Journal of Field Ornithology

J. Field Ornithol. 79(4):438–447, 2008 DOI: 10.1111/j.1557-9263.2008.00197.x

Bias in aerial estimates of the number of nests in White Ibis and Great Egret colonies

Kathryn A. Williams,[1,3] Peter C. Frederick,[1] Paul S. Kubilis,[2] and John C. Simon[1]

[1] *Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, P.O. Box 110430, Gainesville, Florida 32611, USA*

[2] *Department of Statistics, Institute of Food and Agricultural Sciences, University of Florida, 402 McCarty Hall C, P.O. Box 110339, Gainesville, Florida 32611, USA*

Received 3 December 2007; accepted 21 August 2008

ABSTRACT. Estimating detection error, as well as the magnitude of other potential survey biases, is essential when sampling efforts play a role in the estimation of population size and management of wildlife populations. We quantified visual biases in aerial surveys of nesting wading birds (Ciconiiformes) in colonies in the Florida Everglades using a negative binomial count regression model to compare numbers of nests in quadrats counted on the ground with numbers estimated from aerial photographs of the same quadrats. The model also allowed the determination of degree of difference between monitoring results based upon such factors as nest density, vegetative cover, and nest turnover rates. Aerial surveys of White Ibis (*Eudocimus albus*) colonies underestimated the true number of nests found during ground counts by 11.1%, and underestimates were significantly greater ($P = 0.047$) in a colony with high nest turnover. Error rates did not differ for quadrats that varied in the density of White Ibis nests did not differ, and visual bias did not increase with vegetative complexity ($P = 0.73$). Estimates of nest density in colonies of Great Egrets (*Ardea alba*) based on aerial surveys were higher than ground counts for 38% of the quadrats sampled, and mean visual bias was 23.1%. Species misidentification likely contributed to visibility bias for Great Egrets in our study, with some Snowy Egrets almost certainly mistaken for Great Egrets in aerial photos. Biases of the magnitude we observed fro Great Egrets and White Ibises can mask true population trends in long-term monitoring and, therefore, we recommend that detection probability be explicitly evaluated when conducting aerial surveys of nesting birds.

SINOPSIS. **Los errores asociados con el muestreo aéreo del numero de nidos en colonias de *Eudocimus albus* y *Ardea alba***

Es esencial poder estimar el error de detección, así como la magnitud de otros tipos de errores al realizar muestreos cuando estos son usados para estimar el tamaño poblacional y manejar las poblaciones. Cuantificamos los errores de observación en las muestras tomadas desde el aire de aves Ciconiiformes en colonias en los Everglades de Florida, usando un modelo de regresión binomial negativo de conteo para comparar los números de nidos en cuadrantes contadas desde la tierra con los números de nidos estimados usando fotografías aéreas de los mismos cuadrantes. El modelo también permitió la determinación del grado de diferencia entre los resultados del monitoreo basado en factores como la densidad de los nidos, cobertura de la vegetación y la tasa de renovación de nidos. Los muestreos aéreos subestimaron el verdadero numero de nidos en colonias de *Eudocimus albus* (encontradas durante conteos hechas en la tierra) por el 11.1% y estas subestimaciones fueron significativamente mas grandes ($P = 0.047$) en una colonia con una alta tasa de renovación de nidos. Las tasas de error no variaron entre los cuadrantes cuales tenían diferentes densidades de nidos de *E. albus* y el error asociado con la observación visual no incremento con la complejidad de la vegetación ($P = 0.73$). Las estimaciones de la densidad de nidos en las colonias de *Ardea alba* basadas en muestreos aéreos fueron mas altas que los conteos hechos en tierra para 38% de los cuadrantes muestreados; el error promedio de la observación visual fue 23.1%. La mal identificación de las especies probablemente contribuyó al error hecho durante observaciones visuales de *A. alba* en nuestro estudio, con algunos individuos de *Egretta thula* posiblemente identificados como *A. alba* en las fotografías aéreas. A largo plazo, los errores del tamaño que observamos en el monitoreo pueden enmascarar los patrones verdaderos de patrones poblacionales y por eso recomendamos que la probabilidad de detección sea explícitamente evaluado al tomar muestras aéreas de aves que nidifican en colonias.

Key words: *Ardea*, detectability, *Eudocimus*, Everglades, monitoring, survey, waders

Monitoring bird populations can improve our knowledge of the relationship between environmental conditions and demography and permit the use of populations as indicators of ecological change (Temple and Wiens 1989, Stolen et al. 2004). However, evaluating detection

[3]Corresponding author. Current address: BioDiversity Research Institute, 19 Flaggy Meadow Road, Gorham, Maine 04038, USA. Email: kate.williams@briloon.org

probability is essential for sampling efforts that use counts as population indices (Pollock and Kendall 1987; Rosenstock et al. 2002). Detectability has been recognized as a problem in line transects (Dodd and Murphy 1996, Bibby 2000), perimeter counts (Dodd and Murphy 1996), point counts (Bibby 2000, Nichols et al. 2000), and other types of population surveys that use vocal (Simons et al. 2007) or visual counts. Detectability can be a source of bias for several reasons, including individual heterogeneity in behavior (such as frequency of song) and distance- or habitat-related visibility.

