	0.03	0.03	0.90	0.34	1,139
			Pop			4.20	0.02	2,139
Males	49	0.43 \pm 0.27	Pop (LAA)	-0.74	1.53			
Females	95	1.65 \pm 0.29	Pop (TZ)	-2.04	0.77			

Condition and crest morphology

Table 3 summarizes the best models to predict individual body condition and health (details for the other top models with $\Delta AIC_c \leq 2$ are given in Appendix 1). There were significant differences between study populations in all three condition and health indices for both males and females.

Not surprisingly, there is a significant positive relation between tarsus length and body mass in both sexes. In males, crest morphology was not related to body condition in the best model; however, in females, both the pennaceous area at the top of the crest and the amount of new growth significantly predict body condition, controlling for population. Females in better condition tend to have more pennaceous area at top, and less new growth, in the crest ornament.

In males, there was a positive effect of crest width in the best model of WBC concentration; similarly, in females, there was a positive effect of the amount of new crest growth on WBC concentration, but neither of these effects were significant controlling for population. With ectoparasite load, in males, both crest width and top area are significant predictors in the best model (controlling for

population), such that males with wider crests that have less pennaceous area at the top (i.e. are sparse) have greater louse parasitism. No crest measures were significantly related to ectoparasite load in females.

Thus, in females, the amount of new growth at the start of the breeding season is a potential signal of body condition, and possibly also hematological health. In males, the width and area at the top of the crest potentially signal ectoparasite load.

Relation to agonistic behaviours

For males, crest width was the only significant predictor of dominance category in the best model, although the amount of top pennaceous area in the crest was nearly significant (Table 4, Fig. 2; see Appendix 1 for details of other top models with $\Delta AIC_c \leq 2$). Males that have wider crests with less pennaceous area at the top act as the aggressor more frequently on the leks. Among females, the best model for dominance category included non-significant effects of body mass and crest length, but population was the only significant predictor of female agonistic behaviour (Table 4). Thus, crest morphology is a

Table 2. Correlation matrix for measures of crest morphology. Results for Pearson correlations (r , p) are listed for males and females separately; significant relations are highlighted in bold. Sample sizes are $n = 49$ males and $n = 95$ females except where noted because of the exclusion of outliers (see text). Crest new growth area was square root transformed. * $n = 48$; $^+ n = 94$.

		Crest width	Top area	New growth area
Crest length	male	-0.08, 0.61*	0.25, 0.09	-0.17, 0.24
	female	0.27, 0.007	0.40, <0.0001	-0.24, 0.02⁺
Crest width	male		0.45, 0.001*	-0.13, 0.38*
	female		0.66, <0.0001	-0.24, 0.02⁺
Top area	male			-0.46, 0.001
	female			-0.24, 0.02⁺

Table 3. Best models to predict body condition (body mass controlling for tarsus length), WBC concentration, and ectoparasite load of male and female peafowl, from model sets including the following predictors: CrL = crest length, CrW = crest width, CrT = top pennaceous area, CrNG = new growth area, Pop = population, and T = tarsus length (body mass models only). Sample sizes differ where outliers were excluded from models (see text); significant effects are highlighted in bold.

	R ²	Akaike weight	Effect	β	SE	F	p	DF
Body mass								
Males	0.27	0.19	T	0.36	0.13	7.56	0.009	1,43
			CrW	0.01	0.04	0.08	0.77	1,43
			Pop			3.18	0.05	2,43
Females	0.29	0.33	T	0.35	0.10	12.00	0.0008	1,88
			CrT	0.04	0.02	3.96	0.05	1,88
			CrNG	-0.13	0.06	5.28	0.02	1,88
			Pop			6.19	0.003	2,88
WBC								
Males	0.29	0.34	CrW	0.04	0.03	2.25	0.14	1,44
			Pop			8.35	0.0008	2,44
Females	0.18	0.17	CrNG	0.08	0.05	2.70	0.10	1,88
			Pop			6.39	0.003	2,88
Ectoparasite								
Males	0.76	0.45	CrW	0.04	0.02	6.41	0.02	1,43
			CrT	-0.02	0.01	5.38	0.03	1,43
			Pop			59.36	<0.0001	2,43
Females	0.51	0.25	Pop			48.3	<0.0001	2,92

better predictor of dominance status than body size among males, but not among females, in the populations studied here.

