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White Ibis integument color during the breeding season

Julie A. Heath[1] and Peter C. Frederick

Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611-0430 USA

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ABSTRACT. Many birds undergo bare part color changes during the breeding season. Most investigators have focused on color as a signal of individual quality. An alternative, but not exclusive, function of bare part color may be signaling readiness to breed, especially in colonial, asynchronous breeders. White Ibises (*Eudocimus albus*) are colonial waterbirds that show vivid bare part colors on their bills and legs during reproduction. We quantified bill and leg colors to describe color changes and their possible relationship to reproductive status during the breeding season of White Ibises in the Florida Everglades from 1998 to 2001. We also examined the correlation between bare part colors and circulating concentrations of sex steroids to understand the factors that regulate bare part colors. During the display stage, male and female ibises developed dark pink bills and scarlet legs. As the breeding season progressed, bills and legs faded and developed a muted pink hue. The bare part colors of female ibises were correlated with testosterone concentrations, but those of male ibises were not correlated with any hormones. A discriminant function analysis based on principal component scores (representing variation in saturation and hue) and the amount of black on the bill successfully classified ibis reproductive stage 94% of the time. The use of bare part colors to determine reproductive status may be useful for studying reproduction in colonially nesting birds, where access to breeding sites can be difficult and potential for researcher disturbance is high.

SINOPSIS. **Color del integumento en *Eudocinus albus* durante la época de reproducción**
Muchas aves experimentan cambios en la coloración de sus partes desnudas durante la época de reproducción. Muchos investigadores han enfocado el asunto como una señal de la calidad de los individuos. Una alternativa, aunque no exclusiva, es que la función del cambio en coloración puede ser una señal para indicar, que se está listo para reproducirse, particularmente en aves coloniales que anidan asincrónicamente. Cuantificamos el color del pico y las patas del ibis, *Eudocimus albus*, para determinar si los colores en la partes desnudas correlacionaban con niveles de esteroides sexuales y si los cambios en coloración podían ser utilizados para clasificar el estado reproductivo de aves capturadas lejos de sus nidos. Durante la fase de cortejo, tanto el macho como la hembra de ibis desarrollan una coloración rosada en el pico y escarlata en las patas. Con el progreso de la época de reproducción, la coloración se hace más pálida y cambia a rosado tenue. Las partes desnudas de las hembras presentaron una correlación con los niveles de testosterona, pero los cambios en los machos no correlacionaron para ninguna hormona. Una análisis de función discriminativa y la cantidad de negro en el pico permitieron clasificar la etapa reproductiva de los aves,correctamente, en el 94% de las veces. El uso de la coloración en partes desnudas de aves para determinar su estado reproductivo, pudiera ser de utilidad para estudiar la reproducción de especies coloniales en donde los lugares de reproducción sean de difícil acceso o en donde la potencialidad de disturbio por parte del investigador sea muy grande.

Key words: bare part, capture technique, carotenoid, Ciconiiformes, hormone, signal

In many bird species, the color of the unfeathered portions of the integument, including the cere, bill, and legs, becomes more vivid during the breeding season (Burley et al. 1992, Negro et al. 1998). Most studies of integument color have focused on color as a signal of individual quality and, therefore, a component of mate choice. Specifically, color may indicate access to food resources (Hill 1995) or an ability to withstand health challenges (Lozano 1994, Blount et al. 2003, Faivre et al. 2003). Support for these hypotheses has come from direct immunocompetence tests (Faivre et al. 2003, McGraw and Ardia 2003) and in the form of mate choice, because females of some species often choose males with bright colors over duller males (Burley et al. 1992, Blount et al. 2003). An alternative, but not exclusive, hypothesis is that rapidly changing integument, or bare part, colors signal readiness to breed (Baltz and Clark 1996). This may be especially important in species that nest colonially or asynchronously.