Visual estimates based on aerial surveys may have particularly low detection probabilities (Gibbs et al. 1988, Bayliss and Yeomans 1990, Frederick et al. 2003) due to a number of potential visibility biases, including visual occlusion (nests hidden from view by the nesting substrate), high nest densities (Bayliss and Yeomans 1990, Dodd and Murphy 1995), and species misidentification (Barbraud and Gélinaud 2005, Rodgers et al. 2005). For example, Rodgers et al. (1995) found that difficulties in identifying Great Egret (*Ardea alba*) and Wood Stork (*Mycteria americana*) nests from the air led to large and highly variable estimates of bias. Gibbs et al. (1988) found that aerial surveys underestimated true numbers of Great Blue Herons by an average of 13%, and suggested that a correction factor might be used for aerial survey results.

Large colonies of nesting birds may contain a disproportionate percentage of regional breeding populations, and estimating detection bias in these colonies is, therefore, of particular interest. Large colonies may also have high nest densities, multiple species, and vegetation that may reduce nest visibility, and so may be the most likely to produce estimation biases. We examined aerial bias in estimation of numbers of Great Egret and White Ibis (*Eudocimus albus*) nests, colonial species with similar plumage and different nesting habits. Specifically, we compared estimates of the number of nests in colonies derived from both aerial surveys and ground counts in order to obtain estimates of visual bias, and the resulting estimates were used to adjust calculations of colony size. Our prediction was that, for both species, visual bias would result in an underestimation of nest numbers, and degree of error would increase with vegetative density and nest density.

METHODS

We studied Great Egrets and White Ibises in the Water Conservation Areas (WCAs) of the Florida Everglades (Broward and Palm Beach Counties, FL) from March to May 2005–2007. WCA-3A and WCA-1 are large areas of primarily sawgrass (*Cladium jamaicense*) and wet prairie in the northern and central Everglades (Fig. 1). The mixed-species colony at

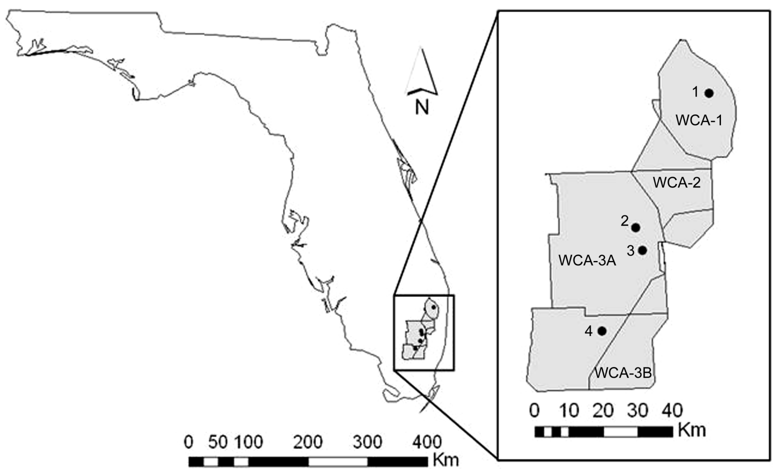

Fig. 1. South Florida and the Water Conservation Areas (WCAs), with the locations of the four colonies numbered in order from north to south. 1 = New Colony 3, 2 = Alley North, 3 = Cypress City, and 4 = Vacation Island colony.

Alley North (WCA-3A; N 26° 11.179′, W 80° 31.431′) included both species in different areas of a single large tree island, as well as Snowy Egrets (*Egretta thula*), Little Blue Herons (*Egretta caerulea*), Tricolored Herons (*Egretta tricolor*), and Black-crowned Night Herons (*Nycticorax nycticorax*). We also studied mixed-species colonies at Vacation Island (WCA-3A, N 25° 54.939′, W 80° 37.813′), Cypress City (WCA-3A, N 26° 07.468′, W 80° 30.283′), and New Colony 3, a White Ibis colony in WCA-1 (N 26° 32.013′, W 80° 17.879′). The emergent woody vegetation in all colonies was mainly willow (*Salix caroliniana*), with a few pond apples (*Anona glabra*). White Ibises at Alley North also nested in cattail (*Typha latifolia*) clumps on the outskirts of the tree island.

Colony-wide counts. Aerial surveys were conducted monthly (January–June 2005–2007) using a Cessna Skyhawk (172) high-wing aircraft (speed approximately 177 kph, altitude 244 m). During surveys, each colony was photographed (Canon EOS 20D, 28–135 mm image stabilizing lens) and photographs were subsequently analyzed with Adobe Photoshop Elements 2.0 or Paint.Net 2.0. The largest single-month count for each colony and species was defined as the maximum (peak) count. Such counts are commonly used to estimate minimum breeding populations for wading birds in the Everglades (Ogden 1994, Cook and Call 2006). Peak counts were later adjusted with species-specific (Great Egret) or colony-specific (White Ibis) estimates of visibility bias to create estimates of minimum population breeding size for each colony.

