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Male ornament variation in a sexually dimorphic seabird with variable male mating success

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ABSTRACT

Questions: Are sex-specific ornaments necessarily under sexual selection? Could previous sexual selection have eliminated meaningful variation in male ornaments, as envisioned by the lek paradox?

Background: The lek paradox proposes that sexual selection on a trait can become limited by the availability of genetic variation. If prolonged directional selection leads to an exhaustion of genetic variation in male ornaments, selection would favour a corresponding decline in choosiness by females. Ornaments that have undergone this evolutionary process should have low phenotypic variation.

Organism: Great frigatebird, *Fregata minor*, whose male ornaments have been assumed to be sexually selected via female mate choice.

Methods: We compared morphological traits of males that did and did not succeed in attracting a mate. We also compared phenotypic variation of these traits versus phenotypic variation in (1) a behavioural trait shown to be sexually selected in this population, and (2) morphological traits shown to be sexually selected in other species.

Conclusion: We found no strong morphological predictors of male mating success and only partial evidence for the reduced phenotypic variation that would be predicted by the lek paradox. Specifically, phenotypic variation in male ornaments was lower than in the behavioural trait shown to be sexually selected in this population but was not low compared with ornaments shown to be sexually selected in other species.

Keywords: *Fregata minor*, lek paradox, ornaments, sexual selection, SWS1 opsin, ultraviolet.

INTRODUCTION

Sexual selection acts on a wide array of behavioural and morphological traits (Andersson, 1994). Indeed, some of the most extravagant features of animals are sexually selected male traits, such as the elaborate train of peacocks (Petrie *et al.*, 1991; Petrie, 1994). Such sexually dimorphic ornamentation is thought to be favoured by sexual selection but opposed by viability

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selection (Keyser and Siefferman, 2005; but see Petrie, 1992), which limits a correlated expression of the trait in the opposite sex (Lande, 1980). However, traits that are exaggerated or expressed in only one sex might not currently be under sexual selection (Westneat, 2006). While the importance of sexual selection in shaping male ornamentation has been well documented (Darwin, 1871; Andersson, 1994; Gontard-Danek and Møller, 1999), it remains important to test adaptive explanations for the form and function of traits (Pigliucci and Kaplan, 2000). In this study, we explore whether sexual selection currently targets male morphological ornaments in the great frigatebird, a sexually dimorphic seabird whose remarkable gular pouch and iridescent feathers have been widely assumed to be sexually selected via female mate choice (Alcock, 1993; Attenborough, 1998, p. 193; Ligon, 1999, p. 75; Knight, 2002). The occurrence of these traits in frigatebirds is especially intriguing because (1) the five species of frigatebirds are the only sexually dichromatic members of a diverse clade of more than 200 species (Dearborn *et al.*, 2001), and (2) comparative analyses have suggested that sexual dichromatism in birds is most often associated with social or genetic mating systems with high variance in male mating success (Owens and Hartley, 1998; Dunn *et al.*, 2001), yet great frigatebirds exhibit nearly strict monogamy (Dearborn *et al.*, 2001).

Ultimately, sexual selection on traits may become limited by the availability of genetic variation. Ornaments are predicted to be under directional sexual selection, and prolonged directional selection has been theorized to lead to an exhaustion of genetic variation in the ornaments and a corresponding loss of benefits to choosiness by females [i.e. the lek paradox, assuming females agree on a preferred type of male (Taylor and Williams, 1982; Kirkpatrick and Ryan, 1991)]. Many processes have been proposed to counter the loss of genetic variation predicted by the lek paradox, including the effects of a changing array of parasites (Hamilton and Zuk, 1982) or a high mutation rate for sexually selected traits (Petrie and Roberts, 2007; see also Hedrick and Dill, 1993; Brown, 1997; Jia *et al.*, 2000; Neff, 2000; Kotiaho *et al.*, 2001; Gorelick and Bertram, 2003; Miller and Moore, 2007). However, the maintenance of variation in sexually selected traits remains a controversial topic.

