

## Morphology and ornamentation in male magnificent frigatebirds: variation with age class and mating status

Article (Published Version)

Madsen, Vinni, Dabelsteen, Torben, Osorio, Daniel and Osorno, José Luis (2007) Morphology and ornamentation in male magnificent frigatebirds: variation with age class and mating status. *American Naturalist*, 169 (S1). S93-S111. ISSN 0003-0147

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/27231/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

### **Copyright and reuse:**

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

# Morphology and Ornamentation in Male Magnificent Frigatebirds: Variation with Age Class and Mating Status

Vinni Madsen,<sup>1,\*</sup> Torben Dabelsteen,<sup>2,†</sup> Daniel Osorio,<sup>3,‡</sup> and José Luis Osorno<sup>1,§</sup>

1. Instituto de Ecología, Universidad Nacional Autónoma de México, México Distrito Federal, México;

2. Animal Behaviour Group, Institute of Biology, University of Copenhagen, Copenhagen, Denmark;

3. School of Life Sciences, University of Sussex, Brighton, United Kingdom

**ABSTRACT:** Male magnificent frigatebird (*Fregata magnificens*) ornamentation includes bright iridescent plumage and a red inflatable gular pouch. These signals are displayed during courtship, along with a drumming sound produced through specialized beak clackings resonating in the gular pouch. The extent of white in the plumage identifies three age classes of nonjuvenile male. Here we investigate how morphological and secondary sexual traits correlate with age class and mating status. Even though several age class-related differences in morphology and visual appearance can be identified, the only features that significantly predict mating success are acoustic components of courtship display. Specifically, males that mate drum at lower fundamental frequencies—that is, they have larger gular pouches—and have a quicker and more constant drumming cadence than unsuccessful males. The fundamental frequency decreases with age class, reflecting an increase in gular pouch size. This implies that females prefer older or possibly more experienced or viable males. Drumming cadence speed and stability might reflect male stamina. Apart from the acoustic differences with mating status, there is a nonsignificant tendency for back-feather iridescence to be of shorter reflectance wavelength spectra in mated than in unmated males, which, when combined with acoustic variables, improves prediction of age class and mating status.

**Keywords:** acoustic communication, female mate preference, *Fregata magnificens*, iridescence, secondary sexual trait expression, structural feather coloration.

\* E-mail: vinni@post.tele.dk.

† E-mail: tdabelsteen@bi.ku.dk.

‡ E-mail: d.osorio@sussex.ac.uk.

§ Deceased.

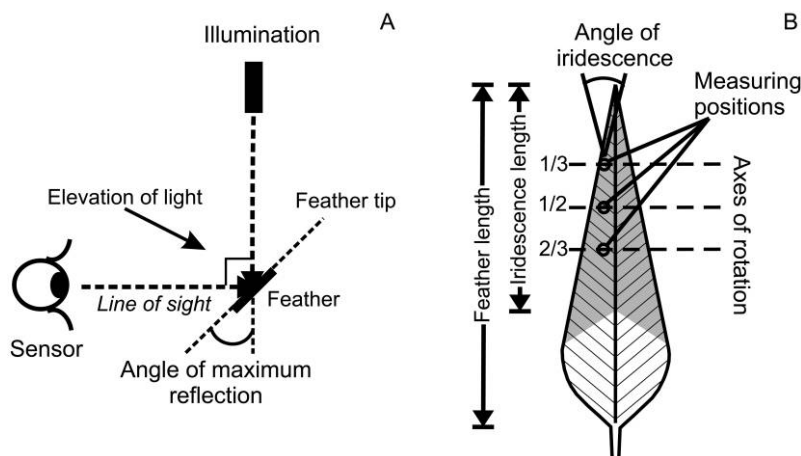
Am. Nat. 2007. Vol. 169, pp. S93–S111. © 2007 by The University of Chicago. 0003-0147/2007/1690S1-40609\$15.00. All rights reserved.

Birds often use multiple signals in their mating displays, from specialized calls and movements to flesh and feather designs and coloration (Andersson 1994; Ligon 1999). To interpret multicomponent signals, it is necessary to establish what information each component conveys to receivers and how this information is used. For instance, different types of feather pigmentation may signal different aspects of condition or quality (Gray 1996; Owens and Hartley 1998; Badyaev and Hill 2000; Senar et al. 2003). Thus, melanin deposition is independent of nutritional limitations (McGraw et al. 2002) and parasite load (McGraw and Hill 2000) at molt, but the extent of melanin pigmentation may signal social status (Rohwer 1975, 1982; Roper 1986; Senar et al. 1993; McGraw et al. 2003). In contrast, carotenoid pigmentation is often used in mate choice, and the quality and/or extent of carotenoid coloration reflects nutritional condition (Hill and Montgomerie 1994; Hill 2000; Johnsen et al. 2003; Tschirren et al. 2003) and parasite load (McGraw and Hill 2000; Figuerola et al. 2003) at time of feather growth. Structural feather coloration is widely used in signaling but has been less studied than pigmentation coloration.

## Ornamentation and Frigatebird Biology

### *Feather Ornamentation*

Structural coloration is produced by interference between light waves reflected from more or less regularly spaced refractive index boundaries within composite structures. In feathers, these materials are keratin, melanin, and, occasionally, air. Owing to their dependence on nanoscale order (Land 1972; Dyck 1976; Fox 1976; Prum et al. 1998, 1999; Andersson 1999; Land and Nilsson 2002; Zi et al. 2003), structural colors could be a rich source of information. Hue, brightness, color purity, and directionality might all reflect condition during or after feather growth. Some structural colors are iridescent in that their color,



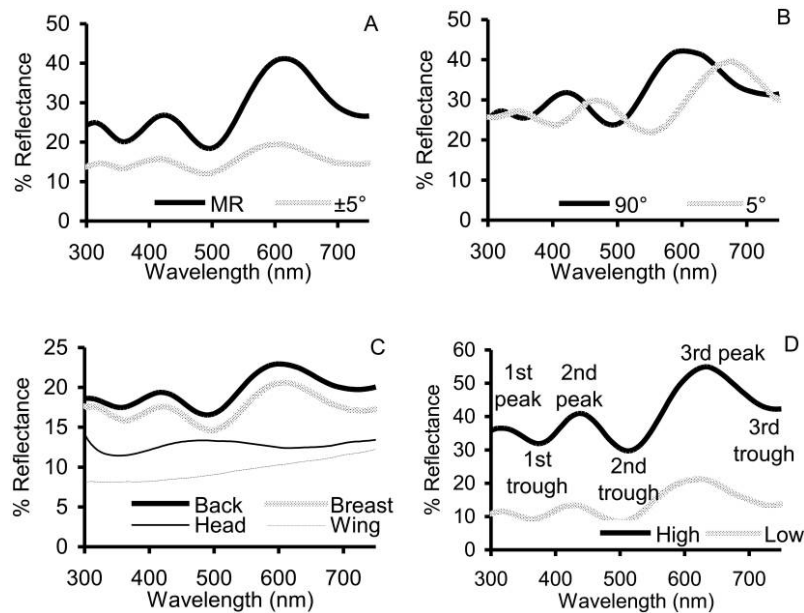
**Figure 1:** A, Viewing geometry. The line of sight was horizontal and the light source placed vertically above the feather, at an elevation of light of  $90^\circ$ . The feather was rotated along the longitudinal axis to the position with maximum reflectance, and spectra were measured at this angle and at  $5^\circ$  to either side (see also Osorio and Ham 2002). B, Sketch of a lanceolated male back feather, with shading indicating area of iridescence. Shown are the three locations where iridescent spectra were measured from a 1-mm-diameter spot on the feather surface. Axes of rotation were in the plane of the main rachis and ran through the viewed point.

that is, wavelength at peak reflectance, changes as the feather moves, and these colors are often directional, resembling colored mirrors. Other structural colors are non-iridescent, with directional properties more like those of ordinary pigmented surfaces. In practice, there is a continuum between these two types (Prum et al. 1998; Osorio and Ham 2002). Relatively noniridescent structural colors in feathers of blue grosbeaks (*Guiraca caerulea*; Keyser and Hill 1999) and blue tits (*Parus caeruleus*; Johnsen et al. 2003) and the iridescent colors of brown-headed cowbirds (*Molothrus ater*; McGraw et al. 2002) are affected by nutritional status during feather growth. Furthermore, features of both types of structural coloration reflect male quality (Keyser and Hill 2000; Siitari and Huhta 2002; Doucet and Montgomerie 2003; Siefferman and Hill 2003; but see Smiseth et al. 2001). Noniridescent structural coloration seems to be used in courtship displays (Hausmann et al. 2003) and in influencing mate choice by bluethroats (*Luscinia s. svecica*; Andersson and Amundsen 1997; Johnsen et al. 1998) and blue tits (Andersson et al. 1998; Hunt et al. 1998, 1999) but not blue grosbeaks (*Passerina caerulea*; Ballentine and Hill 2003). Iridescent colors are used in sexual signaling, as on the peacock's tail, but their role remains little studied. An exception is in the starling (*Sturnus vulgaris*), where iridescent coloration differs with sex (Cuthill et al. 1999) and correlates with mate preference (Bennett et al. 1997; Komdeur et al. 2005) and age (Komdeur et al. 2005). The relationship between structural coloration and mate choice is perhaps best studied in blue tits, where there is evidence that females alter offspring

sex ratio depending on male cap color (Sheldon et al. 1999) and that females mated to "colorful" males invest more in parental care (Limbourg et al. 2003) but "dull" males gain more extrapair paternity (Delhey et al. 2003). The paucity of studies of iridescent plumage may partly be due to the difficulty of obtaining meaningful measurements. These mirrorlike surfaces are highly directional; in some cases a rotation of  $1^\circ$  can cause a twofold change in brightness (Osorio and Ham 2002; D. Osorio, personal observation). Consequently, it is difficult to document their reflective properties. No single viewing geometry (fig. 1A) gives the maximum—or even a nonzero—reflectance from all iridescent feathers (Osorio and Ham 2002). Subjective appearance may also be misleading because multi-peaked reflectance spectra (fig. 2) may mean that iridescent colors have different appearances for humans and birds (Bennett et al. 1994; Hart 2001; Vorobyev 2003), often being more saturated (i.e., colorful) for birds. For instance, spectra that look gray to us may present saturated nonspectral hues to a bird (Osorio and Ham 2002).