Visibility bias. We created 21 rectangular quadrats in Great Egret and White Ibis colonies for comparison of aerial and ground counts of nests. White Ibis quadrats varied from 100 m^2 to 200 m^2, and Great Egret quadrats were either 400 m^2 or 900 m^2. Each quadrat consisted of four landmarks conspicuous enough to be seen from the aircraft. Markers were of four types: (1) 2–4 m^2 spots of white latex paint dispensed from a backpack sprayer, (2) white PVC crosses 1.5 m across, erected atop 3-m high PVC pipes, (3) 1 m^2 pieces of white or pale-colored cotton cloth tied to vegetation (Fig. 2), and (4) 0.5–1.5 m^2 clumps of orange vinyl flagging affixed to vegetation. We erected markers for four quadrats in the ibis colony at Alley North in 2005, 10 quadrats in Alley North (four egret and six ibis) and seven ibis quadrats in New Colony 3 in 2006, and two egret quadrats in Cypress City and two in Vacation Island in 2007. During

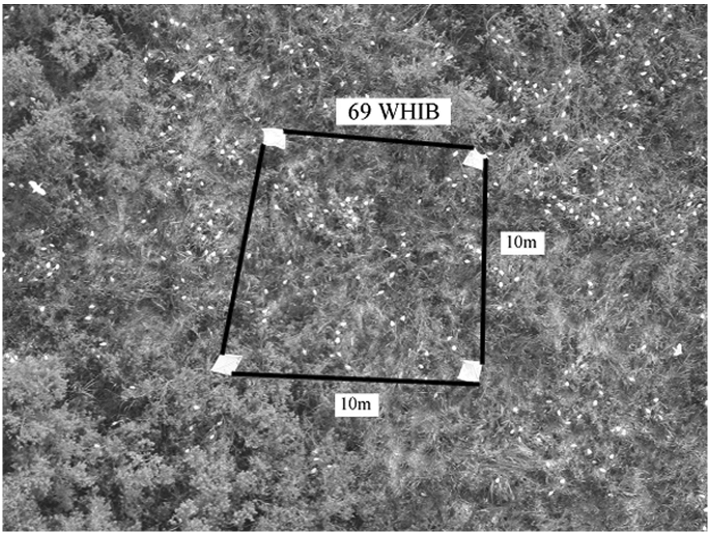

Fig. 2. A 10 × 10 m White Ibis quadrat at Alley North colony in WCA-3A (7 April 2006). White dots in photograph are adult ibises incubating nests. The ground count for this quadrat was 72 nests, and the aerial count from this photograph was 69 nests. Written labels and lines between the four artificial markers were inserted into the photograph using Adobe Photoshop Elements v. 2.0.

ground counts (30–90 min), we marked and counted each nest in a quadrat, and tied vinyl flagging to vegetation between corner markers. This flagging could usually be seen in aerial photographs, permitting delineation of quadrat edges during photographic analysis.

Within 24–36 h of ground counts, we photographed quadrats from the air at an altitude of 152 m (Canon EOS 20D, 28–135 mm image stabilizing lens). The door was removed on the copilot's side of the aircraft to shoot vertically, and photographs were analyzed using the same procedure as with colony-wide counts. On the computer screen, we delineated quadrat edges using colored lines (Fig. 2), and marked nests with colored dots as they were counted.

Statistical analysis. We used mixed effects negative binomial regression (McCullagh and Nelder 1989, Wolfinger and O'Connell 1993, Littell et al. 2006) to characterize the mean error in nest counts of Great Egrets and White Ibises made from aerial photographs compared to corresponding ground counts. An individual quadrat nest count was assumed to follow a negative binomial probability distribution with a mean parameter (expected value) that depended on the method of observation linearly through a log link-function (McCullagh and Nelder 1989). We modeled the log expected nest count as an intercept term plus a coefficient multiplying a 0–1 indicator variable for the aerial method. This latter coefficient can be interpreted as the additive difference between the log mean aerial nest count and the log mean ground nest count. The exponentiated coefficient can be interpreted as the ratio of the mean aerial nest count to the mean ground nest count (the A:G mean ratio). To preserve correspondence (pairing) between aerial and ground counts of the same quadrat (or, equivalently, to account for the within-quadrat correlation between paired aerial and ground nest counts), we modeled quadrat as a "subject" random effect. The complete mixed effect model, consisting of an observation method fixed effect and a quadrat random effect, is analogous to a paired t-test model and has the form

$$\log(\mu_{ij}) = \beta_0 + \beta_1 x_{ij} + \varepsilon_j,$$

where β_0 and β_1 are the regression coefficients, x_{ij} is an indicator variable for observation type for the i^{th} nest count in the j^{th} colony ($x_{ij} = 0$ for a ground observation; $x_{ij} = 1$ for an aerial observation), and ε_j is the random effect for the jth colony (the ε_j are assumed to follow a normal distribution with mean 0 and variance σ^2). Given this parameterization, the population mean μ_G for ground nest counts is estimated by e^{β_0}, the population mean μ_A for aerial nest counts is estimated by $e^{\beta_0+\beta_1}$, and the ratio of the aerial mean count to the ground mean count (μ_A/μ_G) is estimated by e^{β_1}.