Although the lek paradox was initially described for mating systems with no pair bonding and only indirect (i.e. genetic) benefits of female choice, there is growing evidence of genetic benefits of mate choice in species where males also provide direct benefits such as nest sites or parental care (Norris, 1993; Sheldon *et al.*, 1997; Møller and Alatalo, 1999; Forsman and Hagman, 2006). Thus, questions about genetic benefits and the maintenance of variation in sexually selected traits may be relevant to a variety of mating systems. Frigatebirds have an unusual mating system compared with other seabirds, because they exhibit sexual dimorphism, short-term pair bonds, and a lek-like mate choice arena, where choosing females have the opportunity to compare hundreds of courting males (Dearborn *et al.*, 2001). In all five species of frigatebirds, male courtship behaviour highlights their ornaments – a red, inflatable gular pouch and a ruff of lanceolate, iridescent feathers (Nelson, 1975); recent work has shown the gular pouch of great frigatebirds, *Fregata minor*, to contain high concentrations of carotenoids (Juola *et al.*, 2008). These traits have been assumed to be sexually selected via female mate choice (Alcock, 1993; Attenborough, 1998, p. 193; Ligon, 1999, p. 75; Knight, 2002), but few studies have tested for sexual selection on these male morphological ornaments. Results to date have been surprising: female choice was not related to male size, male gular pouch coloration or reflectance spectra of the iridescent ruff feathers in a Mexico population of magnificent frigatebirds, *Fregata magnificens* (Madsen *et al.*, 2007a, 2007b), and date of pairing (for males that succeeded in attracting a mate) was not related to male morphology in a Hawaii population of great frigatebirds (Dearborn and Ryan, 2002). Here we extend this work by examining whether morphological traits predict mating success in great frigatebirds. In this population, previous work has documented limited male–male competition (Dearborn *et al.*, 2005) but a male-biased operational sex ratio and a corresponding skew in male mating success, such that the vast majority of courting males fail to obtain a mate in a given breeding season (Dearborn *et al.*, 2001; Dearborn and Anders, 2006). The main traits that we tested in the current study – ornament size, ornament brightness, and morphological symmetry – are predicted to be under directional selection via female choice. In that case, males with larger, brighter or more symmetrical features should be more likely to be chosen as mates.

To interpret our results, we conducted two follow-up tests. First, we sequenced the SWS1 opsin gene in this species to determine whether frigatebird vision is sensitive to ultraviolet light, as this is relevant to female perception of male ornaments. Second, we compared phenotypic variation of male traits in this species with male traits shown to be under sexual selection in other avian species. If male ornaments currently predict mating success in a species, then variation should still exist in those traits that are the basis of mate choice. If male ornaments do not predict mating success, one possibility is that prolonged sexual selection has reduced genetic variation in male traits, as envisioned by the lek paradox; if so, these traits should have low phenotypic variation compared with traits that are still currently under sexual selection in other species.

METHODS

Study system

Great frigatebirds are sexually dimorphic, long-lived seabirds in the order Pelecaniformes. Mating is serially monogamous, in that a female usually chooses a new mate for each breeding attempt. Males have two prominent ornaments: a bright red, inflatable gular pouch, and a ruff of iridescent, lanceolate feathers. To attract a mate, males perform courtship displays that highlight these ornaments: males erect the ruff to form a collar, and inflate the gular pouch and shake it from side to side; in addition, the male vocalizes while extending and vibrating the wings.

We studied great frigatebirds on Tern Island, French Frigate Shoals, in the Northwestern Hawaiian Islands. Tern Island is 14 ha in size and flat, with a mix of open sandy areas, herbaceous vegetation, and large woody shrubs (*Tournefortia argentea* and *Scaevola taccada*). Frigatebirds display from, and nest on, the tops of the shrubs. During the breeding season, this colony has a strongly male-biased sex ratio (Dearborn *et al.*, 2001), such that fewer than 20% of courting males obtain a mate in a given season (Dearborn and Anders, 2006). Extra-pair fertilizations are essentially absent in this population (Dearborn *et al.*, 2001), so extra-pair paternity does not confound measures of mating success.

Morphology

Early in the 1998 breeding season, we measured several aspects of the morphology of sexually mature but unpaired males. We first hand-captured males at night in the breeding colony. We measured the length of the ruff from the base of the neck to the tip of the lanceolate feathers, and we classified the iridescence into one of three categories (dull, moderate, bright) as seen by humans when illuminated with a standard light source; classification was based on consensus of two observers who were blind to the eventual pairing status of the bird. We then measured:

- body mass;
- length of culmen;
- length of right and left wing (three measurements each);
- length of right outer rectrix and left outer rectrix (three measurements each);
- age and status of those two rectrices.

Frigatebirds vary in the moult sequence of their tail feathers (Metz and Schreiber, 2002), and new feathers are distinctly darker and smoother than old feathers. We classified these feathers as new and intact, old and intact, or broken (meaning that the rachis had broken and some distal segment of the feather was missing), yielding six ordered categories of increasing condition of the two rectrices. Before release, birds were banded and marked with numbered wing tags.

