Comparison and Assessment of Aerial and Ground Estimates of Waterbird Colonies

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ABSTRACT Aerial surveys are often used to quantify sizes of waterbird colonies; however, these surveys would benefit from a better understanding of associated biases. We compared estimates of breeding pairs of waterbirds, in colonies across southern Louisiana, USA, made from the ground, fixed-wing aircraft, and a helicopter. We used a marked-subsample method for ground-counting colonies to obtain estimates of error and visibility bias. We made comparisons over 2 sampling periods: 1) surveys conducted on the same colonies using all 3 methods during 3–11 May 2005 and 2) an expanded fixed-wing and ground-survey comparison conducted over 4 periods (May and Jun, 2004–2005). Estimates from fixed-wing aircraft were approximately 65% higher than those from ground counts for overall estimated number of breeding pairs and for both dark and white-plumaged species. The coefficient of determination between estimates based on ground and fixed-wing aircraft was $\leq$0.40 for most species, and based on the assumption that estimates from the ground were closer to the true count, fixed-wing aerial surveys appeared to overestimate numbers of nesting birds of some species; this bias often increased with the size of the colony. Unlike estimates from fixed-wing aircraft, numbers of nesting pairs made from ground and helicopter surveys were very similar for all species we observed. Ground counts by one observer resulted in underestimated number of breeding pairs by 20% on average. The marked-subsample method provided an estimate of the number of missed nests as well as an estimate of precision. These estimates represent a major advantage of marked-subsample ground counts over aerial methods; however, ground counts are difficult in large or remote colonies. Helicopter surveys and ground counts provide less biased, more precise estimates of breeding pairs than do surveys made from fixed-wing aircraft. We recommend managers employ ground counts using double observers for surveying waterbird colonies when feasible. Fixed-wing aerial surveys may be suitable to determine colony activity and composition of common waterbird species. The most appropriate combination of survey approaches will be based on the need for precise and unbiased estimates, balanced with financial and logistical constraints. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):697–706; 2008)

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Several species of waterbirds are apparently experiencing population declines in the southeastern United States, most notably little blue herons (*Egretta caerulea*, Hunter et al. 2006). However, growing concern exists over whether these decreasing trends are real, owing to the various survey methods and biases associated with these methods. Trends are generally derived from multiple estimates of population size over a period of time. Certain survey methods may be more appropriate for certain species; therefore, incorrect choice of survey methodologies for estimating population size for a given species may result in increased bias and reduced precision (Caughley 1977, Lancia et al. 2005). Aerial survey, using fixed-wing aircraft, is the most common method for estimating the number of waterbirds in a colony (Runde et al. 1991, Michot et al. 2003, Green et al. 2006). Fixed-wing aircraft surveys of colonies have several known disadvantages, including often requiring multiple passes over a colony, especially larger ones, to estimate total size of the colony (Frederick et al. 1996, Rodgers et al. 2005). Investigators must integrate observations from these multiple passes into an estimate without double-counting individual pairs. Additionally, inability of fixed-wing aircraft to hover or fly at a slow speed over colonies presumably makes it more difficult to detect species cryptically colored or nesting in low densities. Helicopters, although more expensive, may alleviate some of these problems associated with fixed-wing aircraft due to their ability to fly at slow speeds and hover.

Ground counts are often conducted on colonies of smaller sizes (<500 pairs) and are considered by many researchers to be the accepted standard of colonial waterbird surveys (Buckley and Buckley 1976, Frederick et al. 1996, Rodgers et al. 2005). However, because ground counts are limited to smaller sized colonies, biologists who survey areas that contain colonies of all sizes may have to use different methods to census the entire area. Ground counts can also be considerably more labor- and time-intensive; therefore, complete coverage of large survey areas may require considerable personnel, funding, and time. Perhaps more importantly, although ground surveys are assumed to be the least error-prone method of surveying waterbird colonies, we are aware of no attempt to estimate the magnitude of errors that might occur with such surveys.