We used PROC GLIMMIX (SAS statistical software; Littell et al. 2006) to fit this regression model to our data and to estimate the A:G mean ratio and 95% confidence bounds. We estimated the percent "visual error" of the aerial method relative to the ground method as 100 × (A:G mean ratio – 1). A –12% error, for example, indicates that the aerial count of a quadrat underestimated the true number of nests found during the ground count by 12%. We examined estimates of visual error for White Ibis for differences due to vegetation complexity, colony year and location, and nest density. We expanded the mixed effect negative binomial regression model to allow the A:G mean ratio to vary across levels of each factor. Because of the limited sample size, we only evaluated the effect of one factor at a time. Three groups or levels were defined for each factor. The colony/survey year factor was split into Alley North colony in 2005, Alley North colony in 2006, and New Colony 3 in 2006. We subjectively ranked the level of tall, potentially occlusive vegetative cover in each quadrat as low (>50% cattails or tall grass cover and <50% willows and other tree cover), medium (10–50% cattails/grass cover, 50–90% tree cover), or high (>90% tree cover). The ground-determined nest density factor was defined as low (<0.5 nests/m^2), medium (0.5–1.0 nests/m^2), or high (>1.0 nests/m^2). The expanded model included the quadrat random effect, the observation method fixed effect, a grouping factor fixed (main) effect, and an interaction effect between observation method and the grouping factor. This model has the form

$$\log(\mu_{ij}) = \beta_0 + \beta_1 x_{ij} + \beta_2 y_{2ij} + \beta_3 y_{3ij} + \beta_4 x_{ij} y_{2ij} + \beta_5 x_{ij} y_{3ij} + \varepsilon_j,$$

where $\beta_2, \beta_3, \beta_4$, and β_5 are additional regression coefficients, and y_{2ij} and y_{3ij} are indicator variables for the second and third levels of the three-level covariate. Under this parameterization, the ground count population means μ_{G1}, μ_{G2}, and μ_{G3} for colony groups defined by the first, second, and third levels of the covariate are estimated by e^{β_0}, $e^{\beta_0+\beta_2}$, and $e^{\beta_0+\beta_3}$. The corresponding aerial count population means μ_{A1}, μ_{A2}, and μ_{A3} are estimated by $e^{\beta_0+\beta_1}$, $e^{\beta_0+\beta_1+\beta_2+\beta_4}$, and $e^{\beta_0+\beta_1+\beta_3+\beta_5}$. The corresponding ratios of mean aerial counts to mean ground counts for the three levels of the covariate are estimated by e^{β_1}, $e^{\beta_1+\beta_4}$, $e^{\beta_1+\beta_5}$. Thus, a test for difference in the mean error rate of aerial counts relative to ground counts among colony groups defined by the three levels of the covariate is a test of the joint null hypothesis, $\beta_4 = 0$ and $\beta_5 = 0$. This test is equivalent to the test for interaction between the observation mode effect (aerial or ground) and the covariate effect.

This model is analogous to a two-way analysis of variance (ANOVA) with one within-quadrat fixed effect (observation method) and one between-quadrat fixed effect (any one of the grouping factors). The interaction effect can be viewed as representing differences in the A:G mean ratio among levels of a grouping factor. We used PROC GLIMMIX to fit the expanded model for each grouping factor. The *F*-test statistics generated by PROC GLIMMIX (Littell et al. 2006) were used to test the significance of the interaction effect for each grouping factor. We used contrasts based on the *t*-statistic (Littell et al. 2006) to compare A:G mean ratios pairwise between levels of a grouping factor or to test for polynomial-based trends in ordered groups. The method of Kenward and Roger (Littell et al. 2006) was used to estimate error degrees of freedom for all tests and comparisons. We obtained level-specific estimates of visual error and bias for each grouping factor by applying the transformations described previously to level-specific A:G mean ratio estimates and 95% confidence bounds from the expanded models. The fit of each regression model was assessed by estimating the square of the Pearson correlation coefficient (Snedecor and Cochran 1989) for the observed nest counts compared to their best least unbiased predicted values (BLUPs; Littell et al. 2006). The overdispersion parameter for each model fit (generalized χ^2 statistic divided by the residual degrees of freedom; Littell et al. 2006) was also examined to determine if observed sample variances agreed with model-based estimates of variance in nest counts.