Because males with wide, sparse crests are apparently in poor health based on their elevated ectoparasite loads (Table 3), I re-examined the best model for male ectoparasite load controlling for dominance status in addition to population. The effect of male dominance category on ectoparasite load was not significant ($F_{2,30} = 0.90$, $p = 0.42$) in this model. There was a significant negative relation between top pennaceous area and ectoparasite load ($F_{1,30} = 6.10$, $p = 0.02$), but the relation with crest width was no longer significant ($F_{1,30} = 1.88$, $p = 0.18$) when controlling for dominance category and population.

Discussion

Peahens have a smaller, less colourful version of the peacock's crest (Fig. 1). The results presented here suggest that, similar to European shags (Daunt et al. 2003), peafowl crest morphology might be related to health and condition in both sexes. Females with more of their crest feathers fully grown prior to the start of the breeding season tend to be in better condition than females with a large area of new

growth at that time, and they may also have fewer body lice. Males typically have all of their crest feathers fully grown at the start of the breeding season, so for most males, this trait is not a useful indicator once courtship begins. In males, the size and pennaceous area of the crest are related to ectoparasite load. These results were significant controlling for differences between study populations, suggesting that this ornament is potentially a useful signal in both sexes in the populations studied here.

Crest length, the only morphological trait that did not differ between the sexes in this study, did not predict individual health or condition, whereas the sexually dimorphic aspects of crest morphology measured here are potentially useful signals: crest width and pennaceous area among males, and the amount of new feather growth among females (Table 3). These results are consistent with the idea that sexual selection drives the evolution of sexual dimorphism and exaggeration in condition-dependent traits (Zahavi 1975, Pomiankowski 1987, Cotton et al. 2004), and with experimental evidence from red jungle fowl *Gallus gallus* demonstrating heightened condition-dependence of sexually dimorphic plumage traits relative to other morphological traits like tarsus length and bill size (Zuk et al. 1990).

In this study, peacocks with wider crests were more often dominant in agonistic interactions on the lek. A possible

Table 4. Best models of agonistic behaviour for male and female peafowl, with dominance modeled as an ordinal logistic response with three levels. Predictors include crest measurements (CrL = crest length, CrW = crest width, CrT = top pennaceous area, CrNG = new growth area), body mass (M), tarsus length (T) and population (Pop). Sample sizes differ where outliers were excluded from models (see text); significant effects are highlighted in bold.

	Pseudo R ²	Akaike weight	n	Effect	β	SE	Wald χ ²	p	DF
Males	0.18	0.09	37	CrW	0.76	0.38	2.02	0.04	1
				CrT	-0.25	0.14	-1.75	0.08	1
Females	0.18	0.06	71	CrL	-1.50	0.96	-1.56	0.12	1
				M	1.50	0.82	1.83	0.07	1
				Pop (LAA)	1.43	0.61	2.33	0.02	
				Pop (TZ)	0.51	0.73	0.69	0.49	

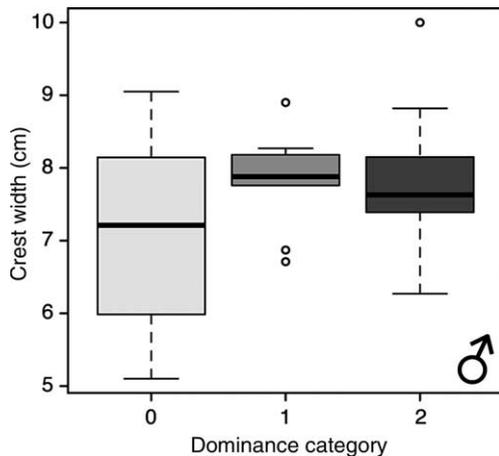


Figure 2. Tukey box plots of crest width in relation to dominance category (0 = no agonistic interactions, 1 = subordinate in at least half of the interactions observed, 2 = dominant in most interactions) in male peafowl ($n = 37$).