To classify gular pouch colour, we surveyed the colony during the daytime for marked males performing courtship displays. Colour was measured by standardized visual comparison to Munsell colour chips. As recommended by the manufacturer (Gretag Macbeth, Grand Rapids, MI) and by the American Society for Testing and Materials (ASTM D 1729, Standard Practice for Visual Evaluation of Color Differences of Opaque Materials), we scored colour when the bird was illuminated by a lightly overcast north sky, with the sun at a 45° angle to the viewed surface of the gular pouch, and the viewer at a 90° angle to the viewed surface. We viewed birds through a hole in a photographic 18% grey card from a distance of 4 m, with the view of the gular pouch filling the hole. Chips from a Munsell colour chart were viewed beside the hole until the chip was chosen that matched the gular pouch. For each viewing, we repeated the process to verify the match between the chip and the gular pouch, and all colour scores were made by the same person. In addition to scoring colour, we scored physical damage to the gular pouch, using a 4-point scale to describe the presence of scars and discoloured patches.

Objective measure of colour is best achieved with spectrometry, as avian colour perception differs from that of humans (Bennett and Thery, 2007). One particular difference is the sensitivity of some bird species to ultraviolet (UV) light. To address the possibility that female frigatebirds might use UV cues in mate choice, we sequenced the SWS1 opsin gene (see below). Outside of the UV region, colour mapping by the human visual system may sometimes correspond with that of some avian species (Vorobyev *et al.*, 1998).

Behavioural measurements

Data collected in this population in 1999 showed that male courtship effort was predictive of pairing success (Dearborn *et al.*, 2005). Sexually mature, unpaired males had been marked with numbered wing tags at the start of the breeding season. Three times each day, we made an island-wide census, recording the presence and behavioural status of marked males. In particular, we described whether each male was engaged in courtship display. Over the breeding season, a male was substantially more likely to become paired with a female if he was displaying on a large proportion of those censuses (Dearborn *et al.*, 2005).

We collected similar data twice per day in 1998, 2000, and 2005 but have not previously analysed or presented these data. For all four years (1998, 1999, 2000, 2005), here we compute for each marked male the proportion of twice-daily colony surveys on which the male was engaged in courtship display, using only the part of the season that each particular male was unmated (i.e. excluding periods when the male had an active nest). This proportion was calculated with a denominator of the total number of surveys when the male was unmated and present on the island. We excluded males that we never saw displaying, to avoid an artificially inflated coefficient of variation (CV) from males that either were non-breeders or were transient on the island; this might exclude some males whose rare displays were undetected. The resulting approach is thus somewhat conservative, as our hypothesis predicts a large coefficient of variation for courtship effort in this species.

SWS1 opsin sequencing

A subset of bird species, including most Passerines, have vision that is strongly UV-sensitive (Bennett and Thery, 2007). Recent work has found genetic predictors of UV sensitivity, based on the sequence of the SWS1 gene, which codes for the opsin protein found in birds' short-wavelength-sensitive cones (Odeen and Hastad, 2003; Carvalho *et al.*, 2007). Short-wavelength sensitivity appears to be roughly dichotomous across species. Some species have peak sensitivity (i.e. λ-max) of SWS1 near 406 nm, in the violet spectrum, whereas other species have SWS1 λ-max near 371 nm, in the ultraviolet spectrum (Odeen and Hastad, 2003; Hastad *et al.*, 2005). We amplified and sequenced the SWS1 opsin gene of one male and one female great frigatebird from our study population, to compare the SWS1 sequence to that of species with known or estimated values of λ-max. Using primers SU149a and SU306b (Odeen and Hastad, 2003), PCR amplification was carried out in 20-μl reactions containing final concentrations of 0.2 mM of each dNTP, 0.4 μM of each primer, 2.5 mM $MgCl_2$, 1 × Applied Biosystems GeneAmp Gold buffer, 0.5 units of AmpliTaq Gold polymerase (Applied Biosystems), and 20 ng of DNA. PCR was initiated by a 7-min denaturing step followed by 37 cycles of 95°C for 30 s, 52°C for 30 s, and 72°C for 30 s, with a final extension step at 72°C for 10 min. We gel-purified PCR products from 2% agarose using GE Healthcare Illustra GFX columns. Sequencing was conducted with Applied Biosystems Big Dye 3.1. We cleaned the sequencing reaction with Agencourt CleanSEQ magnetic beads and separated products by capillary electrophoresis on an ABI 3130XL Genetic Analyser.

Data analysis

For morphological and behavioural traits, we used univariate and multivariate logistic regression or univariate chi-square tests (for categorical variables, such as ruff iridescence) to determine whether male morphology was predictive of male pairing success. Effect size for logistic regression was estimated with Nagelkerke's R^2. Fluctuating asymmetry of wing chord length and outer rectrix length was calculated as the absolute value of the mean of three measurements of the left side minus the mean of three measurements of the right side; repeatability, measured as the intra-class correlation coefficient, was 0.993 for wing length and 0.999 for rectrix length.

Sample sizes differed between analyses, because not all measurements were available for all birds. This was especially the case for gular pouch colour, which was a difficult measure to obtain due to the restrictions involving viewing angle, accessibility, and the ethical constraints of working around endangered and threatened species (e.g. Hawaiian monk seals, green sea turtles).