Many wading birds, such as ibises, egrets, and herons (Ciconiiformes), are colonial nesters and show both plumage and bare part color changes during the breeding season (McVaugh 1972, Rodgers 1978, 1980). Such changes in bare part

[1] Current address: Biology Department, Hofstra University, Hempstead, New York 11549 USA. Email: biojah@hofstra.edu

colors tend to be brief (1–2 weeks) and involve bills and legs becoming a more brilliant yellow or red. Carotenoid pigments that create yellow, orange, and red colors in bare parts (and feathers) are obtained in the diet (Trams 1969, Fox 1976). However, the factors that regulate carotenoid deposition in bare parts remain poorly understood (McGraw et al. 2003). Color changes could be the result of shifts in diet content or quantity, or seasonal changes in metabolism (Trams 1969, Negro et al. 1998, 2000), or changing hormone concentrations (Kimball and Ligon 1999, McGraw et al. 2003).

A number of studies have demonstrated that sex steroids can affect feather coloration (reviewed by Kimball and Ligon 1999). For example, captive House Finches (*Carpodacus mexicanus*) with elevated plasma testosterone (T) concentrations had drabber plumage than control birds even though both groups were given dietary carotenoid supplements (Stoehr and Hill 2001). In other groups (e.g., Anseriformes), high estradiol (E_2) concentrations caused dull coloration, but the absence of E_2 resulted in brightly colored birds (Haase and Schmedemann 1992, Owens and Short 1995). Bare part colors may similarly be affected by circulating hormone concentrations, and bare part color can presumably change more rapidly than feather colors because it does not require the molt of new feathers. If dependent on changing hormone concentrations, bare part coloration might serve as a sensitive indicator of short-term changes in reproductive development.

Seasonal variation in bill and leg colors could also serve as a tool for biologists to classify the reproductive stage of birds, because color changes may progress in a predictable fashion throughout the breeding season. If so, this may allow investigators to avoid invasive techniques, such as capturing adult birds on or near the nests, which may cause temporary or permanent nest abandonment (Jewell and Bancroft 1991). Instead, investigators could capture birds away from the nests, identify the birds' nesting stage from bare part color, and relate physiological or behavioral activities to reproductive condition. The ability to accurately classify birds to reproductive stage requires development of an empirically derived predictive model.

The White Ibis (*Eudocimus albus*) is a colonially breeding, wading bird that feeds on small fish and crayfish (*Procambarus* spp.). These prey items are the most likely source of the carotenoids that affect ibis bare part colors (Trams 1969, Negro and Garrido-Fernandez 2000). During the breeding season, males and females display dramatic changes in bill and leg color. Early in the season, ibises develop red bills and legs. As nesting progresses, these colors fade and the distal portion of the bill turns black (Bildstein 1993). In this article, we quantitatively describe the color changes of White Ibis bills and legs during the breeding season, explore the hormonal correlates of color changes, and develop a model based on bill and leg colors to classify the reproductive stage of White Ibises captured away from the nests.

METHODS

The breeding season of White Ibises consists of five distinct stages based on adult behavior and physiology: prebreeding, display, copulation and egg production, incubation, and chick rearing. The display stage, when birds perform display flights and choose mates, lasts approximately 10 d (Kushlan and Bildstein 1992). Copulation occurs toward the end of display stage and continues during nest building and egg production. Nest building begins during the end of the display stage and continues into the beginning of the egg-production stage. Copulation and egg production occur over approximately the next 10 d. During this time, male ibises stay at the colony to guard the nests and mates and do not make regular foraging trips (Kushlan and Bildstein 1992). Females lay eggs every other day until they complete a clutch of 2 to 4 eggs. Male and female ibises incubate the eggs beginning with the laying of the last egg. Incubation lasts about 3 weeks, and both sexes contribute to chick rearing by brooding and feeding the chicks. Chick rearing continues for approximately 6 weeks.

From January–June 1998–2001, prebreeding and breeding adult White Ibises were captured with mist nets or a rocket net at foraging sites away from colonies in Water Conservation Areas 1 and 3 of the Everglades (Heath 2002, Heath and Frederick 2003). We determined sex based on either size or laparoscopy (Heath et al. 2003). Twenty-seven birds were marked with a radio-transmitter, and all but one of these birds were relocated at a colony in the study area. Prebreeding birds ($N = 15$) were

defined as either those captured prior to nesting activity within the Water Conservation Areas or those that showed no external and internal (via laparoscopy) signs of reproductive activity. Ibises in display stage ($N = 13$) were defined as birds that had begun to attend colonies, birds with distended gular pouches, or both (Bildstein 1993). Female ibises in the egg-production stage ($N = 11$) were identified by palpating the abdomen or via laparoscopy (Heath et al. 2003). In one case, a male ibis was located at his nest via radiotelemetry 25 d after capture. There were three chicks less than 5 d old in his nest, and we backdated to calculate that he was captured during the time his mate was laying eggs (egg-production stage).