Finally, it is unknown whether visibility bias greatly affects estimates of individual species and the species composition of colonies. Variation in the visibility of species might have consequences for waterbird surveys because species plumage varies from highly visible white to cryptic dark coloration (Pollock and Kendall 1987, Martin and Lester 1990, Frederick et al. 1996). Although such bias undoubtedly

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exists, it is unclear how it differentially affects results of aerial and ground surveys.

The coastal wetlands of Louisiana, USA, provide nesting sites for substantial proportions of the continental populations of several species of colonial waterbirds (Martin and Lester 1990). Colony surveys with fixed-wing aircraft have been conducted at infrequent intervals in Louisiana since the 1970s (Portnoy 1977, 1978; Keller et al. 1984; Martin and Lester 1990; Michot et al. 2003; Green et al. 2006). Aerial surveys were used because they allowed single observers to survey large areas over short time periods; furthermore, many colonies are located in remote areas that would be difficult to access from the ground. Although use of fixed-wing aircraft might be the most economical means of surveying these colonies, the importance of this region to several waterbird populations provides impetus for understanding the degree to which species-specific estimates of nests are biased. If these biases are great, relative to helicopter or ground estimates, improvements in estimates might justify use of more expensive survey approaches. We also wanted to quantify error associated with ground estimates by using a marked-subsample method for ground surveys based on the Lincoln–Peterson estimator (see Lancia et al. 2005); similar approaches have been used to quantify aerial survey errors for white-tailed deer (*Odocoileus virginianus*; Potvin et al. 2004) and Canada geese (*Branta canadensis*; Walter and Rusch 1997). Specifically, our objectives were to 1) compare the estimated number of breeding pairs of waterbirds in colonies between fixed-wing aircraft, helicopter, and ground surveys, especially in reference to plumage coloration and body size, 2) evaluate the marked-subsampling estimator as a method for ground estimates, and 3) examine probability of detection and visibility bias associated with ground estimates.

STUDY AREA

We conducted aerial and ground surveys of waterbird colonies in Cameron Prairie, Sabine, Lacassine, and Mandalay National Wildlife Refuges, Rockefeller State Refuge, Avery Island, and portions of the Atchafalaya Basin in south and southwestern Louisiana. We surveyed colonies occupying wetland habitats typical of southern Louisiana including bald cypress (*Taxodium distichum*)–water tupelo (*Nyssa aquatica*) deepwater swamps, flooded timber (e.g., *Salix nigra*), and buttonbush (*Cephalanthus occidentalis*) stands associated with freshwater impoundments and inland and coastal marshes. We attempted to survey all the active colonies in this region that we could access by boat or by foot; we used the survey of Michot et al. (2003) to determine which colonies were most likely to be active.

We observed the following species nesting in our study colonies during 2004–2005: neotropic cormorant (*Phalacrocorax brasilianus*), anhinga (*Anhinga anhinga*), great blue heron (*Ardea herodias*), great egret (*Ardea alba*), snowy egret (*Egretta thula*), little blue heron, tricolored heron (*Egretta tricolor*), cattle egret (*Bubulcus ibis*), green heron (*Butorides virescens*), black-crowned night heron (*Nycticorax nycticorax*), yellow-crowned night heron (*Nyctanassa violacea*), white ibis (*Eudocimus albus*), dark ibis (*Plegadis* spp.), and roseate spoonbill (*Platalea ajaja*). Because of the extreme difficulty of distinguishing between white-faced ibis (*Plegadis chihi*) and glossy ibis (*Plegadis falcinellus*) from the air, we grouped both species into a category of dark ibis.