#### *Skin Ornamentation*

Skin ornaments are included in many displays and may play an important role in mate choice (Zuk et al. 1990a, 1995; Spurrier et al. 1991; Buchholtz 1995; Ligon and Zwartjes 1995; Rintamäki et al. 2000). These ornaments reflect condition (Ligon et al. 1990), parasite load (Zuk et al. 1990b; Spurrier et al. 1991), and testosterone levels (Stokkan 1979; Ligon et al. 1990; Zuk et al. 1995; Papeschi et



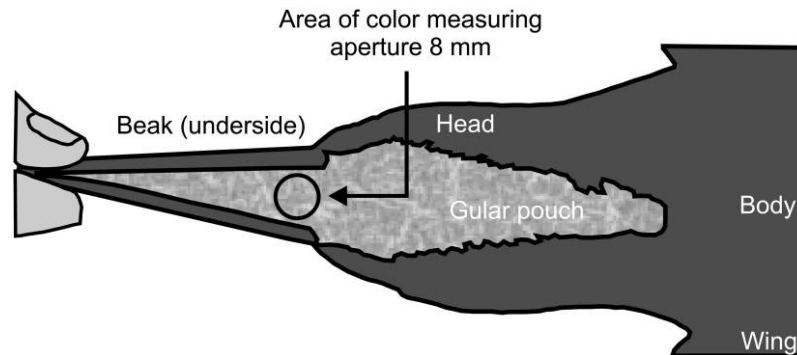
**Figure 2:** Reflectance spectra, relative to a barium sulfate standard. *A*, Spectra at the angle of maximum reflectance (MR) and the average with the feather rotated  $5^\circ$  to either side of the maximum. *B*, Effects of varying the elevation of the light from  $5^\circ$  to  $90^\circ$  above the line of sight. As expected, the reflectance curve is blueshifted as the angular separation of the viewer and light source increases (Osorio and Ham 2002). *C*, Spectra at the angle of maximum reflectance for back, breast, head, and wing feathers from a male magnificent frigatebird. The first three had iridescent coloration. The separate peaks in violet/blue and red parts of the human-visible spectrum account for the purplish color of the back feathers. *D*, Examples of relatively high- and low-reflectance back feathers at the angle of maximum reflectance and the amplitudes and locations of the peaks and troughs used to characterize the spectra. Analyses did not use the first peak because, owing to noise in records, it was not always detectable. The remaining five data points were highly correlated.

al. 2000; Rintamäki et al. 2000). There are, however, few investigations of soft parts included in courtship behaviors, probably as a result of the difficulty of quantifying such traits. In particular, inflatable blood-filled skin ornaments have complex forms and change very rapidly in color and shape. Skin coloration in birds is determined by hemoglobin, carotenoids, and other pigments (Ligon et al. 1990; Negro et al. 2000, 2002) and by structural mechanisms (Prum and Torres 2003).

### *Frigatebird Biology*

Frigatebirds (Fregatidae) are sexually size- and color-dimorphic seabirds with long life span ( $>40$  years for one individual; D. Dearborn, personal communication). Females are larger than males and have drab blackish-brown plumage, whereas males have a predominantly black plumage. Male frigatebirds have two conspicuous morphological sexual traits: an inflatable red gular pouch and lanceolated iridescent plumage (Harrison 1985; Orta 1992; Dearborn and Ryan 2002). Whereas the iridescent plumage is a permanent trait, the gular pouch is a seasonally expressed skin ornament that, after mating, shrinks and re-

verts to the color of the normal skin (Reville 1991; Madsen 2005). Gular pouch coloration varies between males in lightness, hue, and saturation, from pink to orange-red to red, and could therefore give information about current condition. In contrast, the plumage iridescence could be an indicator of long-term male quality, possibly displaying condition outside the breeding season, owing to the effects of feather growth and feather maintenance on color. Mate-seeking males will select a display site, inflate the gular pouch, and commence scanning for overflying mate-seeking females. When a female shows interest, by circling or hovering, the male responds with a high-intensity display, which continues as long as the female remains above him (Diamond 1973; Nelson 1975; Dearborn and Ryan 2002; Madsen 2005). This display includes occasional bouts of drumming (fig. 3), which may give information about several aspects of male quality. For instance, the fundamental frequency is negatively correlated with gular pouch size, which varies considerably between males (Madsen et al. 2004), and if size increases with age, this could signal male viability through the so-called age-based indicator mechanism (Trivers 1972; Manning 1985; Kokko and Lindström



**Figure 3:** Gular pouch color was measured in the area of nonextendable skin between the two sides of the under-beak, where coloration was measured from an 8-mm-diameter spot on the skin surface.

1996; Kokko 1997, 1998). Drumming rhythm cadence and constancy may also indicate stamina.

Magnificent frigatebirds form monogamous pairs, with asymmetric investment in parental care by the two sexes. Males desert after a few months of chick rearing (Diamond 1973; Osorno 1999; Osorno and Székely 2004), whereas females tend the young for a further 18 months and thus breed successfully only every second year (Diamond 1975; Osorno 1999). This results in a male-biased operational sex ratio. In this study, 57.5% (average over 4 years; Madsen 2005) of the courting males obtained a mate each year. Because some males attract a mate most years, whereas others consistently fail (V. Madsen, personal observation), there is scope for relatively strong sexual selection. Among frigatebirds, competition for mates, as defined by Andersson (1994), seems to take place mainly through female mate choice. Male/male aggressive competition (Madsen 2005) and fertilization competition (Dearborn et al. 2001; M. Serrano, personal communication) seem to be practically nonexistent. Female mate preferences may thus be inferred by comparing successful and unsuccessful males.

#### *Aim*

This study of magnificent frigatebirds investigates relationships between visual and auditory signals plus other morphological features and age class and mating success. Theories of age- and condition-dependent expression of sexual traits predict that older males and males of higher quality will have a higher degree of trait expression (Rohwer et al. 1980; McDonald 1989; Wetton et al. 1995; Mountjoy and Lemon 1996; Sundberg and Dixon 1996; Richardson and Burke 1999). We also expected males that mated successfully to display more developed ornamental traits than unsuccessful males (review in Ryan and Keddyc-Hector 1992).

#### **Methods**

##### *General*

Magnificent frigatebirds were studied in a breeding colony of approximately 15,000–16,000 birds (Madsen 2005) at the Mexican national park Isla Isabel (21°52'N, 105°54'W) during September–December, 2000–2002. A total of 252 unmated nonjuvenile males were captured by hand on nights with no moon. Each bird was fitted with a yellow vinyl wing tag with a unique number and color code, which enabled individual recognition at a distance and between years. Males were assigned to age classes according to the extent of white in the plumage: the oldest, completely black males (hereafter called AD); the intermediate age class, where males had some white feathers on the ventral part only (hereafter called SA); and the youngest age class, where males also had some white head feathers (hereafter called JSA). All age classes were presumably sexually mature. The accuracy of this age classification was confirmed by resightings of marked males, where, over a 3-year period, the age score increased in accordance with our assumptions; that is, the extent of white in plumage declined with age (Madsen 2005). The chronological age within each classification is unknown.

The following measurements were done at least twice and registered only once concordant measurements had been obtained. The length of the culmen was measured ( $\pm 0.5$  mm), and the bird was weighed ( $\pm 25$  g). From this information, a short-term condition measure was calculated, expressed as the residual values of body mass to size linear regression (Jakob et al. 1996; Osorno 1996). Culmen length was chosen to represent size because it did not differ with age class (table 1). The residuals were strongly correlated with body mass ( $r = 0.98$ ,  $P < .001$ ,  $N = 236$ ), and because there is some doubt about the validity of using residuals as a condition measure (e.g., Cotton et al. 2004),

**Table 1:** Culmen length, combined tail and tail fork length (TAIL), and body mass for each age class and mating status

	Culmen (mm)	TAIL	Body mass (g)	N
Age class:				
JSA	12.2 ± .39	-.66 ± 1.23 <sup>AB</sup>	1,178 ± 94.2 <sup>A</sup>	27–30
SA	12.2 ± .37	-.23 ± 1.14 <sup>B</sup>	1,206 ± 93.5	28–46
AD	12.3 ± .49	.27 ± 1.11 <sup>A</sup>	1,246 ± 112.5 <sup>A</sup>	125–162
F	.4	10.3	6.6	
df	2, 233	2, 235	2, 233	
P	.69	<.001	<.01	
Mating status: <sup>a</sup>				
Mated	12.3 ± .57	.11 ± 1.32	1,267 ± 103.9	57–60
Unmated	12.2 ± .41	.44 ± .93	1,241 ± 110.5	71–74
F	2.1	2.7	1.8	
df	1, 129	1, 129	1, 129	
P	.15	.10	.18	

Note: Values are presented as mean ± SD. Statistics are based on ANOVA. The three age classes were youngest (JSA), intermediate (SA), and oldest (AD). Superscript letters indicate significant post hoc differences between age classes.

<sup>a</sup> Analyses were performed with AD only.

we decided to include only body mass in the following analyses. The deeply forked tail consists of 12 feathers. The lengths of the outermost tail feathers and the tail fork (i.e., length from the tips of the shortest tail feathers to the tip of the longest tail feather) were measured ( $\pm 0.5$  mm). The length of the longer of the two outermost tail feathers (i.e., a presumably intact and fully grown feather) and the length of the tail fork were significantly correlated ( $r_s = 0.85$ ,  $P < .001$ ,  $N = 238$ ), so they were entered in a principal component analysis. One principal component, hereafter called TAIL, was then extracted based on correlation (eigenvalue = 1.85, eigenvector = 0.71, explained variance = 92.2%). Sample sizes for the various measures vary, for instance, because some birds were set free if they appeared affected by the handling. Also, some equipment was not available in all field seasons, and some samples were omitted because permits were not obtained.

Mating status of marked males was recorded throughout the field season, and individual mating success was assigned when the mating season was nearly over, in late December. Only mated males build a nest, so males that were registered as building nests and/or with a nest at least twice during the fieldwork period were classified as mated. Males were classified as unmated when they had been observed throughout the fieldwork period, had not been building a nest or with a nest, and retained the red and loosely structured gular pouches at the end of the mating season. Males that had not been observed building nests or with nests during the fieldwork period and were not observed at the end of the mating season were classified as being of “unknown mating status.” Final mating status as mated or unmated could be assigned to 200 of the 252 marked males, with 0 out of 24 JSA, 7 out of 32 SA, and

69 out of 144 AD males succeeding in obtaining a mate in the year of marking.

#### Feather Samples

Samples consisting of two feathers each from the head, wing coverts, and back, were collected from 214 males. The two feathers were taken at random from two different positions within the area, under light conditions (headlamps only) that did not allow for prior assessment of iridescence. From 43 males, samples of one feather from each of the two breast patches, situated on either side of the gular pouch, were also collected. Younger males do not have a fully developed ornamental plumage; some of the head feathers are white, and some back feathers are more femalelike in color and shape and lack iridescence. For these males, only fully developed black and/or iridescent feathers were collected. The iridescent coloration is delicate and was never handled; only the noniridescent part of the feather was ever touched.

For spectral measurements, the feathers were manually straightened and mounted on matte black cards. The length of the feather and the iridescent part, when present, were measured with a ruler ( $\pm 0.5$  mm; fig. 1B). This gave the proportion of the total feather length, excluding the feather shaft, that bore iridescent coloration, calculated as the ratio of iridescence to total length of the feather, hereafter called IRIRATIO. Another piece of card, with a 7-mm-diameter round aperture over the area to be measured, was then placed over the feather. For wing feathers, this was to the left of the rachis and 5–6 mm from the tip; for head feathers, it was centered on the rachis and 9–11 mm from the tip; and for breast and back feathers,

it was left of the rachis and within the iridescent part. The more detailed analysis of iridescence on breast and back feathers averaged three locations in the iridescent part along the left side of the rachis. Averaging was done to minimize any color variation due to growth bars (e.g., Murphy et al. 1989; Machmer et al. 1992). The three locations were (1) one-half, (2) midway between one-half and two-thirds, and (3) two-thirds of the way down the iridescent part from the feather tip (fig. 1B).