The nesting stage of many birds captured away from the nest was determined through one or more means. Incubating birds ($N = 11$) were identified by brood patch development (Heath et al. 2003). Brood patch regression and information from radiotelemetry were used to identify chick-rearing birds ($N = 9$). For example, chick-rearing adults (1) had a bare but not highly vascularized patch of skin where the brood patch had been, (2) would return to a portion of a colony where most nests contained chicks, and (3) made many trips away from the colony for at least the following week. Ibises of known nesting stage were also captured at colonies in central Florida (Lake, Polk, and Orange counties) using a cylinder-wire-mesh nest trap designed by Frederick (1986). The nesting stage of these birds was recorded as either incubating (eggs in nest) or chick rearing (chicks in nest). In addition to the known-stage birds, we captured 50 unknown-stage birds (26 females and 24 males). These birds did not have characteristics that allowed us to be sure of their reproductive stage.

Once captured, we collected a 3-ml blood sample from the jugular vein, marked the bird with a U.S. Geological Survey aluminum band, and recorded weight and other morphological measurements. Bill and leg colors were scored by holding a paint swatch (Wal-Mart stores brand numbers 0071–1111; 100 colors total) up to the body part and recording the color that most closely resembled the bill or leg. Colors were scored away from direct sunlight and viewed with paint swatches held under the bill and leg. A similar method using the Munsell color system has proven successful for scoring bird plumage (De Repentigny et al. 1997). The amount of black on the bill (bill black) was quantified to the nearest mm by measuring the black part of the curved length from the most proximal black part of the bill to the bill tip. T, E_2, and progesterone (P) concentrations were determined by radioimmunoassay (Heath et al. 2003).

Standard color swatches that matched ibis bare parts (71 total) were scanned (Hewlett Packard ScanJet 6100C) and scored for red, blue, and green (RGB) content and hue, saturation, and brightness (HSB) using Photoshop 7.0 (Adobe). Although the HSB color scheme is easier to interpret than RGB, the scale of hue (H) is circular and hue values are angles. Hue values did not meet the multivariate-normal assumptions of the statistics used to evaluate seasonal color changes or create a discriminant function model. Therefore, we entered RGB values into a principal components analysis based on a covariance matrix to develop continuous, independent, and linear variables (principal components, PCs) that describe variations in bare part color. After interpreting the PC Eigenvectors, we compared PC scores to HSB values to clarify what each PC represented.

To determine how colors changed during the breeding season and if there were differences between the sexes in color changes, a MANOVA test was performed on color scores collected from known-stage birds ($N = 59$). For this analysis, reproductive stage and gender were the predictor variables, and scores on the PCs for bill and leg color and bill black were the response variables. The interaction terms stage and gender were not significant and were removed from the model. An *a posteriori* Tukey's test was used to compare means among groups where there were differences (Zar 1999).

To examine relationships among color and hormone concentrations, we used data collected from all ibises (known and unknown stage, $N = 109$). Separate canonical correlation analyses were performed for data collected from males and females to control for gender variation in endocrinological processes. Canonical correlation evaluates the relationships among two groups of (continuous) variables (James and McCulloch 1990). This test attempts to maximize correlations between canonical variables from each set of groups; in this case, color scores and hormone concentrations. This test allowed simultaneous examination of correlations among

all hormones, with the potential for interactive effects.

The variables with the lowest *P*-values calculated by the MANOVA (the first two PC scores for leg color, the first PC score for bill color, and the variable "bill black") were used to develop the discriminant function analysis to classify reproductive stage. All data met the assumptions of discriminant analysis (homogeneity of covariance matrices and normality; Manly 1994). Descriptive statistics are reported as mean ± 1 SE. All analyses were performed using SAS 6.12 (SAS Institute 1989) and SAS 8 (SAS Institute 1999) statistical software.