METHODS

We conducted surveys for comparisons between survey methods over 2 sampling periods: 1) helicopter, fixed-wing, and ground surveys (hereafter 3-method comparison or TMC) all conducted during May 2005 and 2) fixed-wing and ground surveys (hereafter fixed-wing–ground comparison or FWGC) during May and June of 2004 and 2005. We identified a priori the surveyed colonies based on the likely ability to conduct simultaneous ground estimates as well as the relative adjacency of colonies to one another (Fig. 1). We used this nonrandom sampling design for logistical and feasibility purposes, specifically to minimize travel time, thereby maximizing the number of colonies we could visit in a given day. For the FWGC, we conducted surveys in early May and early June following protocols established from earlier colonial waterbird surveys in Louisiana (Martin and Lester 1990, Michot et al. 2003). We based this survey schedule on the peak nesting season for most species of wading birds in Louisiana (Martin and Lester 1990). For the TMC, we conducted these surveys from 3 May to 11 May 2005. We surveyed 27 active waterbird colonies, of which 17 colonies were also accessible for ground surveys. We conducted pair-wise comparisons of the TMC: fixed-wing–helicopter ($n = 27$), fixed-wing–ground ($n = 16$), and helicopter–ground ($n = 17$) for comparison of estimates. For the FWGC, we conducted fixed-wing aerial surveys on 3–7 May 2004, 8–9 June 2004, 6–11 May 2005, and 6–7 June 2005 and ground estimates simultaneously during the corresponding 4 periods: 29 April–7 May 2004, 3–8 June 2004, 3–11 May 2005, and 7–14 June 2005. We surveyed 20 different colonies over the 4 sampling periods: May 2004 ($n = 14$), June 2004 ($n = 12$), May 2005 ($n = 16$), June 2005 ($n = 16$).

Aerial Surveys

We conducted fixed-wing aircraft surveys from a single-engine, amphibious aircraft (Cessna 185; Cessna Aircraft Co., Wichita, KS) owned and operated by the United States Geological Survey. The aircraft was configured with a voice–Global Positioning System (GPS)–moving map system that linked the GPS unit of the aircraft with onboard intercom system and onboard laptop computers. Each voice observation, from pilot or observer, was assigned a specific time and position (latitude and longitude). The voice–GPS–moving map system also displayed geospatial points (e.g., colonies), current aircraft position, flight track, and location of recent voice observations on a 1:250,000-scale digital map image from a computer monitor screen mounted on the aircraft's instrument panel. We conducted helicopter surveys using a Bell 206L (Bell Helicopter Textron Inc., Hurst, TX) helicopter owned and operated by Southern Helicopters,