For interpretation of non-significant results, we computed effect sizes as Pearson product–moment correlation coefficients, with 95% confidence intervals calculated by first transforming the correlation coefficients to Z-scores. For reference purposes, we compared our values to the significantly non-zero effect sizes summarized in a meta-analysis by Gontard-Danek and Møller (1999).

Traits that have been under prolonged directional selection (to the point of reduced additive genetic variation) should exhibit lower phenotypic variation than traits known to be under directional sexual selection currently, because comparative work has found a very strong cross-species correlation between phenotypic variation and additive genetic variation in sexually selected traits (Pomiankowski and Møller, 1995). To compare the amount of phenotypic variation in frigatebird traits and the amount of within-population phenotypic variation in sexually selected traits in other species, we searched the literature to locate studies in which morphological or behavioural traits were shown to be under current sexual selection. We then used values from these studies to calculate coefficients of variation for comparison with traits in our focal population of great frigatebirds. If the lack of evidence for strong directional sexual selection on frigatebird morphological traits is because prolonged selection has reduced the variation in these traits, the coefficient of variation in frigatebird morphological traits should be low compared with traits known to be under sexual selection in other species. As a control, we also examined within-species variation in male courtship behaviour, because previous work in this frigatebird population has shown that courtship effort is predictive of pairing success and thus likely to be under sexual selection.

RESULTS

Ornaments and pairing success

In univariate analyses with sequential Bonferroni corrections of alpha (Rice, 1989), we found no relationship between pairing success and the following ornaments:

- gular pouch colour [analysed as hue (all males the same hue), value (Wald chi-square = 0.03, $P = 0.866$, Nagelkerke $R^2 = 0.000$, $n = 115$) and chroma (Wald chi-square = 0.57, $P = 0.449$, Nagelkerke $R^2 = 0.007$, $n = 115$), or as a single principal component of those scores (Wald chi-square = 0.02, $P = 0.885$, Nagelkerke $R^2 = 0.000$, $n = 115$)];
- gular pouch damage (Kendall's tau-b, for four ordered categories of damage, $= -0.062$, $P = 0.469$, $n = 115$);
- ruff iridescence (Kendall's tau-b, for three ordered categories of brightness, $= 0.102$, $P = 0.154$, $n = 217$); or
- ruff length corrected for body size (Wald chi-square = 1.84, $P = 0.175$, Nagelkerke $R^2 = 0.015$, $n = 191$).

The mean effect size observed in these analyses was Pearson's $r = 0.057$ (range among traits: $r = 0.016$ to 0.125), corresponding to the 1.4 percentile (range among traits: 1.1–1.6 percentile) of the distribution of effect sizes for visual traits significantly related to mating success in other species, reviewed by Gontard-Danek and Møller (1999). The mean upper 95% confidence limits for our effect sizes was in the bottom 5.0 percentile (range among traits: 2.5–8.9 percentile) of the distribution of effect sizes for visual traits significantly related to mating success in the review by Gontard-Danek and Møller (1999). Thus our estimated effect sizes and their upper confidence limits were quite small in comparison to effect sizes of known sexually selected traits in other species of birds.

Non-ornament morphology and pairing success

In univariate analyses with sequential Bonferroni corrections of alpha (Rice, 1989), we found no relationship between pairing success and the following morphological traits:

- wing symmetry (Wald chi-square = 6.04, $P = 0.014$, Nagelkerke $R^2 = 0.034$, $n = 250$);
- rectrix symmetry (Wald chi-square = 4.80, $P = 0.028$, Nagelkerke $R^2 = 0.031$, $n = 257$);
- rectrix length (Wald chi-square = 0.04, $P = 0.845$, Nagelkerke $R^2 = 0.000$, $n = 257$);
- rectrix condition (Kendall's tau-b, for six ordered categories of condition, = −0.067, $P = 0.221$, $n = 265$);
- culmen length (Wald chi-square = 3.05, $P = 0.081$, Nagelkerke $R^2 = 0.016$, $n = 257$); or
- mass (Wald chi-square = 4.45, $P = 0.035$, Nagelkerke $R^2 = 0.024$, $n = 254$).

Wing length was weakly predictive of pairing success (longer-winged males more likely to pair; Wald chi-square = 12.03, $P = 0.0005$, Nagelkerke $R^2 = 0.068$, $n = 257$). A multivariate logistic regression of all ornaments and morphological traits, using a stepwise variable selection procedure based on likelihood ratios, retained only wing length as a predictor of pairing success (Wald chi-square = 10.14, $P = 0.001$, Nagelkerke $R^2 = 0.248$, $n = 68$).