RESULTS

The first two PCs based on the RGB values obtained from the paint swatches accounted for 98% of the variation among bill and leg colors. The first PC accounted for variation in saturation (intensity) and the second PC for variation in hue (Table 1). Scores on the first PC negatively correlated with saturation values attained from the original colors (Spearman correlation, $r_s = -0.96$, $P < 0.001$). A low score on the first PC indicated a more vivid color (saturation ~100%) than a higher score (saturation ~20%). Scores on the second PC correlated with hue values of the original colors (angle-linear correlation, $r_s = 0.86$, $P < 0.001$; Zar 1999). Low scores on the second PC indicated more violet–red colors (hue values ~330°) than higher scores that represented more yellow–red colors (hue values ~30°). Each bird was assigned a score from the first two PCs for its bill and leg colors. There were four scores total: bill PC1 (bill saturation), bill PC2 (bill hue), leg PC1 (leg saturation), and leg PC2 (leg hue).

Reproductive changes. There were no differences in color (bill PC1, bill PC2, leg PC1, and leg PC2) between known-stage males ($N = 19$) and females ($N = 40$; Table 2). All ibis integument colors changed across reproductive stages (Table 2). The first PC score for leg color was significantly lower during the display and egg-production phases, and the second PC score for leg color was lower during the display stage. In other words, leg color was most vivid with a violet–red hue during the display phase. Ibis legs became muted with more of a yellow tint as the nesting season progressed (Fig. 1). In general, PC1 scores had more within-stage variation than PC2 scores for leg color (Fig. 1). First PC scores for bill color were lowest during the display and egg-production stages. Scores for the second PC were low during the display, egg-production, and incubation stages. Ibis bills were a vivid shade of pink during the display stage and faded to a light salmon color during chick rearing (Fig. 2). In addition, birds in the display stage showed the highest within-group variation in PC1 and PC2 bill colors (Fig. 2). As bill colors faded, the black tip extended from the distal to the proximal portion of the bill. Ibis bills did not have a significant amount of black until the breeding season started (Fig. 3).

Hormone concentrations and color changes. T, E_2, and P concentrations changed significantly during the breeding season (for complete review, see Heath et al. 2003). Plasma T concentrations for male and female ibises were similarly high during the display stage

Table 1. Eigenvalues and Eigenvectors (below) for principal components created from the variables red, green, and blue measured in White Ibis leg and bill colors ($N = 71$).

Principal component	Eigenvalue	Difference	Proportion	Cumulative
PC1	5852.83	5251.58	0.89	0.89
PC2	601.25	448.74	0.09	0.98
PC3	152.51		0.02	1.00
		Eigenvectors		
Color	PRIN1	PRIN2		PRIN3
Red	0.162	0.501		0.850
Green	0.687	0.561		−0.462
Blue	0.708	−0.659		0.253

Table 2. Effect of reproductive stage and sex of White Ibises on principal component scores for leg and bill colors and amount of black on the bill.

Source	df	SS	*F*	MANOVA *P*
ANOVA: Leg PC1				
Stage	4	1,15,323.01	16.24	0.0001*
Sex	1	273.06	0.15	0.69
Error	45	80,049.89		
ANOVA: Leg PC2				
Stage	4	2906.85	10.77	0.0001*
Sex	1	118.05	1.41	0.24
Error	45	3759.38		
ANOVA: Bill PC1				
Stage	4	59,032.74	9.50	0.0001*
Sex	1	241.38	0.61	0.69
Error	45	69,920.99		
ANOVA: Bill PC2				
Stage	4	2251.20	4.62	0.0052*
Sex	1	89.29	0.68	0.41
Error	45	5942.65		
ANOVA: Black on bill				
Stage	4	2.91	18.68	0.0001*
Sex	1	0.02	0.55	0.46
Error	45	1.75		

Source	Wilk's λ	*F*	Num df	Denom df	*P*
MANOVA: Leg PC1, Leg PC2, Bill PC1, Bill PC2, and black on bill					
Stage	0.063	10.89	20	167	0.0001**
Sex	0.919	0.72	5	41	0.61

* Significant at $\alpha = 0.01$.