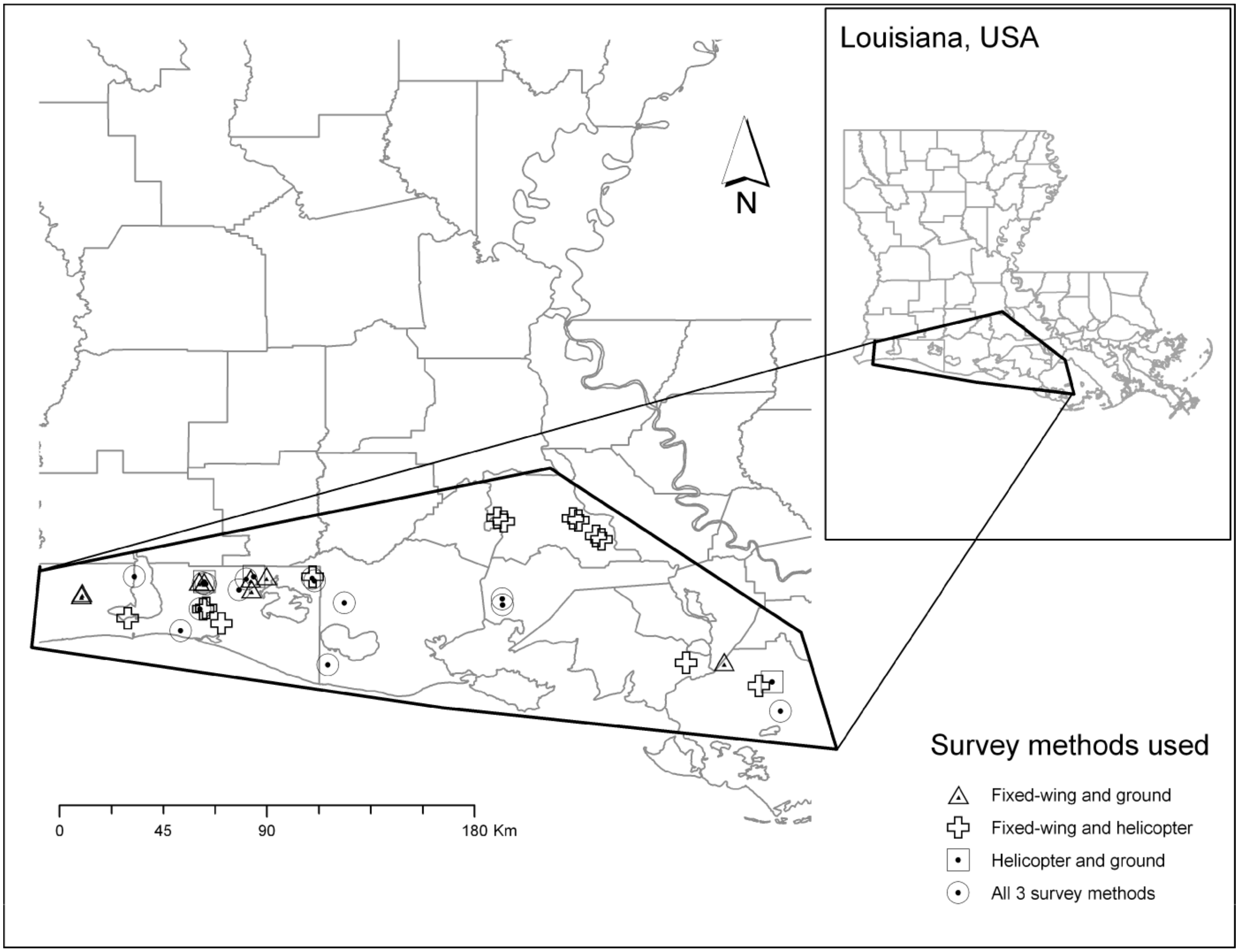

Figure 1. Location of waterbird colonies sampled using fixed-wing aircraft, helicopter, and ground surveys in south–southwestern Louisiana, USA, 2004–2005.

Sunshine, Louisiana. Because we leased this helicopter, which was not normally used for wildlife surveys, we used a hand-held GPS unit containing all colonies in its geospatial database for navigation. Aboard the helicopter, we recorded colony estimates using a hand-held digital voice recorder (IRiver™; IRiver Co., Seoul, Korea). We used the same observer, C. W. Jeske (CWJ), in all aerial surveys. As the experience level of observers has been shown to affect survey estimates, we selected an experienced observer (CWJ) that had participated in numerous colonial waterbird surveys including the most recent surveys conducted in Louisiana (Erwin 1982). Although the observer was the same for all surveys, we used different pilots between the helicopter and airplane surveys. For fixed-wing surveys, the pilot, T. C. Michot, also was the navigator, whereas we used another navigator, M. C. Green (MCG) during helicopter surveys.

We conducted aerial surveys at approximately 150 m above ground level for both the helicopter and airplane surveys. Fixed-wing aircraft speeds during surveys averaged 157 km per hour, whereas helicopter speeds ranged from near-hover to 40 km per hour along elongated colonies (e.g., flooded tree-rows). The observer (CWJ) in either aircraft was responsible for estimating the number of birds, by species, in each colony. We estimated number of individual birds at each colony and assumed that each individual represented a breeding pair. Generally, we made several passes over the colony during fixed-wing surveys, whereas one pass was usually sufficient to estimate number of waterbirds in the colony during helicopter surveys. We transcribed voice observation data from the voice–GPS–moving map system (airplane) and voice recorder (helicopter) after completion of the survey.