The recording apparatus allows adjustment of the position of the light source and the orientation of the feather surface relative to the recording line of sight (fig. 1A); it is described in more detail by Osorio and Ham (2002). The mounted feather was placed in a 160-mm-radius Cardan arm perimeter and illuminated by a 6-mm (i.e., 2.1°) UV-transmitting liquid light guide lit by a 400-W xenon arc. The spectrum from 300 to 750 nm was recorded by focusing light from a 1-mm-diameter spot on the feather surface with a quartz lens onto a 0.2-mm light guide connected to a spectrometer (S2000, Ocean Optics). A matte white Teflon reference was used for calibration. Reflectance spectrum of this reference was measured once relative to a standard of freshly pressed (medical-grade) barium sulfate, and measurements were adjusted accordingly. Before each feather was measured, the setup was recalibrated by taking dark and white references. To establish the stability of the apparatus, a series of nine repeated measurements of the white reference at six wavelengths at the approximate values of the peaks and troughs of the feather spectra was performed. The setup was recalibrated between each measurement. Reflectance spectrum measurements for peaks and troughs were stable at these six wavelengths, with coefficients of variance ranging from 0.0045 to 0.0070 for the nine repeated measurements.

The viewing geometry was with the feather aligned so that the lateral (i.e., widthways) axis of the blade was normal to the line of sight, and its orientation relative to the line of sight could be varied by rotation about this axis (for details, see fig. 1A and Osorio and Ham 2002). Two possible viewing geometries were tested: first, with the line of sight and light source nearly coaxial (separated by 5°), as if the sun were almost directly behind the viewer, and second, with the light source at the pole, elevated 90° above the line of sight, as if male and female frigatebirds were at same level and the sun were directly overhead. As expected, reflectance spectra shifted to shorter wavelengths as the angle between viewer and light sources increased (fig. 2B; Land 1972; Osorio and Ham 2002). For this study, a 90° angle between the light source and the line of sight was used because of its biological relevance and because the setup was more convenient due to the right angles involved.

With an ordinary specular (i.e., mirror) surface, where

the angle between illumination and viewer is 90°, the mirror looks brightest at an orientation of 45°. With the iridescent frigatebird feathers, the angle of maximum reflectance (MR) was close to but not exactly a 45° angle to plane of the feather blade. The deviation from 45° gives the angle of tilt in the iridescent reflector relative to the feather surface (using the terminology of Osorio and Ham 2002). For back feathers, tilt ranged from 0° to -7° (mean = -3.1°,  $N = 214$ ). This corresponds with the results of Cuthill et al. (1999), who found maximum reflectance of iridescent feathers from starlings to be between 40° and 45°. (However, other feathers reflect light at very different angles relative to the plane of the blade; Osorio and Ham 2002). We used measurements with the feather surface oriented to maximize the reflectance and oriented 5° to either side of this maximum. It should be noted that one would not normally measure reflectance spectra of ordinary pigment-based coloration with this viewing geometry. This is because the geometry maximizes spectrally unselective specular reflectance, thus minimizing the saturation of the pigment color. However, iridescent feather surfaces abolish this non-spectrally selective highlight, so that the color's brightness and saturation are maximized simultaneously (Osorio and Ham 2002). This unusual quality helps give iridescent structural coloration its striking visual effect.

After recording, reflectance spectra were smoothed by convolution with a Gaussian mean (SD approximately 3 nm), and reflectance amplitudes were plotted at 5-nm intervals from 300 to 750 nm (fig. 2C). Smoothing removes high-frequency noise but otherwise does not affect the data. Wing feathers lacked iridescent coloration, and head feathers had one small peak (fig. 2C). The spectral locations and amplitudes of peaks and troughs from 43 back feathers and breast feathers were significantly correlated ( $r_s$  range 0.42–0.59,  $N = 43$ ,  $P$  range .01–.001). For analyses of iridescence levels we therefore concentrated on back feathers and characterized their spectra by quantifying wavelengths and amplitudes of reflectance peaks and troughs (fig. 2D). Spectra had three peaks and three troughs in the 300–750 nm range (fig. 2D). For 40 samples, first peaks (fig. 2D) were not discernible because of poor signals at short wavelengths. However, principal components (see “Results”) with or without first peaks were highly correlated (reflectance amplitude:  $r_s = 1.00$ ,  $P < .001$ ; reflectance wavelength:  $r_s = 1.00$ ,  $P < .001$ ; reflectance peak-to-trough ratio:  $r_s = 0.90$ ,  $P < .001$ ;  $N = 174$ ), allowing us to include all samples in the following analyses by excluding all first peaks.

The sinusoidal form of the reflectance spectra (fig. 2) suggests that they can be described by three variables that correspond roughly to brightness, hue, and saturation in human color perception (Mollon 2001). These variables

were reflectance amplitude (RF), wavelength (WL), and peak-to-trough ratio in reflectance amplitude (PT). The peak-to-trough ratio was calculated as the reflectance at the peak divided by the reflectance at the trough. The three calculated ratios were second peak to first trough, third peak to second trough, and second peak to second trough.

To check the stability of measurements at the angle of maximum reflectance, one back feather from each of 10 individuals, chosen at random, was measured twice at this angle. For each measuring, the setup was recalibrated and the feather repositioned and remeasured at three positions for which the mean was calculated. Individual means from the repeated measurements were significantly correlated when tested in Spearman rank-order correlations (RF:  $r_s$  range 0.94–1.00,  $P < .001$ ; WL:  $r_s$  range 1.00–1.00,  $P < .001$ ; PT:  $r_s$  range 1.00–1.00,  $P < .001$ ).

To check the degree of variation introduced when measuring iridescence at a fixed angle compared to that when measuring at the variable angle of maximum reflectance, 10 back feathers were measured at both a fixed angle of 45° and the angle of maximum reflectance. This resulted in a range of individual differences in reflectance amplitude of 13%–63% (mean = 36%). By using a well-defined and adjustable viewing geometry, we thus obtained consistent measurements of the iridescent feather coloration when measuring at a variable angle through maximizing reflectance amplitude. Measuring at a fixed angle of 45° introduced considerable differences (up to 63%) in reflectance amplitude for the same male as a result of slight variations in the tilt of the nanoscale layering of feather materials. Measuring iridescent coloration at a fixed angle may therefore result in data that do not facilitate between-male comparisons. Through measuring the iridescence at the angle of maximum reflectance, we also obtained data for the maximum signal value, which is used most commonly when relating ornamental traits to male mating success.

Before making between-male comparisons, it was essential to establish that measurements of a single iridescent feather were representative of the individual. We therefore tested two back feathers from each of 25 males. The five data points (two peaks and three troughs) for each spectral variable (RF, WL, and PT) were significantly correlated (RF:  $r_s$  range 0.92–0.99,  $P < .001$ ; WL:  $r_s$  range 0.90–0.98,  $P < .001$ ; PT:  $r_s$  range 0.72–0.82,  $P < .001$ ). Comparing the data points for the two feather samples from the same individual resulted in the following correlation coefficients: RF:  $r_s = 0.82$ ,  $P < .001$ ; WL:  $r_s = 0.98$ ,  $P < .001$ ; PT:  $r_s = 0.87$ ,  $P < .001$ .

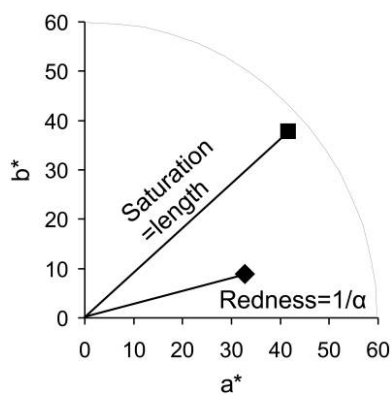
Apart from the reflectance at the angle of maximum reflectance, an important feature of iridescent coloration is its directionality. This is likely to reflect order in the

feather structure and may influence the appearance of a display. To measure directionality as a function of feather orientation (i.e., the angle between line of sight and the sample; Osorio and Ham 2002), we compared reflectance at the angle of maximum reflectance with the mean for 5° to either side of the maximum reflectance. Directionality was calculated by dividing the maximum reflectance minus mean reflectance at  $\pm 5^\circ$  by the maximum reflectance plus mean reflectance at  $\pm 5^\circ$ ; this gives a scale ranging from 0 to 1.

### Gular Pouch Color Measurements

It was not possible to measure the color of an inflated gular pouch during the daytime. It was, however, observed that the color of the nonextendable part between the two sides of the under-beak was visually indistinguishable from the color of the inflated gular pouch. Color measurements were therefore taken from this area at night by placing a colorimeter gently against the skin while the male was lying on its back with the beak extended backward (fig. 3). Measurements of all 139 males were from an 8-mm-diameter spot on the skin surface and were done by one person (V. Madsen) using a Minolta Colorimeter and  $D_{65}$  standard illuminant. The  $D_{65}$  illuminant corresponds to average daylight (380–780 nm). The color was measured using the  $L^*a^*b^*$  color space, which corresponds to the human CIELAB color psychometrics (CIE 1976). In the  $L^*a^*b^*$  color space, lightness is given by  $L^*$  (range 0–100), where 0 is black and 100 is light. The  $a^*$  and  $b^*$  values (range  $\pm 60$ ) are the chromaticity coordinates, where  $+a$  is red,  $-a$  is green,  $+b$  is yellow, and  $-b$  is blue. The  $L^*a^*b^*$  color space thus represents a color sphere with an achromatic center, where  $a^*$  and  $b^*$  are equal to 0. Color saturation is therefore equal to the radius of the circle centered in the center of the color sphere to the point coordinate given by  $a^*$  and  $b^*$ . Hue is indicated by the slope of the line going from the center to the point coordinate given by  $a^*$  and  $b^*$ . Here, we used the inverse of the slope because higher values then indicated a redder color, which was intuitively more useful (fig. 4). The colorimeter was calibrated before each nightly measuring session. Males were measured four or five times each (mean 4.8 times) at slightly varying positions, and an average was calculated. The coefficients of variance for the measures were (mean  $\pm$  SE)  $L^*$ : 2.3%  $\pm$  0.1%;  $a^*$ : 4.1%  $\pm$  0.2%;  $b^*$ : 6.3%  $\pm$  0.3%. Repeatability of measurements was checked by a Pearson correlation analysis of two randomly chosen measurements:  $L^*$ :  $r = 0.95$ ;  $a^*$ :  $r = 0.95$ ;  $b^*$ :  $r = 0.97$ ;  $N = 139$ ).





**Figure 4:** Red ( $a^*$ ) and yellow ( $b^*$ ) parts of the  $L^*a^*b^*$  color sphere. Color saturation in this space is the length of the line from the center of the sphere to the point ( $a^*$ ,  $b^*$ ). Color hue is indicated by the  $\alpha$  of the line from the center to the point ( $a^*$ ,  $b^*$ ); in order for the values to indicate redness, we used the  $1/\alpha$  of the line. Examples of a very saturated (square) and a very red (diamond) gular pouch are shown in the figure.