Correction for visibility bias in colony-wide counts. For White Ibises, mean visibility bias correction factors (G:A mean ratios, obtained by inverting estimated A:G mean ratios) and 95% confidence intervals were estimated separately for each colony in each year, and then multiplied by the colony-wide count to derive a bias-corrected estimate of minimum breeding population size. Because of the small number of quadrats assessed for Great Egrets, colony-wide nest counts were adjusted using an estimate of visibility bias pooled across all colonies and years. Original colony-wide counts were then compared with corresponding bias-corrected estimates and associated confidence intervals to characterize the pattern and frequency of significant error in colony-wide aerial nest counts.

RESULTS

Visibility bias. Overall mean nest density for Great Egrets was 0.05 ± 0.04 nests/m^2. Aerial estimates of nest density were higher than ground counts for 38% of the quadrats sampled, and mean visual bias was 23.1% (95% CI: −26.8% to 107.0%; Table 1). The effect of vegetative cover was not examined because Great Egrets typically nested in the tops of trees. The small number of quadrats precluded tests of other factors. Observed counts showed good agreement with model predictions (r^2 = 0.78). The overdispersion parameter *c* for this model was 1.03, indicating good agreement between observed and model-predicted nest count variances.

For White Ibises, goodness of fit was excellent for each of the models considered ($r^2 > 0.98$ for all model fits; *c* range = 0.96–1.01). Aerial nest counts of ibises averaged 11.1% lower than ground counts (95% CI: −20.9–0.0%; Table 2). The aerial visual error rate estimated for the Alley North colony in 2005 (−39.6%; 95% CI: −58.6– −11.8%) was higher than the overall error rate, and differed significantly ($t_{28} = 2.1$, $P = 0.047$) from the −6.9% error rate for the Alley North colony in 2006 (95% CI: −23.6–13.4%). Aerial visual error rates did not differ ($t_{16.6} = 0.14$, $P = 0.89$) between Alley North and New Colony 3 in 2006 (NC3 error rate in 2006: −8.4%, 95% CI: −20.5–5.6%).

White Ibis nest densities averaged 0.72 ± 0.55 nests/m^2. The aerial visual error rate was

Table 1. Comparison of aerial estimates and ground counts of nests in marked quadrats of White Ibises (WHIB) and Great Egrets (GREG) from 2005 to 2007 in the Everglades of southern Florida.

Species	Year	Ground count	Aerial count	Vegetative cover[a]	Nest density (nests/m^2)	Colony
WHIB	2005	23	20	Low	0.64	Alley North
WHIB	2005	54	21	Medium	1.50	Alley North
WHIB	2005	10	11	High	0.28	Alley North
WHIB	2005	8	4	Low	0.22	Alley North
WHIB	2006	205	173	Low	1.03	Alley North
WHIB	2006	72	69	Low	0.72	Alley North
WHIB	2006	33	30	Low	0.33	Alley North
WHIB	2006	30	24	Medium	0.30	Alley North
WHIB	2006	18	20	Medium	0.18	Alley North
WHIB	2006	67	73	Medium	0.67	Alley North
WHIB	2006	414	467	Medium	0.55	New Colony 3
WHIB	2006	445	491	Low	0.63	New Colony 3
WHIB	2006	139	113	Medium	0.86	New Colony 3
WHIB	2006	303	253	Medium	2.24	New Colony 3
WHIB	2006	96	73	High	1.41	New Colony 3
WHIB	2006	390	319	Medium	0.55	New Colony 3
WHIB	2006	114	99	Medium	0.21	New Colony 3
GREG	2006	14	12	High	0.14	Alley North
GREG	2006	24	19	High	0.06	Alley North
GREG	2006	5	18	High	0.01	Alley North
GREG	2006	16	25	High	0.04	Alley North
GREG	2007	4	1	High	0.01	Vacation Island
GREG	2007	6	4	High	0.02	Vacation Island
GREG	2007	13	6	High	0.04	Cypress City
GREG	2007	11	16	High	0.03	Cypress City

[a]Low = >50% *Typha latifolia* or tall grass cover and <50% *Salix caroliniana* and other tree cover, medium = 10–50% *T. latifolia* or grass cover and 50–90% small *S. caroliniana* and other tree cover, and high = >90% *S. caroliniana* and other tree cover.

Table 2. Regression model estimates of mean percent visual error for counts of White Ibis nests made from aerial photographs relative to counts made by ground observers. Also included are corresponding estimates of the visual bias adjustment factor for correcting colony-wide aerial counts.