Ground Estimates Using Mark–Subsample Method

We conducted ground estimates on selected waterbird colonies during May and June 2004–2005. We conducted our ground estimates within 10 days of corresponding aerial surveys to minimize changes in colony size and species composition. Two observers, M. C. Luent and MCG, conducted ground estimates for all colonies. We conducted all ground surveys from the perimeter of the colony, thereby minimizing disturbance and limiting use of specific survey methods that involve entering the colony (e.g., belt transects). Each observer independently counted number of nests in each colony; however, both observers conducted estimates at the same time. Observers did not share findings during ground surveys. We counted only occupied nests and assumed one nest equaled one breeding pair. For each nest counted, we plotted the location of the nest within the colony on a colony map. At the completion of each count, we compared between observers the nest count, nest location within the colony, and species composition to determine which nests were counted by both observers.

Statistical Analysis

For aerial surveys, we used unadjusted estimates of number of breeding pairs of each species to represent the size of each colony. For ground estimates using tandem observers (marked-subsample), we used Seber's (1973) Peterson estimator to derive estimates of number of breeding pairs, by species, for each colony. From our ground estimates, we obtained total number of nests counted by observer 1 (O_1), total number of nests counted by observer 2 (O_2), and number of nests counted by both observers (B_2). We determined number of nests counted by both individuals from detailed maps of nest locations prepared by both observers. We were able to determine estimated number of nests, by species, for each colony by using Chapman (1951):

$$\hat{N} = \left[\frac{(O_1 + 1)(O_2 + 1)}{B_2 + 1}\right] - 1$$

We estimated variance following Seber (1982):

$$\text{var}(\hat{N}) = \frac{(O_1 + 1)(O_2 + 1)(O_1 - B_2)(O_2 - B_2)}{(B_2 + 1)^2(B_2 + 2)}$$

The marked-subsample method also allowed us to estimate probability of detection for each observer and estimate visibility bias (Lancia et al. 2005). We estimated probability of detection using $P_1 = \text{B}/(\text{O}_2 + \text{B})$ and $P_2 = \text{B}/(\text{O}_1 + \text{B})$ for observer 1 and observer 2, respectively (Magnusson et al. 1978, Caughley and Grice 1982, Walter and Rusch 1997). We determined visibility bias from the inverse of these detection probabilities averaged across the tandem observers ($[1 - (P_1 + P_2)/2]$; Choquenot 1995). We determined coefficients of variation for a given species to assess if variance of estimates of numbers of nesting pairs differed between species (Miller 1991). Following White et al. (1982), we used coefficients of variation as a standardized measure of variance, because colonies varied greatly in size.

We compared estimated number of breeding pairs, by species, in each colony for the TMC. We performed paired *t*-tests to examine the null hypothesis that mean difference in the estimated numbers of breeding pairs for total birds, white birds, and dark birds between survey methods was zero. We also examined differences between mean numbers of species detected by each survey method using paired *t*-tests. When making a related series of pair-wise comparisons, here and in subsequent analyses, we controlled for Type I error using a sequential Bonferroni adjustment of $\alpha = 0.05$ (Miller 1981, Rice 1989).

We used regression to determine how well estimates from a less intensive survey method predicted estimates obtained from a more intensive method. We used bisector regression (S-PLUS 7.0; 2005 Insightful Corp., Seattle, WA) because of measurement errors in both ground and aerial surveys. Bisector regression has been shown to perform considerably better than other regressions (e.g., reduced major-axis) that are commonly used when both X and Y axes contain errors (Isobe et al. 1990). We used the adjusted coefficient of determination of this relationship to determine variation in the ground estimate (dependent variable) that can be explained by number of nesting pairs observed from either aerial method (independent variable). We also examined variation in helicopter estimates (dependent variable) that can be explained by the fixed-wing estimates (independent variable). A low adjusted coefficient of determination would suggest that a less intensive survey method explained little variation in estimates of the number of nesting pairs of a species obtained from the more intensive approach. We also determined if the slope and intercept of the relationship between the numbers of pairs estimated from ground estimates and aerial surveys were not significantly different from one and zero, respectively, which are the expectations if bias did not change with colony size.