explanation is that males use the crest as a status signal during competitive interactions with other males. Although obvious displays involving the crest have not been described in peafowl, competing males often inspect one another while walking in parallel (Petrie et al. 1991; pers. obs.), and they would have ample opportunity to assess each other's crest plumage. Given that the relation between male crest width and dominance status is weak (Fig. 2, Table 4), it is not likely to be the only signal used in male–male interactions; however, in contrast with a previous study of peacocks (Loyau et al. 2005a), tarsus length was not related to male dominance in the lek interactions measured here. The hypothesis that the crest has a signal function in male competition could be tested experimentally by manipulating the ornament prior to the breeding season, or by controlled tests in captivity.

Surprisingly, males with wider crests also have greater ectoparasite loads when controlling for the negative effect of top area (Table 3), suggesting that males with wide, sparse crests tend to be in poor health, in addition to being dominant on the leks (Table 4). It is possible that wide-crested males suffer direct health costs as a result of frequent competitive interactions, leading to increased infestation, or that they devote less time to preening. Among males of a given dominance category, the amount of pennaceous area at the top of the crest predicts ectoparasite load, but crest width does not, and there was no evidence of an effect of male dominance status on ectoparasite load among the birds studied here. Further studies are needed to investigate how agonistic behaviour interacts with condition, health and ornamentation in this species.

Although the results of this study suggest that the crest could serve as a condition indicator in females, the function of this ornament in females is not clear. There was no evidence for a relation between crest morphology and the female agonistic behaviour observed here. Nevertheless, it is possible that the female crest could be used as a status signal in other contexts not observed in this study, such as competition over food sources or nesting territory away from the leks. Another possibility is that the female crest could be an adaptive signal used for individual recognition,

because the extent and pattern of new feather growth is highly variable among females (Fig. 1; Tibbets and Dale 2007) – human observers can learn to recognize some unmarked females in feral populations by their crest plumage alone (pers. obs.). Alternatively, the female crest might have no signal function in this species. The most obvious direct use of the peahen's crest occurs during copulation – when a male successfully mounts a female, he will often grasp her crest with his bill (Petrie et al. 1992; pers. obs.). Experimental manipulations of the ornament, and tests of the effects of stress on crest development, are needed to test the proposed functions of this interesting ornament in males and females.

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Appendix 1. The following tables provide details for the other top models ($\Delta AICc \leq 2$) not summarized in Table 3 and 4 of the main text: for body condition (Table A1), WBC concentration (Table A2) and ectoparasite load (Table A3), as well as agonistic behaviour (Table A4, A5) for both male and female peafowl.

Table A1. Top models with $\Delta AICc \leq 2$ to predict body condition (body mass controlling for tarsus length) of male and female peafowl, from model sets including the following predictors: CrL = crest length, CrW = crest width, CrT = top pennaceous area, CrNG = new growth area, Pop = population, and T = tarsus length. Best models are given in Table 3 in the main text. Sample sizes differ where outliers were excluded from models (see main text); significant effects are highlighted in bold.