Variation in courtship effort

Among males seen performing courtship displays at least once, there was relatively large between-male variation in the percent of detections during which courtship was being performed: 1998 CV = 58.9 (range for individual males: displaying on 5.3% to 100% of survey detections), 1999 CV = 62.7 (range 4.3% to 100%), 2000 CV = 53.6 (range 1.5% to 100%), and 2005 CV = 48.5 (range 5.6% to 100%).

Variation in sexually selected traits in other species

Using only those traits shown to be related to mating success in other species, we found an average within-species CV = 16.4 ± 18.9 (± standard deviation) for ornamental traits ($n = 135$ datasets), CV = 5.05 ± 4.01 for non-ornamental morphological traits ($n = 115$ datasets), CV = 29.9 ± 43.1 for behavioural traits ($n = 29$ datasets), and CV = 129 ± 76.1 for symmetry of traits ($n = 89$ datasets). Figure 1 shows the distribution of these CVs, together with the corresponding values from our data on great frigatebirds.

SWS1 opsin sequence

From the two frigatebird samples, we obtained a clear consensus sequence of 120 bp from the SWS1 opsin gene (Genbank nos. EU651855 and EU651856). In the exon region reported by Odeen and Hastad (2003), the frigatebird nucleotide sequence was found to be 5′-TTCATCTCCTGCATCTTCAGCGTCTTCACCGTC-3′, which translates to Phe Ile Ser Cys Ile Phe Ser Val Phe Thr Val, including the functionally pivotal amino acids Ser86, Ser90, and Thr93 (using position numbers from bovine rhodopsin). This sequence matches 12 species in Odeen and Hastad (2003), all of which were reported to have a calculated SWS1 λ-max of 405 nm; one of those species, *Columba livia*, has had SWS1 λ-max measured by microspectrophotometry (Bowmaker *et al.*, 1997), revealing close correspondence between measured and predicted values (409 nm vs. 405 nm).

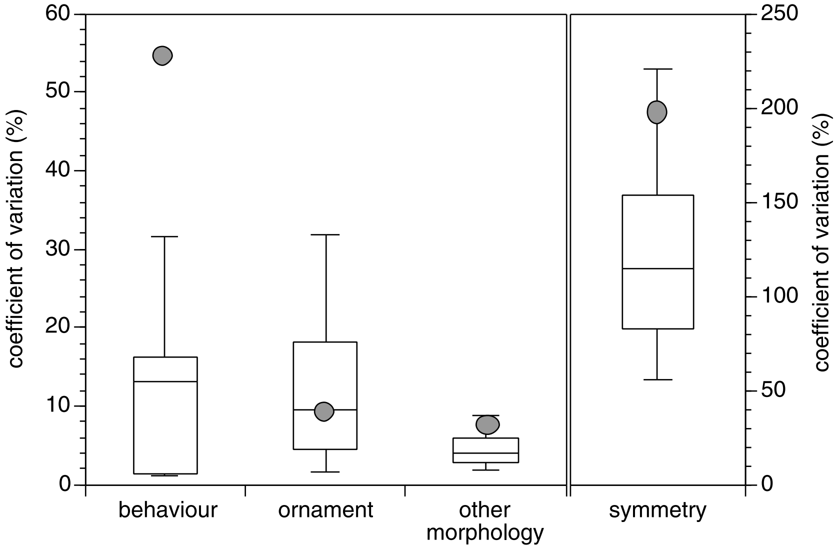

Fig. 1. Boxplots showing the distribution of coefficients of variation (CVs) for different categories of traits found to be under sexual selection in other species. Line shows median, box shows upper and lower quartile, and whiskers show 10th and 90th percentiles. Solid circles show CV from frigatebird traits in this study.

DISCUSSION

Due to their visually striking male ornaments, frigatebirds have been used in textbooks and documentary films as an illustration of sexual selection in action. These assertions – while intuitively appealing – have remained almost entirely untested. In this study of great frigatebirds, we did not find support for the hypothesis that male ornamental traits in frigatebirds are selected for by female mate choice. Specifically, we found no evidence that male mating success is predicted by gular pouch colour, gular pouch damage, ruff length or ruff iridescence, as seen by humans. Male ornaments are also unlikely to function primarily in intra-sexual competition, as their use in courtship displays occurs more than 100 times as often as their use in male–male interactions (Dearborn *et al.*, 2005).

Pairing success also was not predicted by most other morphometrics: wing or tail symmetry, tail length, tail condition, culmen length, or body mass. The only predictor of male mating success was wing length, which poses its own puzzle: males with longer wings were more likely to attract a mate, but males are overall smaller (including shorter wings) than females in this population (unpublished data) and in other populations of this species (Schreiber and Schreiber, 1988; Metz and Schreiber, 2002).