** Significant MANOVA result for the effect of stage, the Bonferroni adjusted $\alpha = 0.01$.

(Males: 1066 ± 181 pg/ml, $N = 5$; Females: 891 ± 156 pg/ml, $N = 13$) and then decreased during egg production, incubation, and chick rearing (Heath et al. 2003). Female ibises' E_2 concentrations tended to be higher during display and chick-rearing than during prebreeding, egg-production, and incubation stages. Males had low E_2 concentrations through egg production, then E_2 concentrations increased during incubation and chick rearing. Female plasma P concentrations increased significantly from prebreeding to the display stage and then were maintained at intermediate concentrations throughout egg production, incubation, and chick rearing. Male ibises showed no changes in plasma P concentrations during the breeding season.

Color changes of female ibises were correlated with T concentrations (Wilk's $\lambda F_{12,85} = 2.78$, $P = 0.003$; Table 3). The first canonical correlation indicated a relationship between T and the first PC score for leg color and the second PC score for bill color (Tables 4 and 5).

These relationships were not as clear for male ibises. None of the canonical correlations approached significance (Wilk's λ $F_{12,56} = 0.65$, $P = 0.61$). Furthermore, none of the canonical variables explained a significant amount of variation among any of the variables.

Classification model. Six ibises were captured on their nests. An additional 53 were captured away from the nest, but had distinctive characteristics that indicated their stage of reproduction (i.e., large gular pouch or egg in oviduct). We used data from these 59 known-stage birds to create a discriminant function model. Four variables (bill PC2, leg PC1, leg PC2, and black on bill) contributed to three significant canonical variables (Table 6). The model correctly identified the stage of reproduction 94% of the time (resubstitution validation; Fig. 4; Manly 1994).

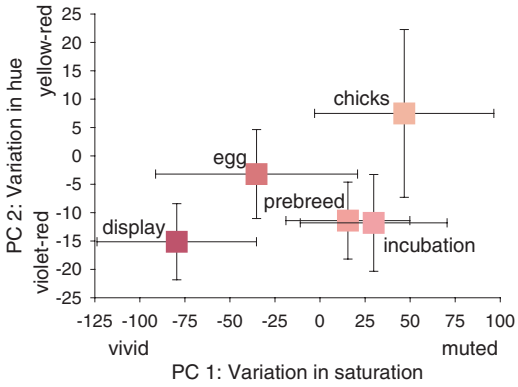

Fig. 1. Changes in White Ibis leg color during the breeding season. The first principal component scores accounts for variation in saturation. The second principal component scores accounts for variation in hue. Boxes are average principal component scores. Fill colors are the graphical representation of the average scores for each stage. Error bars represent standard deviation. During the display stage, the legs are darkest with a violet–red hue.

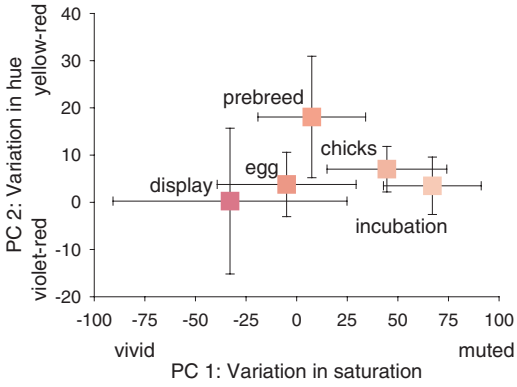

Fig. 2. Changes in White Ibis bill color during the breeding season. The first principal component scores accounts for variation in saturation. The second principal component scores accounts for variation in hue. Boxes are average principal component scores. Fill colors are the graphical representation of the average scores for each stage. Error bars represent standard deviation. During the display stage, the bills are darkest.

DISCUSSION

Male and female White Ibises exhibited color changes in their bare parts during the breeding season, which were consistent with the nesting stage. Ibises developed extended gular areas, vivid pink bills, and scarlet legs during the display stage. As the breeding season progressed, ibis bills faded and developed black tips. Male and female ibises showed similar color changes throughout the breeding season.