To determine if low sample sizes might explain apparent weak relationships between fixed-wing surveys and ground estimates (see Results), we also conducted an expanded FWGC. For this comparison, we included surveys conducted over the 4 sampling periods (May, Jun 2004; May, Jun 2005) and used the same procedure of analyses described previously for the TMC. For statistical analyses we assumed that measurement errors of observations of the same colony made in different years or months were independent. Colony composition changed greatly from month to month and across years partially justifying this assumption. We did not have to make the assumption of independence of errors for the TMC because we only surveyed all colonies once during the sampling period. If the expanded comparison had larger coefficients of determination and less evidence of systematic over or under counts than the TMC, we could attribute some of the poor performance of the fixed-wing survey in the latter comparisons to insufficient sample sizes.

We tested differences among species in visibility bias during ground surveys using analysis of variance (PROC ANOVA; SAS Institute, Cary, NC). We conducted Tukey's post hoc multiple comparisons to further examine the variation in visibility bias among species. We conducted a similar analysis of coefficients of variation. Because the visibility biases exhibited a skewed distribution, we evaluated differences among species with a Kruskal–Wallis Test (PROC NPAR1WAY; SAS Institute, Cary, NC) and a Dunn's multiple-comparisons test.

RESULTS

Three-Method Comparison

For the comparison between ground and fixed-wing surveys, estimates from fixed-wing survey ($\bar{x} \pm \text{SE} = 311.94 \pm 63.01$) for total number of nesting pairs of waterbirds were

Table 1. Regressions assessing ability of fixed-wing counts (independent variable) to estimate numbers of nesting birds determined in ground counts (dependent variable) of colonies in south–southwestern Louisiana, USA, during May 2005 ($n = 16$).

Group or species[a]	R^2	P	Slope	SE	$P_{S=1}$	Intercept	SE	$P_{I=0}$
Overall	0.41[b]	0.004[c]	0.74	0.13	0.062[d]	−27.97	38.06	0.474
White species	0.90	<0.001	0.84	0.02	0.001	−5.91	13.20	0.661
Dark species	0.26	0.003	0.46	0.18	0.008	−0.35	17.52	0.984
Neotropic cormorant	0.32	0.012	0.45	0.18	0.009	−0.04	15.86	0.997
Great blue heron	0.00	0.481						
Great egret	0.88	<0.001	0.82	0.02	<0.001	−0.52	13.98	0.971
Snowy egret	0.00	0.950						
Cattle egret	0.16	0.070						
Roseate spoonbill	0.66	<0.001	1.21	0.10	0.051	−3.33	3.23	0.318

[a] We do not show individual species found in ≤6 colonies (anhinga, little blue heron, tricolored heron, black-crowned night heron) due to small sample size.

[b] As R^2 approaches one, precision of the counts increases; P is associated with the test of the null hypothesis that $R^2 = 0$.

[c] In comparisons where $P < 0.05$, based on a sequential Bonferroni adjustment of alpha, slope and intercept values (and SEs) are based on ordinary least squares bisector regression.

[d] P-values, $P_{S=1}$ and $P_{I=0}$, are associated with tests of the null hypotheses that the slope and intercept were not significantly different from one and zero, respectively.

higher than the ground estimate ($\bar{x} = 203.56 \pm 45.72$; $t_{15} = 2.316$, $P = 0.035$); however, this difference was not significant following Bonferroni adjustment. There were no other large differences in the overall estimates of nesting pairs or white- or dark-plumaged birds made by 3 survey methods. Fixed-wing surveys ($\bar{x} = 3.6 \pm 0.5$) estimated fewer species than ground surveys ($\bar{x} = 4.5 \pm 0.5$; $t_{15} = -2.46$, $P = 0.027$) as well as fewer species in comparison to helicopter surveys (fixed-wing: $\bar{x} = 3.9 \pm 0.4$; helicopter: $\bar{x} = 5.2 \pm 0.5$; $t_{26} = -3.16$, $P = 0.004$). Ground surveys ($\bar{x} = 4.8 \pm 0.4$) also appeared to detect a greater mean number of species per colony than did helicopter surveys ($\bar{x} = 4.2 \pm 0.4$; $t_{16} = -2.06$, $P = 0.056$) although the difference was not statistically significant.