We now consider two non-evolutionary interpretations for our results: we may have failed to find a relationship between male ornaments and male mating success due to low statistical power or due to a 'mismeasurement' of traits because of bias imposed by human perceptual systems. We first explore the possibility that we lacked statistical power to detect a biologically meaningful effect. The effect sizes observed in our study were not statistically different from zero, possibly because the true effect sizes are small or zero, or it could be a result of limited sample size. To assess the latter possibility, we calculated the upper confidence limit on the effect size estimates and compared those values to a distribution of effect sizes in studies where sexual selection was demonstrated (Gontard-Danek and Møller, 1999). Our mean observed effect size was smaller than 98% of the significant effect sizes in that review paper, and the mean upper confidence limit on our effect sizes was smaller than 95% of the significant effect sizes in that review paper. Thus, if male ornaments do have an undetected influence on pairing success in our population, the effect size is likely quite small compared with sexually selected traits in other species.

A second possible explanation for two of the negative results (gular pouch colour and ruff iridescence) is the well-documented difference between human and avian visual systems (Bennett and Thery, 2007). This cannot be discounted, as it is certain that female frigatebirds perceive colour differently from human observers. However, this does not explain the lack of evidence for current sexual selection on other ornaments such as ruff length and gular pouch damage, or for non-ornamental traits such as wing and tail symmetry. In addition, our findings on gular pouch colour and ruff iridescence are consistent with studies of magnificent frigatebirds that used spectrometry to measure reflection spectra of ruff feathers and gular pouches; those studies likewise found no relationship between ornament coloration and male mating success (Madsen *et al.*, 2007a, 2007b). Furthermore, our sequencing of the SWS1 opsin gene suggests that great frigatebirds belong to the broad group of birds with the ancestral state of violet-sensitive vision (VS) rather than the derived shift to ultraviolet sensitivity (UVS) (Hunt *et al.*, 2004). Current evidence suggests five origins of UVS vision in birds, arising via two different genetic mechanisms: either Ser86 changing to Phe86, or Ser90 changing to Cys90 (Carvalho *et al.*, 2007); frigatebirds have neither of these mutations. Based on calculations (Odeen and Hastad, 2003) and microspectrophotometry of a species with the same SWS1 amino acid sequence [*Columba livia* (Bowmaker *et al.*, 1997)], SWS1 in great frigatebirds probably has a λ-max of 405–410 nm. Although the gular pouch of great frigatebirds has recently been shown to have a very small reflective peak at 360 nm (Juola *et al.*, 2008), the SWS1 sequence suggests that frigatebirds' spectral sensitivity is likely low or absent in this wavelength range. Previous work has suggested very little UV reflectance in the iridescent ruff feathers of great frigatebirds (Dearborn and Ryan, 2002). Taken together, this evidence suggests that the lack of a relationship between male mating success and our assessment of male coloration is probably not due to an undetected pattern of female choice based on UV reflectance of male ornaments.

After finding no strong relationship between male ornaments and male pairing success, we tested a prediction of a genetic-exhaustion hypothesis: if male traits are not subject to current female choice because prolonged sexual selection has greatly reduced the additive genetic variance in these traits, we would expect low phenotypic variation when compared against traits known to be currently under sexual selection in other species. Our literature survey found that coefficients of variation for frigatebird morphological traits were roughly in the middle of those from studies demonstrating sexual selection on morphology in other species. In contrast, the coefficient of variation for frigatebird courtship effort – a trait strongly predictive of mating success in this population – was higher than 93% of coefficients of variation from studies demonstrating sexual selection on behavioural traits in other species. Thus, our findings are only partially supportive of an exhaustion-of-variation hypothesis: the coefficient of variation for the frigatebird behavioural trait that predicts mating success was larger than those for the frigatebird morphological traits that do not predict mating success, but these morphological coefficients of variation were not unusually small compared with those of sexually selected morphological traits in other species.

If the morphological ornaments in frigatebirds reflect environmentally induced variation in condition, rather than variation in genetic quality, then an exhaustion-of-genetic-variation hypothesis is not applicable. However, condition dependence does not account for the lack of evidence for current sexual selection. If condition-dependent variation in ornament phenotype exists, then mate choice via ornaments should be beneficial to females in both magnificent frigatebirds and great frigatebirds, where males perform important parental care that is condition dependent (Osorno, 1999; Dearborn, 2001). There is limited data on possible condition dependence of these traits: in magnificent frigatebirds, gular pouch colour varied with parasite infection, but these variables did not translate to mating success (Madsen *et al.*, 2007b). Thus, there remains the difficulty of explaining the current function of ornaments whose variation does not appear to be correlated with mating success.

In a broad sense, our work with *Fregata minor* and Madsen's work with *F. magnificens* has found little or no effect of male morphology on male pairing success (Madsen *et al.*, 2007a, 2007b; this study) or pairing date (Dearborn and Ryan, 2002) but has found that some aspect of male courtship behaviour is predictive of male pairing success (Madsen *et al.*, 2004; Dearborn *et al.*, 2005). Frigatebirds thus may belong with red-winged blackbirds (Westneat, 2006) in that category of species with multiple secondary sexual traits, only some of which seem to be cues used currently in mate choice [the 'unreliable signal hypothesis' of Møller and Pomiankowski (1993)].