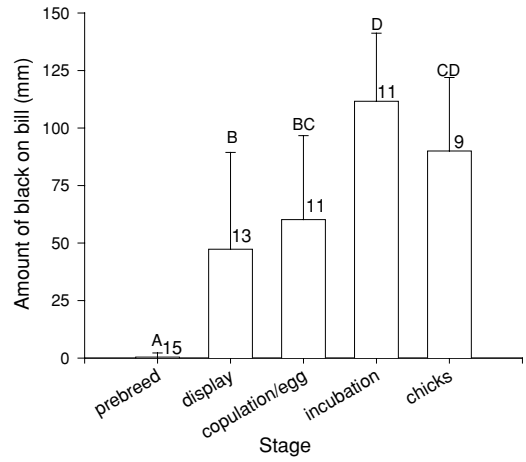

Fig. 3. Changes in the amount of black on White Ibis bills during the breeding season (mean ± 1 SD). Bills are most black during the incubation stage, as face and bill areas lose their red color. Means with the same letters are not significantly different. Sample sizes are indicated by the number at the upper right corner of the bar.

Although many bird species have different bare part coloration during breeding as compared to nonbreeding seasons, within-breeding season color changes are rarely described (but see Rodgers 1980, Burley et al. 1992). Unless color changes are dramatic (e.g., White Ibises), within-season variation in bare part color may be difficult to measure with subjective methods such as matching color swatches with bare parts. Objective measures of color quality with ultraviolet and visible wavelength spectrophotometry may permit better detection of within-season differences and quantification of color changes that are more relevant to bird vision (Hill 1998). Our study was limited to human-perceived differences in colors by our subjective scoring method. Nonetheless, we were able to detect significant differences in both saturation and hue of bare part color among reproductive stages.

The short-term, sexually monomorphic phenomenon of color changes in the bare parts of White Ibis suggests that integument color may

Table 3. Eigenvalues for the canonical correlation between hormone concentrations and color scores for female White Ibis.

Canonical correlation	Eigenvalue	Difference	Proportion	Cumulative
1	0.8645	0.6159	0.7540	0.7540*
2	0.2486	0.2152	0.2168	0.9709
3	0.0334		0.0291	1.0000

* $P < 0.05$.

Table 4. Squared multiple correlations between hormone concentrations and color scores for female White Ibis.

Hormone	Color canonical variable 1	Color canonical variable 2
Estradiol	0.0884	0.2455
Testosterone	**0.4531**	0.4558
Progesterone	0.0251	0.0251

Numbers in bold indicate large contribution to canonical variable.

Table 5. Squared multiple correlations between female White Ibis color scores and the first two canonical variables of the hormone variables.

Color score	Hormone canonical variable 1	Hormone canonical variable 2
Leg PC1	**0.3610**	0.3612
Leg PC2	0.0005	0.0369
Bill PC1	0.0587	0.1262
Bill PC2	**0.2446**	0.2629

Numbers in bold indicate large contribution to canonical variable.

act as a signal of breeding readiness. White Ibises exhibit a high amount of breeding asynchrony both within-breeding colonies and within-breeding systems (e.g., Florida Everglades). During the 4 yr of our study, nest initiations by ibises ranged from February through June each year. At feeding sites and within colonies, ibises group together with birds in a variety of reproductive stages. Thus, a visual cue such as bill and leg color changes may aid in communication of breeding readiness, because high carotenoid deposition in female bills may advertise that female birds are ready to deposit immunostimulatory carotenoids into oocytes during egg production (Baltz and Clark 1996, Vershinin 1999, Blount et al. 2000).

White Ibis bill PC1 scores (saturation) varied most during the display stage when birds were choosing mates. Such variation suggests that integument color may also serve as a signal of individual quality. Other studies have also revealed that bill color affects mate choice. Female Zebra Finches (*Taeniopygia guttata*) selected carotenoid-supplemented males with redder bills over control males (Blount et al. 2003). Carotenoid-supplemented males also had better cell-mediated immune function as compared to control birds who had not received carotenoid supplements (Blount et al. 2003). This link between immune function and female preference suggests that bill color is an indicator of mate quality. However, in some cases, birds may select mates with vivid bare part color over muted birds, because bare part color corresponds

Table 6. Eigenvalues for the canonical variables used to classify reproductive stage of White Ibis.

Canonical variable	Eigenvalue	Difference	Proportion	Cumulative
1	2.880	1.69	0.62	0.62*
2	1.185	0.57	0.25	0.87*
3	0.613	0.61	0.13	0.99*
4	0.002		0.00	1.00

* $P < 0.0001$.

Equations for canonical variables that discriminate among groups.