#### Sound Recording and Analysis

A total of 86 wing-tagged males were recorded. Of these, 61 were captured during the present investigation, and a subsample of 20 were measured the same year in which they were sound recorded. Because morphological size was not expected to change after the juvenile stage, we included all males in a correlation test between fundamental frequency (gular pouch size) and morphological size. However, only adult males captured the same year in which they were sound recorded were included in correlation tests between acoustic components of the drumming and body mass.

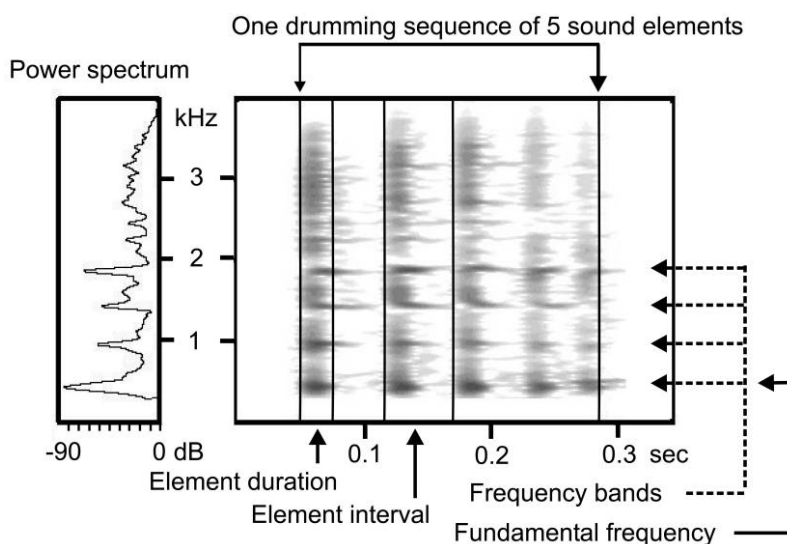
The drumming was recorded at close range (1.5–15 m) using a SONY WM-DC6 tape recorder and a Sennheiser MKH70 P48 directional microphone. Great care was taken in choosing recording sites that did not disturb neighboring breeding birds, and consequently, no nest losses due to our presence were observed. The drumming was digitized (16-bit, 8-kHz sampling frequency) and analyzed in Avisoft, version 4.15 (Avisoft 2002) using the spectrogram window (FFT 512, frame 100%, Hamming window, frequency resolution 15 Hz, overlap 98.43%, time resolution 1 ms). We reduced ambient noise using the lower cutoff frequency filter option set at 0.3 kHz. In accordance with the procedure of Madsen et al. (2004), a drumming sequence was defined as two or more sound elements in close continuation, that is, with less than 0.1 s between the start of each sound element. A minimum of five sequences and a maximum of 25 sequences were analyzed per male (mean  $18.4 \pm 0.86$  sequences). Each sound element within a drumming sequence contains several fre-

quency bands, of which the lowest frequency band's peak frequency, hereafter called the fundamental frequency, is negatively correlated with gular pouch size (Madsen et al. 2004). Descriptive acoustic components of a drumming sequence were fundamental frequency (Hz), frequency band interval (Hz), sound element duration (ms), element interval (ms; fig. 5), and the coefficient of interval variation. The peak frequency (frequency with maximum amplitude; fig. 5) for each frequency band was measured in the power spectrum as the average for the sequence. Individual male averages were calculated per frequency band over all sequences analyzed, and frequency band intervals were calculated by subtracting these frequency band averages. Sound element duration and element intervals in seconds for each sound element in a sequence were obtained from the "automatic parameter measures" (threshold of  $-10$  dB, hold time of 1 ms). The few elements that could not be correctly separated (e.g., because of background noise) were excluded from subsequent analyses. Average sound element durations and element intervals were calculated per sequence, and individual male averages were calculated together with the coefficient of interval variation over all sequences analyzed.

#### Statistics

Analyses used the statistical programs Statistica, release 4.3 (StatSoft 1993), and JMP, version 3.2.1 (SAS Institute 1989–1997). All data were tested for within-group normal distribution using the Shapiro-Wilk  $W$ -test. Normally distributed and log-transformed variables were tested for differences related to age class and mating status using MANOVAs, ANOVAs, and Student  $t$ -tests. Correlation analyses used Pearson product-moment correlation or Spearman rank-order correlation. Analyses for mating status-related differences were performed with the oldest age class (AD) only, to avoid confounding the results with possible age class-related differences. Discriminant function analyses for age class and mating status were performed on normally distributed and log-transformed variables with significance level for entry set at 1.0 and tolerance at 0.01. All statistical tests were two-tailed, with probability levels  $<0.05$  in general being considered significant. Adjusting significance levels, when testing several variables independently, was done using sequential Bonferroni technique (Rice 1989). Significant differences among more than two groups were post hoc tested using a Tukey HSD test.

When males were sound recorded more than once in the same year, we used the recording with the most drumming sequences for analyses of the effects of age class and mating status. If there was no difference in number of drumming sequences, one recording was chosen at ran-



**Figure 5:** *Right*, spectrogram of a magnificent frigatebird courtship drumming sequence of five sound elements; *left*, mean power spectrum for the same sequence. Four frequency bands can be identified. The lowest frequency band, called the fundamental frequency, has a frequency of about 440 Hz. Element duration and element interval are indicated.

dom. For males that were rerecorded the following year, the recording from the first year was generally used in the analyses for differences with age class and mating status. The only exception was one male for whom mating status could be assigned in only the second year; here, the second-year recording was included in the analyses.

## Results

### *Morphological Measures*

All measures were obtained for 167 males, distributed with 27 in the youngest age class (JSA), 28 in the intermediate age class (SA), and 113 in the oldest age class (AD). Measures varied significantly with age class (MANOVA: Wilks's  $\lambda = 0.83$ ,  $df = 8, 324$ ,  $P < .001$ ). When each of the variables was tested, only culmen length did not vary with age class (table 1). Post hoc analyses showed that JSA males had significantly shorter tail and tail fork lengths (the combined measure TAIL) than both SA and AD males and that SA males also had significantly shorter TAIL than AD males (table 1). Young JSA males also weighed significantly less than AD males, with SA being a nonsignificant intermediate (table 1). Mating status was assigned to a total of 100 males from the AD age class, distributed with 38 mated and 62 unmated males. Measures did not vary significantly with mating status (MANOVA: Wilks's  $\lambda = 0.98$ ,  $df = 4, 95$ ,  $P = .81$ ; table 1).

### *Feather Iridescence*

The iridescent reflectance spectra from the 214 samples analyzed showed substantial variation between individuals (table 2). Within the multip peaked spectrum reflectance amplitudes, reflectance wavelengths and difference in reflectance of peaks to troughs were significantly correlated, and one principal component was therefore extracted based on correlations. This principal component reduced the three or five data points for each of the three variables to one composite variable per individual per variable. For RF,  $r$  range = 0.95–0.99,  $P < .001$ , eigenvalue = 4.86; eigenvector = 0.45; explained variance = 97%. For WL,  $r$  range = 0.73–0.96,  $P < .001$ ; eigenvalue = 4.50; eigenvector range 0.41–0.46; explained variance = 90%. For PT,  $r$  range = 0.77–0.84,  $P < .001$ ; eigenvalue = 2.61; eigenvector range 0.57–0.59; explained variance = 87%.

With regard to directionality of the iridescence, the mean ratio of decrease in reflectance at  $\pm 5^\circ$  to the angle of maximum reflectance was  $0.4 \pm 0.07$  ( $N = 214$ ). This is almost a halving of reflectance for a  $5^\circ$  rotation of the feather (fig. 2A), implying that light from a point source is directed into an ellipse just over  $20^\circ$  across its vertical axis (fig. 1B). Iridescence is, therefore, visible only within a restricted angle; otherwise, feathers are very black (<4% reflectance). As expected, the angle over which light is directed was inversely related to the maximum reflectance, so that the total amount of light reflected probably was relatively constant (fig. 6). Thus, feathers with the greatest maximum brightness tend also to reflect light over a nar-

**Table 2:** Iridescent color spectrum variables, as obtained from analysis of maximum reflectance of 214 back feathers from male magnificent frigatebirds

	Reflectance (%)		Wavelength (nm)		Peak/trough reflectance ratio	
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
First trough	20.87 $\pm$ 5.05	7.3–34.9	359.2 $\pm$ 9.47	330–393		
Second peak	25.50 $\pm$ 6.08	9.4–41.5	420.9 $\pm$ 11.92	380–460	1.22 $\pm$ .06	.99–1.22
Second trough	19.12 $\pm$ 4.80	7.8–35.6	492.9 $\pm$ 13.84	447–535	1.73 $\pm$ .14	1.26–1.73
Third peak	33.01 $\pm$ 8.30	11.8–55.4	604.7 $\pm$ 17.73	543–652	1.34 $\pm$ .08	1.03–1.34
Third trough	24.33 $\pm$ 6.25	6.3–39.9	730.5 $\pm$ 13.74	677–750		

rower angle. This effect is likely to be indicative of nano-scale order within the feather and should enhance the visual display (i.e., intensity modulation) produced by the brightest feathers.

All measures concerning feather iridescence were obtained for 211 males, distributed with 28 JSA, 42 SA, and 141 AD (table 3). The variables differed significantly with age class (MANOVA: Wilks's  $\lambda = 0.89$ ,  $df = 10, 408$ ,  $P < .01$ ). When each variable was tested, only the ratio of iridescence length to total feather length (IRIRATIO) differed significantly, with a post hoc analysis showing that the difference was between the oldest and the youngest birds, with older males having a higher ratio (table 3). The similarity of different age classes in iridescence spectrum data is consistent with the field observation that iridescence levels of back feathers were not useful for age-classifying males. JSA males do not, however, have a completely developed plumage; they still have back feathers of a more femalelike appearance, that is, rounded, not lanceolated, blackish/brown feathers with no iridescence. Also, they have white feathers on the head. Therefore, the overall appearance of the youngest males is distinctly different from that of the older age classes. Mating status was assigned to a total of 121 males from the AD age class, distributed with 52 mated and 69 unmated males. Feather iridescence variables did not differ significantly with mat-

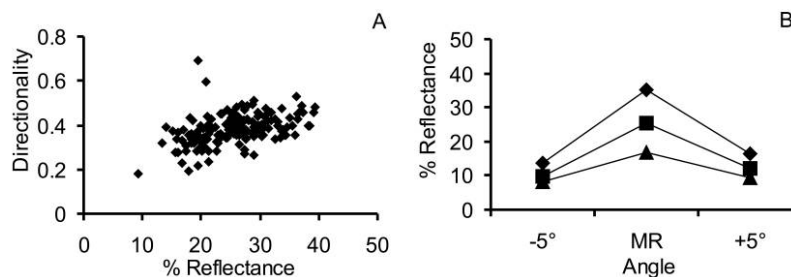
ing status (MANOVA: Wilks's  $\lambda = 0.94$ ,  $df = 5, 113$ ,  $P = .25$ ; table 3). There was, however, a tendency for successfully mating males to have lower iridescence of lower wavelength (WL in table 3).