Even if the observed variation in ornaments does not currently determine male mating success, it is likely that a male lacking entirely a gular pouch and an iridescent ruff would fail to attract a mate, because such a male would not appear to be the correct species and age/reproductive class. Thus, the presentation of ornaments now may be a necessary contribution to allow a male to join the pool of candidates – akin to a password (Hauber *et al.*, 2001) – even though the current natural range of variation in ornaments does not differentiate males that are and are not chosen by females. If the cost of having the ornaments were large enough, the ornaments might not be simply a relic of past selection but instead could serve to increase the variation between males in costly behavioural traits (Kodric-Brown and Brown, 1984) such as male courtship effort in frigatebirds (Dearborn *et al.*, 2005).

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REFERENCES

Alcock, J. 1993. *Animal Behavior: An Evolutionary Approach*. Sunderland, MA: Sinauer Associates.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Attenborough, D. 1998. *The Life of Birds*. Princeton, NJ: Princeton University Press.

Bennett, A.T.D. and Thery, M. 2007. Avian color vision and coloration: multidisciplinary evolutionary biology. *Am. Nat.*, **169**: S1–S6.

Bowmaker, J.K., Heath, L.A., Wilkie, S.E. and Hunt, D.M. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vision Res.*, **37**: 2183–2194.

Brown, J.L. 1997. A theory of mate choice based on heterozygosity. *Behav. Ecol.*, **8**: 60–65.

Carvalho, L.S., Cowing, J.A., Wilkie, S.E., Bowmaker, J.K. and Hunt, D.M. 2007. The molecular evolution of avian ultraviolet- and violet-sensitive visual pigments. *Mol. Biol. Evol.*, **24**: 1843–1852.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.

Dearborn, D.C. 2001. Body condition and retaliation in the parental effort decisions of incubating great frigatebirds (*Fregata minor*). *Behav. Ecol.*, **12**: 200–206.

Dearborn, D.C. and Anders, A.D. 2006. Demography and reproductive ecology of great frigatebirds. *Atoll Res. Bull.*, **543**: 159–171.

Dearborn, D.C. and Ryan, M.J. 2002. A test of the Darwin-Fisher theory for the evolution of male secondary sexual traits in monogamous birds. *J. Evol. Biol.*, **15**: 307–313.

Dearborn, D.C., Anders, A.D. and Parker, P.G. 2001. Sexual dimorphism, extrapair fertilizations, and operational sex ratio in great frigatebirds (*Fregata minor*). *Behav. Ecol.*, **12**: 746–752.

Dearborn, D.C., Anders, A.D. and Williams, J.B. 2005. Courtship display by great frigatebirds, *Fregata minor*: an energetically costly handicap signal? *Behav. Ecol. Sociobiol.*, **58**: 397–406.

Dunn, P.O., Whittingham, L.A. and Pitcher, T.E. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, **55**: 161–175.

Forsman, A. and Hagman, M. 2006. Calling is an honest indicator of paternal genetic quality in poison frogs. *Evolution*, **60**: 2148–2157.

Gontard-Danek, M.C. and Møller, A.P. 1999. The strength of sexual selection: a meta-analysis of bird studies. *Behav. Ecol.*, **10**: 476–486.

Gorelick, R. and Bertram, S.M. 2003. Maintaining heritable variation via sex-limited temporally fluctuating selection: a phenotypic model accommodating non-Mendelian epigenetic effects. *Theory Biosci.*, **122**: 321–338.

Hamilton, W.D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**: 384–387.

Hastad, O., Ernstdotter, E. and Odeen, A. 2005. Ultraviolet vision and foraging in dip and plunge diving birds. *Biol. Lett.*, **1**: 306–309.

Hauber, M.E., Russo, S.A. and Sherman, P.W. 2001. A password for species recognition in a brood parasitic bird. *Proc. R. Soc. Lond. B*, **268**: 1041–1048.

Hedrick, A.V. and Dill, L.M. 1993. Mate choice by female crickets is influenced by predation risk. *Anim. Behav.*, **46**: 193–196.

Hunt, D.M., Cowing, J.A., Wilkie, S.E., Parry, J.W.L., Poopalasundaram, S. and Bowmaker, J.K. 2004. Divergent mechanisms for the tuning of shortwave sensitive visual pigments in vertebrates. *Photochem. Photobiol. Sci.*, **3**: 713–720.

Jia, F.Y., Greenfield, M.D. and Collins, R.D. 2000. Genetic variance of sexually selected traits in waxmoths: maintenance by genotype × environment interaction. *Evolution*, **54**: 953–967.