Effect	Visual error%[a] (95%CI)	Visual bias[a] (95% CI)
All quadrats	−11.1 (−20.9–0.0)	1.12 (1.00–1.26)
Alley North 2005	−39.6 (−58.6– −11.8)	1.65 (1.13–2.42)
Alley North 2006	−6.9 (−23.6–13.4)	1.07 (0.88–1.31)
New Colony 3 2006	−8.4 (−20.5–5.6)	1.09 (0.95–1.26)
Low vegetative cover	−5.7 (−24.4–17.6)	1.06 (0.85–1.32)
Medium vegetative cover	−13.1 (−26.1–2.3)	1.15 (0.98–1.35)
High vegetative cover	−18.7 (−46.3–23.1)	1.23 (0.81–1.86)
Low nest density	−11.4 (−30.9–13.6)	1.13 (0.88–1.45)
Medium nest density	−2.2 (−16.2–14.0)	1.02 (0.88–1.19)
High nest density	−24.3 (−38.1– −7.3)	1.32 (1.08–1.62)

[a]Visual error and visibility bias were both estimated using a mixed effects negative binomial count regression model that accounted for the within-quadrat pairing of aerial and ground nest counts. Visual error (%) = ((aerial:ground mean ratio)-1) × 100. Visual bias = ground:aerial mean ratio.

Table 3. Colony-wide counts, visibility bias, and bias-adjusted minimum breeding population size for three Great Egret (GREG) and three White Ibis (WHIB) colonies in the Florida Everglades during the 2005–2007 breeding seasons.

Colony (species)	Year	Colony-wide count	Visibility bias[a] (95% CI)	Minimum breeding population size (95% CI)
Vacation Island (GREG)	2007	200	0.81 (0.48–1.37)	162 (96–274)
Cypress City (GREG)	2007	1912	0.81 (0.48–1.37)	1549 (918–2619)
Alley North (GREG)	2006	1193	0.81 (0.48–1.37)	966 (573–1634)
Alley North (WHIB)	2005	12,750	1.65 (1.13–2.42)	21,038 (14,408–30, 855)
Alley North (WHIB)	2006	13,566	1.07 (0.88–1.31)	14,516 (11,938–17,771)
New Colony 3 (WHIB)	2006	4800	1.09 (0.95–1.26)	5232 (4560–6048)

[a]Visibility bias, the ratio of the mean ground nest count to the mean aerial nest count, was estimated using a mixed effects negative binomial count regression model that accounted for the within-quadrat pairing of aerial and ground nest counts. For Great Egrets, visibility bias was estimated from quadrats pooled across all colonies and years, and for White Ibises, visibility bias was estimated separately for each colony in each year.

−11.4% (95% CI: −30.9–13.6%) for low nest density quadrats (<0.5 nests/m^2) and −2.2% (95% CI: −16.2–14.0%) for medium nest density quadrats (0.5–1.0 nests/m^2). Although the error rate for quadrats with high nest density (>1.0 nests/m^2) was higher (−24.3%, 95% CI: −38.1 −7.3%), differences were not significant ($F_{2,14.2} = 2.6$, $P = 0.11$). A polynomial contrast test for quadratic trend in ordered groups was only marginally significant ($t_{13} = 1.8$, $P = 0.1$). Visual error rates from aerial surveys did not differ with vegetative cover ($F_{2,12.5} = 0.3$, $P = 0.73$). Although error increased with increasing cover (low = −5.7% error rate, medium = −13.1%, and high = −18.7%), a polynomial contrast test for linear trend in ordered groups was not significant ($t_{16.8} = 0.7$, $P = 0.51$).

Correction for visibility bias in colony-wide counts. Mean visibility bias was greatest in the Alley North ibis colony in 2005 (1.65, 95% CI: 1.13–2.42; Table 3). Unadjusted colony-wide aerial nest counts for this colony may be biased significantly downward relative to the true number of nests. Mean visibility bias was lower in the other colonies, with bias estimates closer to one (1.07 for the Alley North White Ibis colony in 2006, 1.09 for the New Colony 3 White Ibis colony in 2006, and 0.84 for three Great Egret colonies in 2005 and 2006).

DISCUSSION

We found that aerial surveys underestimated the actual number of nests for White Ibises and overestimated numbers for Great Egrets. Bias for ibises was comparable to that reported previously for Great and Snowy (*Egretta thula*) egrets and White Ibises in Florida (Kushlan 1979), and Squacco Herons (*Ardeola ralloides*) in France (Barbraud et al. 2004). The variation in aerial bias was similar to that reported in other studies (Gibbs et al. 1988, Dodd and Murphy 1995, Rodgers et al. 1995), and appears to be a function of colony characteristics and species effects.

Causes of visibility bias. High nest densities may have affected visibility bias for White Ibises. The visual error rate for high-density ibis quadrats (−24.3%) was higher than for either low- (−11.4%) or medium- (−2.2%) density samples. Although this increase was not considered significant, Gibbs et al. (1988) reported that nest density did affect aerial counts of Great Blue Heron (*Ardea herodias*) nests. Nest density may be a little-recognized source of visual error in aerial surveys.