#### Gular Pouch Coloration

All measures were obtained for 139 males, distributed with 20 JSA, 17 SA, and 102 AD. Measures did not vary significantly with age class (MANOVA: Wilks's  $\lambda = 0.93$ ,  $df = 6, 268$ ,  $P = .11$ ). When each variable was tested, there was a tendency for saturation to be lower in younger males (table 4). With regard to mating success, data were obtained from 36 mated and 78 unmated males, of which 36 mated and 52 unmated males were of the AD age class. Gular pouch coloration measures did not differ significantly with mating status (MANOVA: Wilks's  $\lambda = 0.95$ ,  $df = 3, 110$ ,  $P = .14$ ; table 4).

#### Drumming

The five acoustic components of the drumming differed among the 86 males analyzed, as shown by the range of component values (table 5). A Pearson product-moment correlation analysis found three of the five variables to be significantly correlated: fundamental frequency with fre-



**Figure 6:** Directionality was calculated at the angle  $\pm 5^\circ$  from the angle of maximum reflectance ( $[(RFMR - (RFMR \pm 5^\circ)) / (RFMR + (RFMR \pm 5^\circ))]$ ; fig. 2A). A, Excluding possible outliers, directionality was inversely related to reflectance amplitudes with  $r_s = -0.40$  and  $P < .001$ , as visualized in B, where mean maximum reflectance amplitudes for the 25 lowest (triangles), 25 middle (squares), and 25 highest (diamonds) values are plotted against the reflectance amplitudes at  $\pm 5^\circ$  from the angle of maximum reflectance.

**Table 3:** Color spectrum variables representing wavelength (WL), reflectance (RF), and ratio between peak and trough reflectance (PT), as obtained from principal component analyses for 214 back feathers from male magnificent frigatebirds, and ratio of length of iridescence to total feather length (IRIRATIO;  $N = 211$ ) for each age class and mating status

	WL	RF	PT	IRIRATIO	<i>N</i>
Age class:					
JSA	-.16 ± 2.60	-.51 ± 2.32	.11 ± 1.52	.47 ± .06 <sup>a</sup>	28
SA	.33 ± 1.35	.18 ± 1.98	.39 ± 1.08	.50 ± .05	42
AD	-.06 ± 2.20	.05 ± 2.24	-.13 ± 1.75	.51 ± .05 <sup>a</sup>	141–144
<i>F</i>	.6	.9	2.6	6.3	
df	2, 211	2, 211	2, 211	2, 208	
<i>P</i>	.53	.40	.17	<.01	
Mating status: <sup>b</sup>					
Mated	-.50 ± 2.18	.09 ± 1.97	-.30 ± 1.88	.50 ± .05	51–52
Unmated	.32 ± 2.02	-.16 ± 2.22	-.00 ± 1.45	.52 ± .05	68–69
<i>F</i>	4.6	.4	1.0	2.6	
df	1, 119	1, 119	1, 119	1, 117	
<i>P</i>	<.05 <sup>c</sup>	.53	.33	.11	

Note: Values are presented as mean ± SD. Statistics are based on ANOVA. The three age classes were youngest (JSA), intermediate (SA), and oldest (AD).

<sup>a</sup> Pairwise significant post hoc differences between age classes.

<sup>b</sup> Analyses were performed with AD only.

<sup>c</sup> Not significant after sequential Bonferroni adjustment of significance level (Rice 1989).

quency band distance ( $r = 0.64$ ,  $P < .001$ ,  $N = 81$ ), fundamental frequency with sound element duration ( $r = -0.38$ ,  $P < .001$ ,  $N = 81$ ), and sound element duration with frequency band distance ( $r = -0.30$ ,  $P < .01$ ,  $N = 81$ ). Only the three noncorrelated components—fundamental frequency, element interval, and coefficient of interval variation—were included in the following analyses of differences with age class and mating status.

In total, 24 males were recorded twice during the same field season. The fundamental frequency increased significantly with recording date (mean 429.6–451.7 Hz,  $t_{\text{paired}} = -2.76$ ,  $P < .05$ ,  $N = 24$ ), whereas neither element interval nor coefficient of interval variation changed significantly between recordings (interval:  $t_{\text{paired}} = 0.36$ ,  $P = .72$ ,  $N = 21$ ; coefficient:  $t_{\text{paired}} = 0.38$ ,  $P = .71$ ,  $N = 21$ ). Recording date was therefore included as a covariate in the continued analyses of the fundamental frequency.

Correlational analyses between the three acoustic components and size (culmen length;  $N = 56$ –58) and body mass ( $N = 19$ ) resulted in only nonsignificant  $r$  values (fundamental frequency:  $r = -0.24$  and  $-0.43$ , respectively; element interval:  $r = 0.08$  and  $0.15$ , respectively; coefficient of interval variation:  $r = -0.08$  and  $0.12$ , respectively). Hence, size of the males did not seem to have an effect on the acoustic components of the drumming. This is concordant with a previous study (Madsen et al. 2004).

All measures were obtained for 82 males, distributed

with 3 JSA, 10 SA, and 69 AD. Measures varied significantly with age class (MANOVA: Wilks's  $\lambda = 0.82$ ,  $df = 6, 154$ ,  $P < .05$ ). When each variable was tested, only fundamental frequency varied significantly with age class (ta-

**Table 4:** Gular pouch color lightness, redness, and saturation for each age class and mating status

	Lightness <sup>a</sup>	Redness	Saturation	<i>N</i>
Age class:				
JSA	45.5 ± 4.69	1.5 ± .53	32.7 ± 5.39	20
SA	44.0 ± 3.71	1.8 ± .61	30.1 ± 3.89 <sup>b</sup>	17
AD	44.1 ± 5.32	1.7 ± .58	34.0 ± 6.33 <sup>b</sup>	102
<i>F</i>	.8	1.9	3.2	
df	2, 136	2, 136	2, 136	
<i>P</i>	.46	.15	<.05 <sup>c</sup>	
Mating status: <sup>d</sup>				
Mated	44.6 ± 6.05	1.8 ± .68	32.7 ± 8.78	36
Unmated	43.4 ± 4.57	1.7 ± .49	34.7 ± 4.25	52
<i>F</i>	.9	.4	2.0	
df	1, 86	1, 86	1, 86	
<i>P</i>	.35	.54	16	

Note: Color data defined by CIELAB measures of lightness ( $L$ ), redness ( $a$ ), and saturation ( $[(a^2 + b^2)^{1/2}]$ ; see "Gular Pouch Color Measurements." Values are presented as mean ± SD. Statistics are based on ANOVA. The three age classes were youngest (JSA), intermediate (SA), and oldest (AD).

<sup>a</sup> Analyses were performed on log-transformed data.

<sup>b</sup> Significant post hoc differences between age classes.

<sup>c</sup> Not significant after sequential Bonferroni adjustment of significance level (Rice 1989).

<sup>d</sup> Analyses were performed with AD only.

**Table 5:** Grand mean  $\pm$  SD and range of the means of five acoustic components of magnificent frigatebird courtship drumming

Acoustic component	Grand mean		<i>N</i>
	$\pm$ SD	Range	
Fundamental frequency (Hz)	444.6 $\pm$ 44.5	367–625	86
Frequency band distance (Hz)	535.9 $\pm$ 94.2	422–963	81
Element duration (ms)	25 $\pm$ 3.1	19–33	82
Element interval (ms)	63 $\pm$ 4.1	52–74	82
Coefficient of interval variation (%)	12 $\pm$ 3.3	5–22	82

ble 6). Post hoc analyses showed that significant differences were between the SA and AD age classes, with the oldest males having the lowest fundamental frequency (table 6). Mating status was assigned to a total of 62 males of the AD age class, distributed with 21 mated and 41 unmated males. Measures varied significantly with mating status (MANOVA: Wilks's  $\lambda = 0.68$ ,  $df = 3, 58$ ,  $P < .001$ ; table 6). Testing each of the three acoustic components showed that all three differed significantly with mating status, with mated males having lower fundamental frequency, shorter element interval, and lower coefficient of interval variation than unmated males (table 6).

#### *Combining the Measures*

Correlational analysis found gular pouch lightness negatively correlated with gular pouch redness ( $r = -0.80$ ,  $P < .001$ ,  $N = 139$ ) and both correlated with body mass (lightness:  $r = -0.43$ ,  $P < .001$ ,  $N = 126$ ; redness:  $r = 0.44$ ,  $P < .001$ ,  $N = 126$ ). Gular pouch coloration saturation was negatively correlated with fundamental frequency ( $r = -0.51$ ,  $P < .001$ ,  $N = 25$ ). Remaining correlation coefficients were lower ( $r$  range  $-0.32$  to  $0.32$ ), and even though some were significant, this was mostly due to large sample sizes.

We checked the predictive value of the significant results, including the two tendencies found for gular pouch coloration saturation and feather iridescence wavelength, by entering them in discriminant analyses for age class and mating status. For the analysis of age-related differences at the year of marking, the fundamental frequency was included when recording age was equal to age at marking. With regard to the analysis for mating status-related differences at the year of sound recording, the iridescent wavelength was included because some back feathers were still found to be partly in their sheaths during the mating season, and no distinct molting season of the ornamental plumage has ever been observed. This indicated that the ornamental plumage might have a more continuous molt cycle, as also found for tail feathers that molt at a cycle of about 3 years (Madsen 2005). All the variables tested were included in the resulting discriminant models (i.e.,

five for the acoustic components and four for the measures of gular pouch and feather color), leading to maximum percentages of correctly classified males per age class of 96% (100% JSA, 83% SA, and 100% AD;  $F = 2.7$ ,  $df = 10, 36$ ,  $P < .05$ ,  $N = 25$ ) and per mating status of 84% (83% mated and 84% unmated;  $F = 4.0$ ,  $df = 4, 26$ ,  $P < .05$ ,  $N = 31$ ). When the acoustic components were tested alone—that is, without WL—for mating status, it resulted in a total of 82% (67% mated and 90% unmated;  $F = 9.1$ ,  $df = 3, 58$ ,  $P < .01$ ,  $N = 31$ ) males classified per mating status, which is practically the same total, but with more skew between groups.

#### **Discussion**

Our key finding is that mostly auditory signals best distinguish mated from unsuccessful males. Of the visual signals investigated, none of the gular pouch coloration features differed with mating success, and an indication of a difference only in iridescence hue with mating success was found. The most noticeable feature of the courting male magnificent frigatebirds, namely, the red gular pouch, thus seems to be a mostly auditory signal when used in competition for mates. With regard to gular pouch size, the apparent emphasis on the auditory signal compared to the visual signal may very well result from the produced sound being a robust and honest signal, in comparison to the visual signal of the gular pouch, where angle of vision and male posture may greatly influence perceived size. Despite the lack of differences in visual traits with mating status, several of the traits differed significantly with age.