Coefficients of determination were ≤0.41 for regressions of estimates from fixed-wing and ground surveys for most groupings and species with exception of white birds grouping, great egrets, and roseate spoonbills (Table 1; Fig. 2). For estimates of white and dark birds and specifically great egrets and neotropic cormorants, slopes were significantly different from one. Estimates of slope found to be significantly different from one were all <1, indicating that we overestimated birds as colony size increased. Regressions of estimates from ground and helicopter surveys resulted in estimates of coefficients of determination ≥0.67, with the exception of 3 species, snowy egrets, great blue herons, and cattle egrets (Table 2). For all 7 species and groupings with significant regressions between ground and helicopter surveys, the slope and intercept of the relationship was not significantly different from one and zero, respectively, indicating no evidence of bias for our comparisons of ground and helicopter surveys. Coefficients of determination were ≤0.56 for regressions of fixed-wing and helicopter surveys with the exception of great egrets and little blue herons which had coefficients of determination ≥0.88 (Table 3). For the overall estimated number of pairs as well as for great egret pairs, fixed-wing surveys appeared to overestimate nesting pairs as colony size increased. For little blue herons, nesting pairs were underestimated by fixed-wing surveys as colony size increased.

Expanded Fixed-Wing–Ground Comparison

Fixed-wing aircraft surveys ($\bar{x} \pm \mathrm{SE} = 439.62 \pm 89.16$) estimated a greater number of mean breeding pairs per colony than did ground estimates ($\bar{x} = 198.55 \pm 21.99$, $t_{57} = 2.903$, $P = 0.005$). Estimates for white (fixed-wing: $\bar{x} = 233.47 \pm 48.13$; ground: $\bar{x} = 145.29 \pm 21.04$, $t_{53} = 2.236$, $P = 0.029$) and dark (fixed-wing: $\bar{x} = 195.47 \pm 66.65$; ground: $\bar{x} = 44.35 \pm 6.77$, $t_{54} = 2.302$, $P = 0.025$) species also were greater from fixed-wing aircraft than ground estimates. Mean number of species detected during the fixed-wing aircraft surveys ($\bar{x} = 3.3 \pm 0.25$) was fewer than the number detected during ground surveys ($\bar{x} = 5.1 \pm 0.32$; $t_{57} = -6.66$, $P \leq 0.001$).

There was a significant relationship between ground estimates and estimates from fixed-wing aircraft for 2 groupings and 6 species (Table 4), indicating that aerial surveys reflected trends in numbers of nesting pairs. Although often significant, the strength of the relationship, as measured by the coefficient of determination was ≤0.14 for 9 of the 13 groupings. This estimate of the coefficient of determination was higher for estimates of white-plumaged birds than for dark-plumaged birds; however, estimates of coefficient of determination were ≤0.44 for all species except great egrets.

Of the 8 groupings and species where there was a significant correlation between the 2 estimates of colony size, only 3 of the cases had a slope that was not significantly different from one, suggesting most estimates were biased. In all cases where slope differed from one, bias was unidirectional as estimated slopes were <1.0. In these cases, we counted more pairs in aerial surveys then we estimated in ground counts. As intercepts for all regressions did not significantly differ from zero (Table 4), slopes <1.0 meant overestimates of breeding pairs increased with colony size. For most dark-plumaged species, the relationship between