Our results suggest that vegetative cover did not affect visual bias. Although a larger sample of ibis quadrats in areas with high vegetative cover would have been beneficial (quadrat locations were limited by ground accessibility), variation in aerial bias was larger within than between vegetative cover groups. This suggests that, at least for White Ibises, vegetative cover may not be a key factor in determining the extent of aerial bias. For Great Egrets, there was no variation in cover and, therefore, we could not evaluate effects on visual bias. However, Great Egrets typically nest in the tops of trees, and we suspect that vegetative cover may not affect visibility bias for this species in the Everglades (Rodgers et al. 1995).

Visual bias was likely affected by colony characteristics relating to nesting synchrony and nest success. Error rates were higher in the Alley North White Ibis colony in 2005 than in either Alley North or New Colony 3 in 2006. Nest densities were not higher in the Alley North 2005 quadrats than in 2006 samples, and vegetative complexity may be assumed to be roughly equivalent between years. However, the Alley North colony had several mass abandonment and renesting episodes in 2005. Aerial estimates are usually made when most nests are in incubation stage, and each nest is represented in aerial views by a single incubating adult. Due to high nest turnover and nesting asynchrony in 2005, nests in a single quadrat were more likely to be in varying stages of development and incubation, and this may have resulted in higher error rates in aerial estimates. Such error rates can clearly mask true population trends. Although peak counts from 2005 to 2006 seasons suggest that the colony expanded by almost 1000 nests, bias-corrected estimates indicate a high probability that Alley North colony decreased substantially in size.

Species misidentification likely contributed to visibility bias for Great Egrets in our study, with some Snowy Egrets possibly mistaken for Great Egrets in aerial photos. This source of bias was apparently larger on average than any bias due to the density of vegetation that would have caused underestimates rather than overestimates. The eight Great Egret quadrats were located in an area where Snowy Egrets, Little Blue Herons, and Tricolored Herons also nested. Adult Snowy and Great egrets can be difficult to differentiate from the air, especially in a photograph where behavioral clues are eliminated. Small heron nests of the genus *Egretta* can be reliably distinguished from Great Egret nests by sight on the ground. However, because adult birds are not present during ground counts, nests of different *Egretta* species cannot be readily differentiated from each other, particularly during the incubation and early nestling stages. For this reason, the number of Snowy Egret nests present in the ground counts of quadrats was unknown, and we were unable to correct for aerial bias due to species misidentification. This appears to be a fairly intractable problem for multispecies colonies. Although separation of vegetative occlusion from species misidentification bias might be achieved by comparing bias estimates from single- and mixed-species areas, this would require the assumption that vegetation was similar at both sites. Alternatively, more invasive and expensive methods may be attempted, such as the use of blinds or helicopters to allow better identification of species in the quadrats. In any case, because the two types of error (visual occlusion and misidentification) may generally be inseparable for multispecies colonies (King 1976), estimates of bias from multispecies colonies should be applied to single-species colonies with extreme caution, and vice versa.

Method of statistical analysis. The negative binomial regression technique worked well for predicting visual bias in our study. Although we had a relatively small sample size of White Ibis quadrats, the regression models fit the data well and we believe this type of analysis was probably the most efficient option. Similar analyses have been used in other systems, as recommended by White and Bennetts (1996) and demonstrated with Orange-crowned Warblers (*Vermivora celata*). However, we still had relatively low power to detect differences between groups. Several P values were about 0.1, and larger sample sizes might have increased our ability to identify factors that affected levels of visual bias.

Applying visual bias estimates to colony-wide counts. Our results indicate that, in some cases, aerial surveys of White Ibis colonies may produce biased results due to visual occlusion of nests. Estimating visual bias may be particularly important when aerial counts are complicated by high levels of nest turnover. Because nest turnover rates and detectabilities for White Ibises may vary among years, it may be necessary to estimate visual bias each year. Visual bias did not increase with either the complexity of the vegetation or nest density alone, but the need to measure bias may be especially great when nests are both densely packed and located on multilayered substrates. Vegetation is often the cause of this type of visual bias (Frederick et al. 2003), but similar problems may arise for colonies where nests are occluded by rock crevices or ledges (Steinkamp et al. 2003). For aerial surveys of Great Egret colonies, we found no systematic bias due to vegetative occlusion, but species misidentification appears to be a problem for this species. Thus, our results indicate that visual bias should be explicitly measured in aerial surveys of colonies because several sources of error can affect estimates of the size of breeding populations.

ACKNOWLEDGMENTS

We thank R. Borkhataria, C. Hand, S. Edmonds, C. Enloe, G. Gardner, C. Jester, B. Shoger, A. Smith, B. Smith, A. Spees, and E. Trum, as well as everyone at Unusual Attitudes, Inc., particularly K. Lung, M. Alexander, and S. Diehl. K.W. also thanks S. Robinson and K. Sieving for their comments on an earlier version of this manuscript. This research was conducted as part of a grant from the U.S. Army Corps of Engineers.