#### *Age Class–Related Differences in Morphology and Ornamentation*

Young, probably sexually mature magnificent frigatebird males differed noticeably from older males in weighing less and having less developed plumage features. Some plumage features were directly used in age classification; only the youngest males still had white feathers on the head and/or ventral area. They were also characterized by having a mixture of noniridescent and nonlanceolated

**Table 6:** The three noncorrelated acoustic components of magnificent frigatebird courtship drumming for each age class and mating status

	Fundamental frequency (Hz) <sup>a</sup>	Interval (Hz)	Coefficient of interval variance	N
Age class:				
JSA	445.8 ± 17.54	66 ± 2.1	9 ± 2.3	3
SA	484.3 ± 69.83 <sup>b</sup>	61 ± 4.3	11 ± 3.0	10
AD	439.1 ± 38.34 <sup>b</sup>	63 ± 4.1	12 ± 3.3	69–73
<i>F</i>	5.3	1.6	1.0	
df	2, 82	2, 79	2, 79	
<i>P</i>	<.01	.20	.39	
Mating status: <sup>c</sup>				
Mated	418.4 ± 33.17	61 ± 3.1	10 ± 2.2	21–23
Unmated	451.1 ± 35.54	64 ± 3.9	13 ± 3.5	41–42
<i>F</i>	9.5	7.9	7.9	
df	1, 62	1, 60	1, 60	
<i>P</i>	<.01	<.01	<.01	

Note: Values are presented as mean ± SD. Statistics are based on ANOVA. The three age classes were youngest (JSA), intermediate (SA), and oldest (AD).

<sup>a</sup> Analyses were performed with recording date as covariate.

<sup>b</sup> Significant post hoc differences between age classes.

<sup>c</sup> Analyses were performed with AD only.

femalelike back feathers, and they had shorter tail and tail fork lengths and lower ratios of length of iridescence to total feather length in ornamental back feathers than did older males. Young males did not differ from older males in morphological size, as indicated by culmen length, iridescent spectrum variables, gular pouch coloration lightness and redness, or drumming interval and coefficient of interval variance. There was a (nonsignificant) tendency for saturation of gular pouch color to be lower in young males, which was also the only gular pouch coloration variable that did not correlate with body mass. Instead, saturation was negatively correlated with the fundamental frequency of the drumming, where younger males had higher frequencies than older males, which is indicative of smaller gular pouches (Madsen et al. 2004). Individual between-year re-recordings reconfirmed this: the fundamental frequency decreased from the first year of recording to the next. The increases in plumage development and body mass with age class suggest that the general lack of age class–related differences in ornamentation does not stem from a total lack of age-related differences. In a study of starlings, age-related differences were also found, with older males being more ornamented than second-year birds (Komdeur et al. 2005). The variable that differed with age in starlings was a principal component primarily consisting of tip length (i.e., the lanceolated part of the ornamental feather), iridescence ratio, and a hue index, suggesting that age-related differences in starlings involve more ornamental aspects of plumage than these differences in frigatebirds. Finally, it is worth noting that for gular pouch coloration lightness and redness, other factors, such

as blood parasite prevalence and testosterone levels, seem to influence the development more than age class does (Madsen et al., forthcoming). The correct classification of 96% in a discriminant analysis for age class indicated that most age class–related differences in this data set had been identified.

#### Measurement and Analysis of Iridescent Spectra

The method used here for measuring iridescent spectra is that described by Osorio and Ham (2002). The object is to obtain a meaningful description of the visual effect of the iridescent structural coloration of bird plumage with a limited number of measurements (fig. 1). It is immediately obvious for the feathers described here, and for almost all other structurally colored plumage, that no pre-selected viewing geometry will yield the maximum brightness or hue saturation (or indeed, any measurable reflectance). Moreover, certain feathers (e.g., of hummingbirds and birds of paradise) reflect light from a point into a cone of <5° across (Osorio and Ham 2002; D. Osorio, unpublished data). It is therefore highly desirable to continuously adjust the viewing geometry, in particular, to obtain a maximum signal. A fixed set of viewing geometries (e.g., Cuthill et al. 1999) is less satisfactory for iridescent plumage. Given continuously adjustable viewing geometry, one can go on to investigate the effects of varying the orientation of the feather relative to the viewer (and/or the light source) and hence begin to understand how the intensity and chromaticity of an iridescent display would appear to a viewer under natural conditions.

Regarding the general problem of measuring dark iridescent plumage coloration, this study shows convincingly that it is possible to obtain replicable measurements and that reflectance measured at one point on one feather of an individual fairly accurately predicts reflectance across an entire plumage region (fig. 2). With casual visual inspection of the feathers, or indeed, entire birds, it was not at all obvious that this would be the case. We can therefore commend our method of measurement for all work on structurally colored surfaces, such as feathers and fish scales, that resemble thin-layer interference reflectors (Land 1972; Prum et al. 1999).

The iridescent spectra were analyzed by measuring a number of simple parameters describing the resulting curve, namely, locations and magnitudes of the peaks and troughs, and by extracting one principal component for each of three variables, maximum reflectance, wavelength, and peak/trough ratio. This was in contrast to the more generally used method, where principal components are estimated for the reflectance spectra themselves (Cuthill et al. 1999). The reason for our approach is that the parameters are (a) directly related to the physical mechanism causing reflectance (Prum et al. 1999; Land and Nilsson 2002) and (b) not highly correlated (fig. 2).

#### *Feather Iridescence and Mating Success*

Among the oldest age class, a tendency was found for mated males to have back-feather iridescence of slightly shorter reflectance wavelength than that of unmated males. The implications of this are obscure because little is known about condition-dependent effects of the growth of iridescent plumage (Hill et al. 2005). The apparent insignificance of iridescent coloration reported here is consistent with observations of great frigatebirds from Hawaii, where feather reflectance was scored as dull, moderate, or bright under standardized light conditions at night, and total length of the iridescent back feathers was measured (Dearborn and Ryan 2002). Dearborn and Ryan (2002) found that none of the measured features differed between early- and later-mating great frigatebirds. For magnificent frigatebirds, such a comparison would not be appropriate because males arrive at the colony throughout the approximately 3-month mating period (V. Madsen, personal observation), and no consistent pattern of enhanced breeding success for early breeders seems to exist (Madsen 2005). The apparent insignificance of iridescent coloration differs from results of other work on structural coloration and mate choice (Andersson and Amundsen 1997; Andersson et al. 1998; Johnsen et al. 1998; Hunt et al. 1999; Hill et al. 2005; but see Ballentine and Hill 2003). One possibility is that the magnificent frigatebird is the only frigatebird species known to have purple back-feather hue

(Harrison 1985), suggesting that it is used for identification of the species.

#### *Gular Pouch Coloration and Mating Success*

We did not find any indications of female preference for any feature of gular pouch coloration; successfully and unsuccessfully mating males from the oldest age class did not differ in any of these. This differs from the general findings, for instance, in galliforms, where female mate preferences are based on the color and size expression of condition-associated and testosterone-mediated soft parts (Ligon et al. 1990; Zuk et al. 1990a, 1990b; Holder and Montgomerie 1993; Buchholz 1995; Rintamäki et al. 2000). Our finding was, however, in accordance with the result of an investigation of great frigatebirds on the Hawaiian Tern Island, which also failed to find any female preference for gular pouch color, as scored by use of Munsell cards at standardized angles to the light during the day (Dearborn and Ryan 2002). The color spectrum visible to birds includes the ultraviolet colors, which neither of the two investigations included; this, however, should not affect the results because a pilot study using a spectrometer to measure gular pouch coloration did not indicate any significant reflectance peaks within the ultraviolet range (J. L. Osorno, unpublished data).

#### *Selection Pressures for Visual Ornamentation*

Overall, there is no apparent female preference in frigatebird for the expression of the two morphological male sexual traits, gular pouch coloration and feather iridescence amplitude. The red gular pouch coloration is easily distinguishable against green vegetation, and with iridescence amplitudes of over 50% and a very narrow angle of iridescence ( $\sim 20^\circ$ ), movements will result in sharp flashes of light. In a densely populated frigatebird breeding colony, increased detectability of individuals of the correct sex, age class, and mating status may assist males in attracting female attention and assist females in homing in on the individuals of interest. We therefore suggest that gular pouch coloration and plumage iridescence have been selected for through male competition for attracting females and/or through reduced search cost to females reacting to the signals. Unlike the visual components, the acoustic components of male ornamentation showed distinct differences with mating success.

#### *Female Preference for Older Males*

The drumming of successfully mating older males had lower fundamental frequencies, indicating larger gular pouches, and these males drummed at a faster and more

constant cadence than unsuccessful males. Because we also found gular pouch size to be an age class–related trait, the possible female preference for lower frequencies indicates that females prefer older males, even within the oldest age class. The actual age span of this age class is unknown, but a report of some great frigatebirds (*Fregata minor*) being 44 years old (D. Dearborn, personal communication) does indicate that the age span might be considerable. We suggest that by choosing an older male, a female may obtain a direct benefit if older males, perhaps through more breeding experience, have higher breeding success. In frigatebirds, breeding success is greatly reduced as a result of nest usurpation by unmated males leading to loss not only of the nest but also of the egg or the chick (Reville 1988, 1991; V. Madsen, personal observation). In our breeding colony, nest usurpation happened frequently during the last one and a half months of the mating season, when nests were most abundant (V. Madsen, personal observation), and perhaps experienced males were less likely to lose the nest than inexperienced males. The indirect benefit a female may obtain through choosing an old male may be superior genes, as indicated by the higher viability of older males (i.e., an age-based indicator mechanism; Trivers 1972; Manning 1985; Kokko and Lindström 1996; Kokko 1997, 1998; but see Brooks and Kemp 2001).

Successfully mating males also drummed with a higher and more constant cadence than unsuccessful males. In another seabird, the blue petrel (*Halobaena caerulea*), signaling cadence mirrored male condition, as expressed by the body mass of the male. The call cadence thus provided females with information about male condition: heavy birds produced calls of high cadence, and light individuals produced calls of low cadence (Genevois and Bretagnolle 1994). Likewise, female swamp sparrows (*Melospiza georgiana*) showed more solicitation response to more physically demanding vocal performances, which included trills at a high cadence (Ballentine et al. 2004). Lambrechts and Dhondt (1986) found that male quality in great tits (*Parus major*), as indicated by winter dominance and survival, was negatively related to cadence shifts during the song, with only high-quality males being able to maintain a constant cadence throughout the song. We therefore suggest that drumming cadence speed and constancy in magnificent frigatebirds might reflect male stamina. High stamina might be imperative for breeding success because the incubating/brooding bird cannot leave the nest before the return of the mate. Otherwise, the nest will be lost by other males tearing it apart or taking it over. Together with female preference for older males, the preference for high stamina would probably benefit the female by ensuring that the present condition and/or quality of the male were sufficiently high. This way, males that had recently become sick would not be chosen as mates, which would be of

direct benefit to females. The predictive value of the three acoustic components of the drumming was an 82% correct classification of mating status. When reflectance wavelength of the iridescent back feathers, which is the only other variable that was found tending to vary with mating status, was included, not only did the percentage of correctly classified males increase to 84%, but the skew between groups also leveled out. This indicates that the four variables included in the model might explain most of the differences between successfully and unsuccessfully mating males in this data set, but it also points out that there are some variable(s) that remain to be identified. One such variable may be aspects of the male courtship display, or more specifically, the courting during the several-day-long pair formation period, which was not included in this study.