	Rank	R ²	Akaike weight	$\Delta AICc$	Effect	β	SE	F	p	DF
Body mass										
Males	2	0.22	0.12	0.92	T	0.34	0.13	6.64	0.01	1,44
					CrL	0.19	0.11	2.91	0.09	1,44
					CrW	0.04	0.04	0.75	0.39	1,44
	3	0.30	0.11	1.17	T	0.33	0.13	6.59	0.01	1,42
					CrL	0.13	0.11	1.41	0.24	1,42
					CrW	0.02	0.04	0.19	0.67	1,42
					Pop			2.37	0.11	2,42
	4	0.16	0.09	1.50	T	0.38	0.13	8.32	0.006	1,45
					CrW	0.03	0.04	0.52	0.47	1,45
Females	2	0.26	0.14	1.80	T	0.38	0.10	13.47	0.0004	1,89
					CrNG	-0.17	0.06	8.56	0.004	1,89
					Pop			4.22	0.02	2,89

Table A2. Top models with $\Delta AICc \leq 2$ to predict WBC concentration of male and female peafowl, from model sets including the following predictors: CrL = crest length, CrW = crest width, CrT = top pennaceous area, CrNG = new growth area, and Pop = population. Best models are given in Table 3 in the main text. Sample sizes differ where outliers were excluded from models (see main text); significant effects are highlighted in bold.

	Rank	R ²	Akaike weight	$\Delta AICc$	Effect	β	SE	F	p	DF
WBC										
Males	2	0.31	0.17	1.37	CrW	0.06	0.03	3.33	0.08	1,43
					CrT	-0.02	0.02	1.13	0.29	1,43
					Pop			4.06	0.02	2,43
	3	0.33	0.14	1.76	CrL	-0.08	0.09	0.79	0.38	1,44
					CrT	-0.02	0.02	1.07	0.31	1,44
					Pop			4.44	0.02	2,44
Females	2	0.20	0.14	0.39	CrW	-0.03	0.03	1.82	0.18	1,87
					CrNG	0.05	0.05	1.12	0.29	1,87
					Pop			7.34	0.001	2,87
	3	0.19	0.12	0.75	CrW	-0.04	0.02	3.10	0.08	1,89
					Pop			10.26	<0.0001	2,89
	4	0.16	0.07	1.71	Pop			8.60	0.0004	2,90
	5	0.19	0.07	1.85	CrL	-0.07	0.10	0.417	0.52	1,87
					CrNG	0.07	0.05	1.86	0.18	1,87
					Pop			6.55	0.002	2,87

Table A3. Top models with $\Delta AICc \leq 2$ to predict ectoparasite load of female peafowl, from model sets including the following predictors: CrL = crest length, CrW = crest width, CrT = top pennaceous area, CrNG = new growth area, and Pop = population. For males, there were no models with $\Delta AICc \leq 2$ relative to the top model for ectoparasite load. Best models are given in Table 3 in the main text. Significant effects are highlighted in bold.

	Rank	R ²	Akaike weight	$\Delta AICc$	Effect	β	SE	F	p	DF
Ectoparasite										
Females	2	0.52	0.22	0.30	CrL	0.10	0.07	1.87	0.18	1,91
					Pop			46.39	<0.0001	2,91

Table A4. Top models with $\Delta AICc \leq 2$ to predict agonistic behaviour for male peafowl, with dominance modeled as an ordinal logistic response with three levels. Predictors include crest measurements (CrL=crest length, CrW=crest width, CrT=top pennaceous area, CrNG=new growth area), body mass (M), tarsus length (T) and population (Pop). The best model is given in Table 4 in the main text. Significant effects are highlighted in bold.

	Rank	Pseudo R ²	Akaike weight	$\Delta AICc$	n	Effect	β	SE	Wald χ^2	p	DF
Males	2	0.22	0.06	0.73	37	CrL	-1.93	1.01	-1.92	0.055	1
						CrW	0.78	0.37	2.12	0.03	1
						M	1.71	1.09	1.57	0.12	1
	3	0.15	0.05	0.97	37	CrL	-1.22	0.82	-1.49	0.14	1
						CrW	0.71	0.36	2.00	0.046	1
	4	0.09	0.05	1.03	37	CrW	0.56	0.34	1.68	0.09	1
	5	0.20	0.04	1.39	37	CrW	0.76	0.38	2.01	0.045	1
						CrT	-0.26	0.14	-1.83	0.07	1
						M	0.93	0.94	0.98	0.32	1
	6	0.20	0.04	1.41	37	CrW	0.81	0.39	2.09	0.04	1
						CrT	-0.35	0.19	-1.83	0.07	1
						Pop (LAA)	0.75	0.94	0.80	0.43	
						Pop (TZ)	1.08	1.24	0.87	0.38	
	7	0.19	0.03	1.94	37	CrL	-0.64	0.96	-0.66	0.51	1
CrW						0.79	0.38	2.09	0.04	1	
CrT						-0.20	0.17	-1.17	0.24	1	