LITERATURE CITED

BARBRAUD, C., AND G. GÉLINAUD. 2005. Estimating the sizes of large gull colonies taking into account nest detection probability. Waterbirds 28: 53–60.

———, Y. KAYSER, D. COHEZ, M. GAUTHIER-CLERC, AND H. HAFNER. 2004. Detection probability of nests of Squacco Herons in southern France. Journal of Field Ornithology 75: 172–175.

BAYLISS, P., AND K. M. YEOMANS. 1990. Use of low-level aerial photography to correct bias in aerial survey estimates of Magpie Goose and Whistling Duck density in the Northern Territory. Australian Wildlife Research 17: 1–10.

BIBBY, C. J. 2000. Bird census techniques. Academic Press, London.

COOK, M. I., AND E. M. CALL (EDS.). 2006. South Florida wading bird report, vol. 12. South Florida Water Management District, Everglades Division, West Palm Beach, FL. Available at: www.sfwmd.gov/org/wrp/wrp_evg/projects/2_wrp_evg_projects.html (27 July 2007).

DODD, M. G., AND T. MURPHY. 1995. Accuracy and precision of techniques for counting Great Blue Heron nests. Journal of Wildlife Management 59: 667–673.

———, ANDT. M. MURPHY. 1996. The status and distribution of wading birds in South Carolina, 1988–1996. South Carolina Marine Resources, Columbia, SC.

FREDERICK, P. C., B. A. HYLTON, J. A. HEATH, AND M. RUANE. 2003. Accuracy and variation in estimates of large numbers of birds by individual observers using an aerial survey simulator. Journal of Field Ornithology 74: 281–287.

GIBBS, J. P., S. WOODWARD, M. L. HUNTER, AND A. E. HUTCHINSON. 1988. Comparison of techniques for censusing Great Blue Heron nests. Journal of Field Ornithology 59: 130–134.

KING, K. A. 1976. Colonial wading bird survey and census techniques. In: Wading birds: research report no.7 of the National Audubon Society (A. Sprunt IV, J. C. Ogden, and S. Winckler, eds.), pp. 155–159. Plenum Press, New York.

KUSHLAN, J. A. 1979. Effects of helicopter censuses on wading bird colonies. Journal of Wildlife Management 43: 756–760.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, R. D. WOLFINGER, AND O. SCHABENBERGER. 2006. SAS for mixed models, 2nd ed. SAS Institute, Cary, NC.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. Chapman and Hall/CRC Press, New York.

NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117: 393–408.

OGDEN, J. C. 1994. A comparison of wading bird nesting dynamics, 1931–1946 and 1974–1989, as an indication of changes in ecosystem conditions in the southern Everglades. In: Everglades: the ecosystem and its restoration (S. Davis, and J. C. Ogden, eds.), pp. 533–570. St. Lucie Press, Del Ray Beach, FL.

POLLOCK, K. H., AND W. L. KENDALL. 1987. Visibility bias in aerial surveys: a review of estimation procedures. Journal of Wildlife Management 51: 502–510.

RODGERS, J. A., P. S. KUBILIS, AND S. A. NESBITT. 2005. Accuracy of aerial surveys of Waterbird colonies. Waterbirds 28: 230–237.

———, S. B. LINDA, AND S. A. NESBITT. 1995. Comparing aerial estimates with ground counts of nests in Wood Stork colonies. Journal of Wildlife Management 59: 656–666.

ROSENSTOCK, S. S., D. R. ANDERSON, K. M. GIESEN, T. LEUKERING, AND M. F. CARTER. 2002. Landbird counting techniques: current practices and an alternative. Auk 119: 46–53.

SIMONS, T. R., M. W. ALLDREDGE, K. H. POLLOCK, AND J. M. WETTROTH. 2007. Experimental analysis of the auditory detection process on avian point counts. Auk 124: 986–999.

SNEDECOR, G. W., AND W. G. COCHRAN. 1989. Statistical methods, 8th ed. Iowa State University Press, Ames, IA.

STEINKAMP, M., B. PETERJOHN, V. BYRD, H. CARTER, AND R. LOWE. 2003. Breeding season survey techniques for seabirds and colonial waterbirds throughout North America. North American Waterbird Conservation Plan. Available at: http:// www.nawcp.org/pubs/PSGManual03.pdf (24 March 2008)

STOLEN, E. D., D. R. BREININGER, AND P. C. FREDERICK. 2004. Using waterbirds as indicators in estuarine systems: successes and perils. In: Estuarine indicators (S. A. Bortone, ed.), pp. 409–423. CRC Press, Boca Raton, FL.

TEMPLE, S. A., AND J. A. WIENS. 1989. Bird populations and environmental changes: can birds be bio-indicators? American Birds 43: 260–270.

WHITE, G. C., AND R. A. BENNETTS. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77: 2549–2557.

WOLFINGER, R., AND M. O'CONNELL. 1993. Generalized linear mixed models: a pseudo-likelihood approach. Journal of Statistical Computation and Simulation 48: 233–243.