#### Multiple-Ornament Theory

The increase in accuracy of mating status classification, when more variables were included in the discriminant function analysis model, could indicate that females evaluated males based on multiple traits. The multiple-ornament theory states that several traits might function as either backup signals (signal same aspect of male quality) or multiple messages (signal different aspects of male quality; Møller and Pomiankowski 1993; Johnstone 1995, 1996). In magnificent frigatebirds, two of the acoustic components, the cadence and constancy of cadence, could function as indicators of present male quality, as expressed through his stamina. The plumage feature was more probably a signal of male quality at time of molt, which would be a very long-term condition measure, if back-feather molt were continuous, as observed in the tail feathers. Otherwise, it would be an indicator of condition outside the mating season, namely, during the period of molt. Finally, the third acoustic component, the fundamental frequency, could indicate overall male viability because it decreased with age class. Different traits signaling different aspects of male quality have also been found in other bird species, such as plumage and territory in yellow-browed warblers (*Phylloscopus inornatus*; Marchetti 1998), bill and plumage colors in northern cardinals (*Cardinalis cardinalis*; Jawor et al. 2003), and plumage and bower features in satin bowerbirds (*Ptilonorhynchus violaceus*; Doucet and Montgomerie 2003). The manner in which females evaluate several traits could be through composite trait preference, as found for feather features in California quail (*Callipepla californica*), where females showed preferences for several features in combination compared to the same features separately (Calkins and Burley 2003). We do not yet have direct evidence that female magnificent frigate-



birds assess any of the variables analyzed, but this will have to be tested through future manipulations.

It has recently been suggested that males have a multitude of different traits because females of different ages evaluate the males differentially (Coleman et al. 2004). In our study population, this could not be investigated because only females in adult plumage mated, so that no age class distinctions could be made in female preferences.

### Conclusion

The very nature of iridescent coloration is suggestive of it having an important role in sexual signaling, as supported by findings in starlings (*Sturnus vulgaris*) that not only does the displaying sex have higher levels of iridescence but iridescence is also displayed on especially modified or enlarged feathers (Cuthill et al. 1999). However, the striking visual effects of iridescence, together with the low cost of its components, melanin and keratin, pointedly pose the question of what information it may provide. We show here that a modified goniometer (figs. 1, 2; Osorio and Ham 2002) measures iridescent reflectance reliably and efficiently, so as to identify maximum reflectance and the effects of small changes in viewing angle, and we commend the method for characterizing iridescent plumage. Whereas the acoustic signal is a good predictor of mating success, the apparent absence or weakness of any correlation of iridescent coloration on the back plumage with measures of age, size, and mating success is therefore noteworthy. Nonetheless, given that morphological and ornamental development continues beyond the juvenile stage, we believe that magnificent frigatebirds might be a good subject for investigating multicomponent displays and age-related male strategies with regard to resource allocation between current and future reproductive effort (e.g., Roff 1992; Gustafsson et al. 1995) and optimal lifetime advertisement strategies (e.g., Kokko 1997).

### Acknowledgments

We thank A. Bennett and M. Théry for their great work with this special issue and the Center for Sound Communication at the Animal Behaviour Group, Institute of Biology, for support with equipment for fieldwork and analyses. V.M. was funded by a PhD fellowship from Universidad Nacional Autónoma de México (UNAM), and the practical expenses were funded by the Danish Research Agency. Some support was also received by J.L.O. from the Instituto de Ecología, UNAM, and Consejo Nacional de Ciencia y Tecnología (grant 34899-V). D.O. was supported by the Biotechnology and Biological Sciences Research Council and wishes to thank A. Ham for her help and advice. T. J. S. Balsby, D. Dearborn, A. W. Diamond,

J. Hadfield, K. Renton, and several anonymous referees provided fruitful ideas and comments to earlier drafts of this article. We are grateful to the numerous international volunteers that enthusiastically assisted V.M. with her fieldwork throughout the years, with special mention of F. C. Joelving, who assisted with the recordings in 2001, and C. Schlögl, who assisted twice in the fieldwork and who supplied invaluable data from the spring period during his first 6 months' stay. We thank the administrators of the national park Isla Isabel (Secretaría del Medio Ambiente y Recursos Naturales) for permissions and logistic support and the fishermen of San Blas for their company and support on the island.

### Literature Cited

- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.
- Andersson, S. 1999. Morphology of UV reflectance in a whistling-thrush: implications for the study of structural color signaling in birds. *Journal of Avian Biology* 30:193–204.
- Andersson, S., and T. Amundsen. 1997. Ultraviolet color vision and ornamentation in bluethroats. *Proceedings of the Royal Society B: Biological Sciences* 264:1587–1591.
- Andersson, S., J. Örnberg, and M. Andersson. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B: Biological Sciences* 265:445–450.
- Avisoft. 2002. Avisoft SASLab Pro sound analysis and synthesis laboratory. Version 4.15. Avisoft, Berlin.
- Badyaev, A. V., and G. E. Hill. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnean Society* 69:153–172.
- Ballentine, B., and G. E. Hill. 2003. Female mate choice in relation to structural plumage coloration in blue grosbeaks. *Condor* 105: 593–598.
- Ballentine, B., J. Hyman, and S. Nowicki. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology* 15:163–168.
- Bennett, A. T. D., I. C. Cuthill, and K. J. Norris. 1994. Sexual selection and the mismeasure of color. *American Naturalist* 144:848–860.
- Bennett, A. T. D., I. C. Cuthill, J. C. Partridge, and K. Lunau. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proceedings of the National Academy of Sciences of the USA* 94: 8618–8621.
- Brooks, R., and D. J. Kemp. 2001. Can older males deliver the good genes? *Trends in Ecology & Evolution* 16:308–313.
- Buchholtz, R. 1995. Female choice, parasite load and male ornamentation in wild turkeys. *Animal Behaviour* 50:929–943.
- Calkins, J. D., and N. T. Burley. 2003. Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Animal Behaviour* 65:69–81.
- CIE. 1976. Colorimetry: official recommendations of the International Commission on Illumination. CIE, Paris.
- Coleman, S. W., G. L. Patricelli, and G. Borgia. 2004. Variable female preferences drive complex male display. *Nature* 428:742–745.
- Cotton, S., K. Fowler, and A. Pomiankowski. 2004. Do sexual ornaments demonstrate heightened condition-dependent expression

- as predicted by the handicap hypothesis? *Proceedings of the Royal Society B: Biological Sciences* 271:771–783.
- Cuthill, I. C., A. T. D. Bennett, J. C. Partridge, and E. J. Maier. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *American Naturalist* 153:183–200.
- Dearborn, D. C., and M. J. Ryan. 2002. A test of the Darwin-Fisher theory for the evolution of male secondary sexual traits in monogamous birds. *Journal of Evolutionary Biology* 15:307–313.
- Dearborn, D. C., A. D. Anders, and P. G. Parker. 2001. Sexual dimorphism, extrapair fertilizations, and operational sex ratio in great frigatebirds (*Fregata minor*). *Behavioral Ecology* 12:746–752.
- Delhey, K., A. Johnsen, A. Peters, S. Andersson, and B. Kempenaers. 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (*Parus caeruleus*). *Proceedings of the Royal Society B: Biological Sciences* 270:2057–2063.
- Diamond, A. W. 1973. Notes on the breeding biology and behaviour of the magnificent frigatebird. *Condor* 75:200–209.
- . 1975. Biology and behaviour of frigatebirds *Fregata* spp. on Aldabra Atoll. *Ibis* 117:302–323.
- Doucet, S. M., and R. Montgomerie. 2003. Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behavioral Ecology* 14:503–509.
- Dyck, J. 1976. Structural colors. *Proceedings of the International Ornithological Congress* 16:426–437.
- Figuerola, J., J. Domènech, and J. C. Senar. 2003. Plumage color is related to ectosymbiont load during moult in the serin, *Serinus serinus*: an experimental study. *Animal Behaviour* 65:551–557.
- Fox, D. L. 1976. *Animal biochromes and structural colors*. Cambridge University Press, Cambridge.
- Genevois, F., and V. Bretagnolle. 1994. Male blue petrels reveal their body mass when calling. *Ethology Ecology and Evolution* 6:377–383.
- Gray, D. A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. *American Naturalist* 148:453–480.
- Gustafsson, L., A. Qvarnström, and B. C. Sheldon. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature* 375:311–313.
- Harrison, P. 1985. *Seabirds: an identification guide*. Rev. ed. Helm, London.
- Hart, N. S. 2001. The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research* 20:675–703.
- Hausmann, F., K. E. Arnold, N. J. Marshall, and I. P. F. Owens. 2003. Ultraviolet signals in birds are special. *Proceedings of the Royal Society B: Biological Sciences* 270:61–67.
- Hill, G. E. 2000. Energetic constraints on expression of carotenoid-based plumage colorations. *Journal of Avian Biology* 31:559–566.
- Hill, G. E., and R. Montgomerie. 1994. Plumage color signals nutritional condition in the house finch. *Proceedings of the Royal Society B: Biological Sciences* 258:47–52.
- Hill, G. E., S. Doucet, and R. Buchholz. 2005. The effect of coccidial infection on iridescent plumage coloration in wild turkeys. *Animal Behaviour* 69:387–394.
- Holder, K., and R. Montgomerie. 1993. Context and consequences of comb displays by male rock ptarmigan. *Animal Behaviour* 45:457–470.
- Hunt, S., A. T. D. Bennett, I. C. Cuthill, and R. Griffiths. 1998. Blue tits are ultraviolet tits. *Proceedings of the Royal Society B: Biological Sciences* 265:451–455.
- Hunt, S., I. C. Cuthill, A. T. D. Bennett, and R. Griffiths. 1999. Preferences for ultraviolet partners in the blue tit. *Animal Behaviour* 58:809–815.
- Jakob, E. M., S. D. Marshall, and G. W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77:61–67.
- Jawor, J. M., S. U. Linville, S. M. Beall, and R. Breitwisch. 2003. Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). *Behavioral Ecology* 14:515–520.
- Johnsen, A., S. Andersson, J. Örnborg, and J. T. Lifjeld. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. *Proceedings of the Royal Society B: Biological Sciences* 265:1313–1318.
- Johnsen, A., K. Delhey, S. Andersson, and B. Kempenaers. 2003. Plumage color in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proceedings of the Royal Society B: Biological Sciences* 270:1263–1270.
- Johnstone, R. A. 1995. Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology* 177:87–94.
- . 1996. Multiple displays in animal communication: “backup signals” and “multiple messages.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 351:329–338.
- Keyser, A. J., and G. E. Hill. 1999. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society B: Biological Sciences* 266:771–777.
- . 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* 11:202–209.
- Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* 41:99–107.
- . 1998. Good genes, old age and life-history trade-offs. *Evolutionary Ecology* 12:739–750.
- Kokko, H., and J. Lindström. 1996. Evolution of female preference for old mates. *Proceedings of the Royal Society B: Biological Sciences* 263:1533–1538.
- Komdeur, J., M. Oorebeek, T. van Overveld, and I. C. Cuthill. 2005. Mutual ornamentation, age and reproductive performance in the European starling. *Behavioral Ecology* 16:805–817.
- Lambrechts, M., and A. A. Dhondt. 1986. Male quality, reproduction, and survival in the great tit (*Parus major*). *Behavioral Ecology and Sociobiology* 19:57–63.
- Land, M. F. 1972. The physics and biology of animal reflectors. Pages 75–106 in J. A. V. Butler and D. Noble, eds. *Progress in biophysics and molecular biology*. Pergamon, Oxford.
- Land, M. F., and D.-E. Nilsson. 2002. *Animal eyes*. Chap. 6. Oxford University Press, Oxford.
- Ligon, J. D. 1999. *The evolution of avian breeding systems*. Oxford University Press, Oxford.
- Ligon, J. D., and P. W. Zwartjes. 1995. Ornate plumage of male red jungle fowl does not influence female mate choice. *Animal Behaviour* 49:117–125.
- Ligon, J. D., R. Thornhill, M. Zuk, and K. Johnson. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in red jungle fowl. *Animal Behaviour* 40:367–373.
- Limbou, T., A. C. Mateman, S. Andersson, and C. M. Lessels. 2003. Female blue tits adjust parental effort to manipulated male UV attractiveness. *Proceedings of the Royal Society B: Biological Sciences* 271:1903–1908.
- Machmer, M. M., H. Esselink, C. Steeger, and R. C. Ydenberg. 1992.