Table A5. Top models with $\Delta AICc \leq 2$ to predict agonistic behaviour for female peafowl, with dominance modeled as an ordinal logistic response with three levels. Predictors include crest measurements (CrL=crest length, CrW=crest width, CrT=top pennaceous area, CrNG=new growth area), body mass (M), tarsus length (T) and population (Pop). The best model is given in Table 4 in the main text. Significant effects are highlighted in bold.

	Rank	Pseudo R ²	Akaike weight	$\Delta AICc$	n	Effect	β	SE	Wald χ^2	p	DF
Females	2	0.15	0.05	0.33	71	M	1.14	0.78	1.45	0.15	1
						Pop (LAA)	1.42	0.61	2.35	0.02	
						Pop (TZ)	0.67	0.72	0.92	0.36	
	3	0.11	0.05	0.38	71	Pop (LAA)	1.51	0.60	2.52	0.01	
						Pop (TZ)	0.85	0.70	1.21	0.23	
	4	0.20	0.04	1.14	71	CrL	-1.79	1.00	-1.78	0.07	1
						CrNG	-0.47	0.46	-1.04	0.30	1
						M	1.38	0.84	1.64	0.10	1
						Pop (LAA)	1.27	0.64	1.99	0.05	
						Pop (TZ)	0.23	0.79	0.29	0.77	
	5	0.13	0.03	1.27	71	CrL	-0.98	0.89	-1.10	0.27	1
						Pop (LAA)	1.52	0.60	2.53	0.01	
						Pop (TZ)	0.78	0.71	1.10	0.27	
	6	0.16	0.03	1.27	71	M	1.36	0.81	1.68	0.09	1
						T	-0.92	0.83	-1.11	0.27	1
						Pop (LAA)	1.98	0.81	2.44	0.01	
						Pop (TZ)	0.80	0.74	1.08	0.28	
	7	0.16	0.03	1.46	71	CrW	-0.23	0.22	-1.02	0.31	1
						M	1.41	0.83	1.70	0.09	1
						Pop (LAA)	1.51	0.62	2.45	0.01	
						Pop (TZ)	0.45	0.75	0.59	0.55	
8	0.16	0.03	1.60	71	CrL	-1.39	0.95	-1.47	0.14	1	
					CrNG	-0.59	0.44	-1.34	0.18	1	
					Pop (LAA)	1.32	0.63	2.12	0.03		
9	0.13	0.03	1.62	71	Pop (TZ)	0.39	0.77	0.51	0.61		
					CrNG	-0.38	0.41	-0.93	0.35	1	
					Pop (LAA)	1.37	0.62	2.21	0.03		
10	0.19	0.03	1.75	71	Pop (TZ)	0.62	0.75	0.83	0.41		
					CrL	-1.37	0.99	-1.39	0.16	1	
					CrW	-0.16	0.23	-0.70	0.48	1	
					M	1.67	0.86	1.94	0.052	1	
11	0.19	0.03	1.79	71	Pop (LAA)	1.49	0.62	2.40	0.02		
					Pop (TZ)	0.36	0.76	0.48	0.63		
					CrL	-1.32	1.01	-1.31	0.19	1	
					M	1.59	0.83	1.91	0.056	1	
					T	-0.59	0.86	-0.68	0.50	1	
					Pop (LAA)	1.77	0.81	2.19	0.03		
					Pop (TZ)	0.61	0.75	0.80	0.42		