$Z_1 = (0.4683)$ leg PC1 $+ (0.3308)$ leg PC2 $+ (0.5258)$ bill PC2 $+ (0.6505)$ black on bill,

$Z_2 = (0.5117)$ leg PC1 $+ (0.4325)$ leg PC2 $+ (0.0575)$ bill PC2 $+ (-0.6450)$ black on bill,

$Z_3 = (0.6011)$ leg PC1 $+ (0.6511)$ leg PC2 $+ (-0.5271)$ bill PC2 $+ (0.3331)$ black on bill.

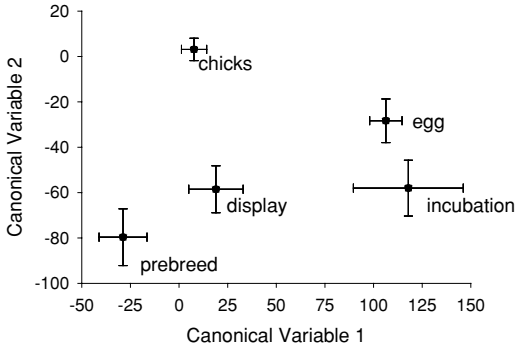

Fig. 4. Mean (±1 SE) values of canonical variables one and two created from principal component scores of White Ibis bill and leg colors during different the reproductive stages.

with reproductive condition. For example, cere color of Budgerigars (*Melopsittacus undulates*) corresponds with the level of ovary development (ceres darken as ovaries develop), and males prefer to mate with females with dark ceres (Baltz and Clark 1996). As quantification of color becomes more accurate, within-season measurements of changes in bare part color may become an important aspect of the study of sexual signaling for many bird species. Concurrent study of the physiological systems and mechanisms that underlie these changes (e.g., hormone concentrations and dietary carotenoids) should provide additional insight to the evolutionary ecology of reproductive behavior and mating systems. We predict that interactions between physiology and bare part color change may be particularly important for species with long breeding seasons or high nesting asynchrony, where birds may benefit from a visual signal of reproductive status.

Although dietary carotenoids are necessary for the development of vivid red colors (Trams 1969, Bildstein 1993), carotenoid intake was probably not the only factor affecting ibis color expression (Bortolotti et al. 1996, Negro et al. 1998). Ibises with display-stage coloration regularly foraged in the same areas as birds in other stages and did not appear to forage selectively for particular prey items. Likewise, variation in the bill pigmentation of Zebra Finches did not correspond with variation in food intake (McGraw et al. 2003). McGraw et al. (2003) suggested that other factors, such as pigment transport, may contribute more to differences in coloration.

In our study, color scores of female ibises were correlated with T concentrations, suggesting that changes in integument color may be related to hormone concentrations. Males displayed similar patterns of bare part coloration as females, but male color scores were not significantly correlated with high T concentrations. Similarly, Bortolotti et al. (1996) found that bare part coloration of male American Kestrels (*Falco sparverius*) was not correlated with androgen levels. In many birds that display secondary sexual characteristics, males and females respond similarly to T (Eens et al. 2000). Although we did not detect a significant correlation, male ibises had the most vivid and red colors during the display stage when T levels were highest. T may modulate carotenoid deposition in male bare parts, but T also plays a role in many other aspects of the male breeding cycle (Wingfield and Farner 1993, Heath et al. 2003), and the complex roles of T in White Ibis breeding biology may make correlations between bare part coloration and T difficult to detect. In addition, evidence from birds exposed to polychlorinated biphenyls suggests that thyroid hormones may also play a role in bare part coloration (Bortolotti et al. 2003). Based on endocrine control of other traits (e.g., behavior), there are likely many species- and gender-specific hormonal patterns associated with integument color.

Color changes in the bills and legs of White Ibises can be quantified and used to classify their reproductive stages. We were able to use this information to determine the reproductive stages of White Ibises captured away from the nests (Heath et al. 2003). This allowed us to identify birds that underwent physiological changes associated with reproduction and address questions concerning nonbreeding behavior and abandonment. Unfortunately, the color swatches used in our study were not standardized and the model we created to discriminate among reproductive stages will need to be recreated using a standardized set of colors. However, this does not diminish the novelty and usefulness of this technique. Other investigators may use similar color-change models, especially those based on objective spectrophotometry methods, to identify reproductive stage or other information (e.g., age or social status) that may be conveyed through plumage and integument colors.

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