- The occurrence of fault bars in the plumage of nestling ospreys. *Ardea* 80:261–272.
- Madsen, V. 2005. Female mate choice in the magnificent frigatebird (*Fregata magnificens*). PhD diss. Universidad Nacional Autónoma de México, Mexico City.
- Madsen, V., T. J. S. Balsby, T. Dabelsteen, and J. L. Osorno. 2004. Bimodal signalling of a sexually selected trait: gular pouch drumming in the magnificent frigatebird. *Condor* 106:157–161.
- Madsen, V., G. Valkiunas, T. A. Izhova, C. Mercade, M. Sanchez, and J. L. Osorno. Forthcoming. Testosterone levels and gular pouch coloration in courting magnificent frigatebird (*Fregata magnificens*): variation with age-class, visited status and blood parasite infection. *Hormones and Behavior*.
- Manning, J. T. 1985. Choosy females and correlates of male age. *Journal of Theoretical Biology* 116:349–354.
- Marchetti, K. 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Animal Behaviour* 55:361–376.
- McDonald, D. B. 1989. Cooperation under sexual selection: age-graded changes in a lekking bird. *American Naturalist* 134:709–730.
- McGraw, K. J., and G. E. Hill. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society B: Biological Sciences* 267:1525–1531.
- McGraw, K. J., E. A. Mackillop, J. Dale, and M. E. Hauber. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology* 205:3747–3755.
- McGraw, K. J., J. Dale, and E. A. Mackillop. 2003. Social environment during moult and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 53:116–122.
- Møller, A. P., and A. Pomiankowski. 1993. Why have birds got multiple ornaments? *Behavioral Ecology and Sociobiology* 32:167–176.
- Mollon, J. D. 2001. The origins of modern color science. Pages 1–39 in S. Shevell, ed. *The science of color*. Elsevier, New York.
- Mountjoy, D. J., and R. E. Lemon. 1996. Female choice for complex song in the European starling: a field experiment. *Behavioral Ecology and Sociobiology* 38:65–71.
- Murphy, M. E., B. T. Miller, and J. R. King. 1989. A structural comparison of faultbars with feather defects known to be nutritionally induced. *Canadian Journal of Zoology* 67:1311–1317.
- Negro, J. J., J. L. Tella, G. Blanco, M. G. Forero, and J. Garrido-Fernández. 2000. Diet explains interpopulation variation of plasma carotenoids and skin pigmentation in nestling white storks. *Physiological and Biochemical Zoology* 73:97–101.
- Negro, J. J., J. M. Grande, J. L. Tella, J. Garrido, D. Hornero, J. A. Donazar, J. A. Sanchez-Zapata, J. R. Benítez, and M. Barcell. 2002. An unusual source of essential carotenoids. *Nature* 416:807–808.
- Nelson, J. B. 1975. Breeding biology of frigatebirds: a comparative review. Pages 113–155 in D. A. Lancaster, ed. *The living bird*. Laboratory of Ornithology at Cornell University, Ithaca, NY.
- Orta, J. 1992. Family Fregatidae (frigatebirds). Pages 362–374 in J. del Hoyo, A. Elliott, and J. Sargatal, eds. *Handbook of the birds of the world*. Lynx, Barcelona.
- Osorio, D., and A. D. Ham. 2002. Spectral reflectance and directional properties of structural coloration in bird plumage. *Journal of Experimental Biology* 205:2017–2027.
- Osorno, J. L. 1996. Evolution of breeding behaviour in the magnificent frigatebird: copulatory pattern and parental investment. PhD diss. University of Florida, Gainesville.
- . 1999. Offspring desertion in the magnificent frigatebird: are males facing a trade-off between current and future reproduction? *Journal of Avian Biology* 30:335–341.
- Osorno, J. L., and T. Székely. 2004. Sexual conflict and parental care in magnificent frigatebirds: full compensation by deserted females. *Animal Behaviour* 68:337–342.
- Owens, I. P. F., and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society B: Biological Sciences* 265:397–407.
- Papeschi, A., F. Briganti, and F. Dessi-Fulgheri. 2000. Winter androgen levels and wattle size in male common pheasants. *Condor* 102:193–197.
- Prum, R. O., and R. Torres. 2003. Structural coloration of avian skin: convergent evolution of coherently scattering dermal collagen arrays. *Journal of Experimental Biology* 206:2409–2429.
- Prum, R. O., R. H. Torres, S. Williamson, and J. Dyck. 1998. Coherent light scattering by blue feather barbs. *Nature* 396:28–29.
- . 1999. Two-dimensional Fourier analysis of the spongy medullary keratin of structurally colored feather barbs. *Proceedings of the Royal Society B: Biological Sciences* 266:13–22.
- Reville, B. J. 1988. Effects of spacing and synchrony on breeding success in the great frigatebird (*Fregata minor*). *Auk* 105:252–259.
- . 1991. Nest spacing and breeding success in the lesser frigatebird (*Fregata ariel*). *Condor* 93:555–562.
- Rice, W. R. 1989. Analysing tables of statistical tests. *Evolution* 43:223–225.
- Richardson, D. S., and T. Burke. 1999. Extra-pair paternity in relation to male age in Bullock's orioles. *Molecular Ecology* 8:2115–2126.
- Rintamäki, P. T., J. Höglund, E. Karvonen, R. V. Alatalo, N. Björklund, A. Lundberg, O. Rätti, and J. Vouti. 2000. Combs and sexual selection in black grouse (*Tetrao tetrix*). *Behavioral Ecology* 11:465–471.
- Roff, D. A. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29:593–610.
- . 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist* 22:531–546.
- Rohwer, S., S. D. Fretwell, and D. M. Niles. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *American Naturalist* 115:400–437.
- Roper, T. J. 1986. Badges of status in avian societies. *New Scientist* 109:38–40.
- Ryan, M. J., and A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. *American Naturalist* 139(suppl.):S4–S35.
- SAS Institute. 1989–1997. *JMP*. Version 3.2.1. SAS Institute, Cary, NC.
- Senar, J. C., M. Camerino, J. L. Copete, and N. B. Metcalfe. 1993. Variation in black bib of the Eurasian siskin (*Carduelis spinus*) and its role as a reliable badge of dominance. *Auk* 110:924–927.
- Senar, J. C., J. Figuerola, and J. Domènech. 2003. Plumage coloration and nutritional condition in the great tit *Parus major*: the roles of carotenoids and melanins differ. *Naturwissenschaften* 90:234–237.
- Sheldon, B. C., S. Andersson, S. C. Griffith, J. Örnberg, and J. Sen-decka. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402:874–877.
- Siefferman, L., and G. E. Hill. 2003. Structural and melanin color-

- ation indicate parental effort and reproductive success in male eastern bluebirds. *Behavioral Ecology* 14:855–861.
- Siitari, H., and E. Huhta. 2002. Individual color variation and male quality in pied flycatchers (*Ficedula hypoleuca*): a role of ultraviolet reflectance. *Behavioral Ecology* 13:737–741.
- Smiseth, P. T., J. Örnborg, S. Andersson, and T. Amundsen. 2001. Is male plumage reflectance correlated with paternal care in blue-throats? *Behavioral Ecology* 12:164–170.
- Spurrier, M. F., M. S. Boyce, and B. F. J. Manly. 1991. Effects of parasites on mate choice by captive sage grouse. Pages 389–398 in J. E. Loye and M. Zuk, eds. *Bird-parasite interactions: ecology, evolution and behaviour*. Oxford University Press, Oxford.
- StatSoft. 1993. *Statistica for Windows*. Release 4.3. StatSoft, Tulsa, OK.
- Stokkan, K.-A. 1979. Testosterone and daylength-dependent development of comb size and breeding plumage of male willow ptarmigan (*Lagopus lagopus lagopus*). *Auk* 96:106–115.
- Sundberg, J., and A. Dixon. 1996. Old, colorful male yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations. *Animal Behaviour* 52:113–122.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man 1871–1971*. Aldine, Chicago.
- Tschirren, B., P. S. Fitze, and H. Richner. 2003. Proximate mechanisms of variation in the carotenoid-based plumage coloration of nestling great tits (*Parus major* L.). *Journal of Evolutionary Biology* 16:91–100.
- Vorobyev, M. 2003. Colored oil droplets enhance color discrimination. *Proceedings of the Royal Society B: Biological Sciences* 270:1255–1261.
- Wetton, J. H., T. Burke, D. T. Parkin, and E. Cairns. 1995. Single-locus DNA fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow (*Passer domesticus*). *Proceedings of the Royal Society B: Biological Sciences* 260:91–98.
- Zi, J., X. Yu, Y. Li, X. Hu, C. Xu, X. Wang, X. Liu, and R. Fu. 2003. Coloration strategies in peacock feathers. *Proceedings of the National Academy of Sciences of the USA* 100:12576–12578.
- Zuk, M., R. Thornhill, and J. D. Ligon. 1990a. Parasites and mate choice in red jungle fowl. *American Zoologist* 30:235–244.
- Zuk, M., R. Thornhill, J. D. Ligon, K. Johnson, S. Austad, S. Ligon, N. W. Thornhill, and C. Costin. 1990b. The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. *American Naturalist* 136:458–473.
- Zuk, M., T. S. Johnsen, and T. Maclarty. 1995. Endocrine-immune interactions, ornaments and mate choice in red jungle fowl. *Proceedings of the Royal Society B: Biological Sciences* 260:205–210.

Symposium Editors: Andrew T. D. Bennett and Marc Théry