Juola, F.A., McGraw, K. and Dearborn, D.C. 2008. Carotenoids and throat pouch coloration in the great frigatebird (*Fregata minor*). *Comp. Biochem. Physiol. B*, **149**: 370–377.

Keyser, A.J. and Siefferman, L.M. 2005. Viability selection against highly ornamented males. *Evol. Ecol. Res.*, **7**: 595–606.

Kirkpatrick, M. and Ryan, M.J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature*, **350**: 33–38.

Knight, J. 2002. Sexual stereotypes. *Nature*, **415**: 254–256.

Kodric-Brown, A. and Brown, J.H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am. Nat.*, **124**: 309–323.

Kotiaho, J.S., Simmons, L.W. and Tomkins, J.L. 2001. Towards a resolution of the lek paradox. *Nature*, **410**: 684–686.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**: 292–305.

Ligon, J.D. 1999. *The Evolution of Avian Breeding Systems*. Oxford: Oxford University Press.

Madsen, V., Balsby, T.J.S., Dabelsteen, T. and Osorno, J.L. 2004. Bimodal signaling of a sexually selected trait: gular pouch drumming in the Magnificent Frigatebird. *Condor*, **106**: 156–160.

Madsen, V., Dabelsteen, T., Osorio, D. and Osorno, J.L. 2007a. Morphology and ornamentation in male magnificent frigatebirds: variation with age class and mating status. *Am. Nat.*, **169**: S93–S111.

Madsen, V., Valkiunas, G., Iezhova, T.A., Mercade, C., Sanchez, M. and Osorno, J.L. 2007b. Testosterone levels and gular pouch coloration in courting magnificent frigatebird (*Fregata magnificens*): variation with age-class, visited status and blood parasite infection. *Horm. Behav.*, **51**: 156–163.

Metz, V.G. and Schreiber, E.A. 2002. Great Frigatebird (*Fregata minor*). In *The Birds of North America*, No. 681 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Academy of Natural Sciences/Washignton, DC: The American Ornithologists' Union.

Miller, C.W. and Moore, A.J. 2007. A potential resolution to the lek paradox through indirect genetic effects. *Proc. R. Soc. Lond. B*, **274**: 1279–1286.

Møller, A.P. and Alatalo, R.V. 1999. Good-genes effects in sexual selection. *Proc. R. Soc. Lond. B*, **266**: 85–91.

Møller, A.P. and Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments. *Behav. Ecol. Sociobiol.*, **32**: 167–176.

Neff, B.D. 2000. Females aren't perfect: maintaining genetic variation and the lek paradox. *Trends Ecol. Evol.*, **15**: 395.

Nelson, J.B. 1975. The breeding biology of frigatebirds: a comparative review. *Living Bird*, **14**: 113–155.

Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature*, **362**: 537–539.

Odeen, A. and Hastad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.*, **20**: 855–861.

Osorno, J.-L. 1999. Offspring desertion in the magnificent frigatebird: are males facing a trade-off between current and future reproduction? *J. Avian Biol.*, **30**: 335–341.

Owens, I.P.F. and Hartley, I.R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond. B*, **265**: 397–407.

Petrie, M. 1992. Peacocks with low mating success are more likely to suffer predation. *Anim. Behav.*, **44**: 585–586.

Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, **371**: 598–599.

Petrie, M. and Roberts, G. 2007. Sexual selection and the evolution of evolvability. *Heredity*, **98**: 198–205.

Petrie, M., Halliday, T. and Sanders, C. 1991. Peahens prefer peacocks with elaborate trains. *Anim. Behav.*, **41**: 323–332.

Pigliucci, M. and Kaplan, J. 2000. The fall and rise of Dr. Pangloss: adaptations and the Spandrels paper 20 years later. *Trends Ecol. Evol.*, **15**: 66–70.

Pomiankowski, A. and Møller, A.P. 1995. A resolution of the lek paradox. *Proc. R. Soc. Lond. B*, **260**: 21–29.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.

Schreiber, E.A. and Schreiber, R.W. 1988. Great frigatebird size dimorphism on two Central Pacific atolls. *Condor*, **90**: 90–99.

Sheldon, B.C., Merila, J., Qvarnstrom, A., Gustafsson, L. and Ellegren, H. 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. Lond. B*, **264**: 297–302.

Taylor, P.D. and Williams, G.C. 1982. The lek paradox is not resolved. *Theor. Pop. Biol.*, **22**: 392–409.

Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. and Cuthill, I.C. 1998. Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A*, **183**: 621–633.

Westneat, D.F. 2006. No evidence of current sexual selection on sexually dimorphic traits in a bird with high variance in mating success. *Am. Nat.*, **167**: E171–E189.