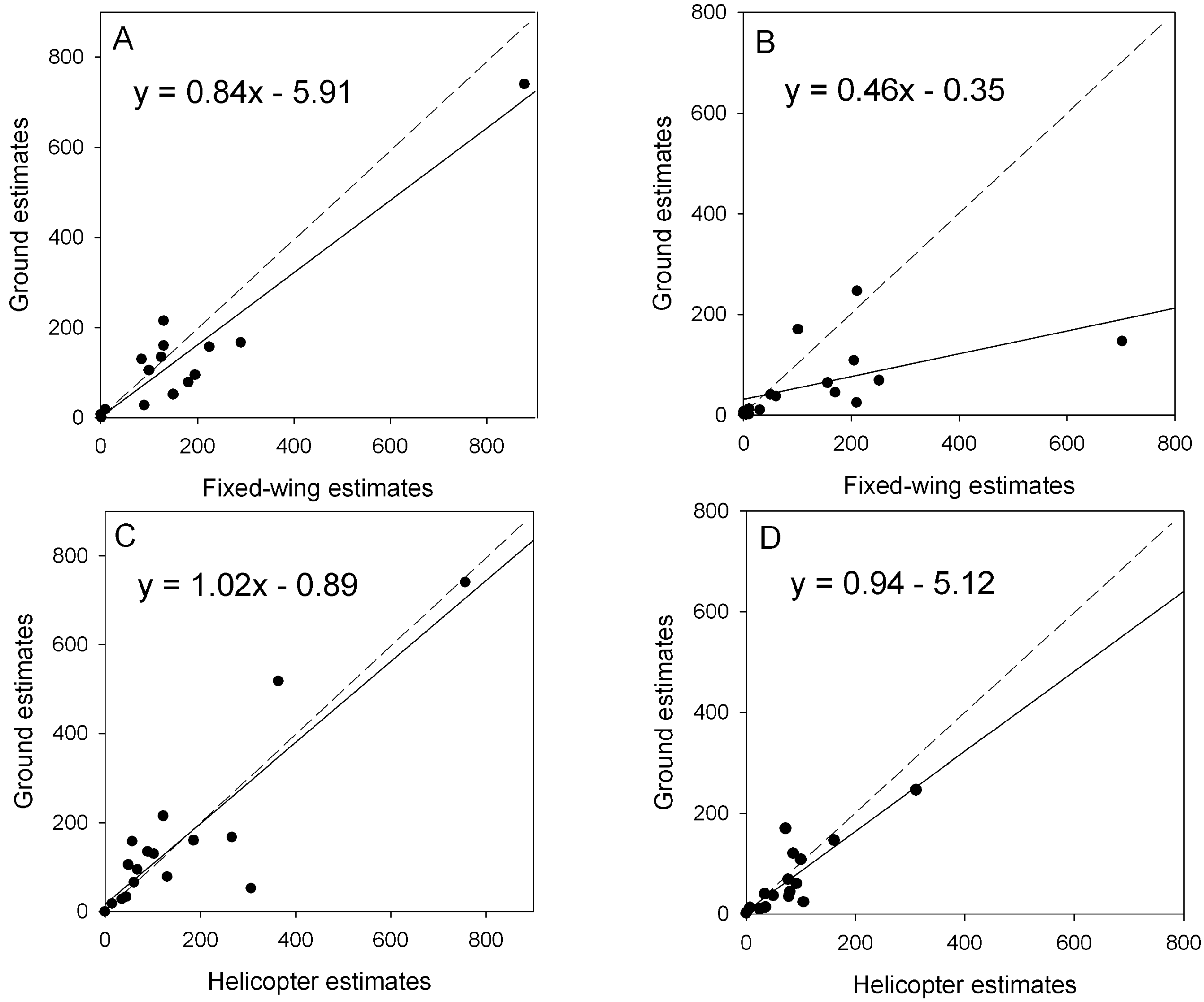

Figure 2. Relationships between ability of fixed-wing surveys to estimate the total number of white-plumaged (A) and dark-plumaged (B) nesting birds determined in ground estimates and between ability of helicopter surveys to estimate the total number of white-plumaged (C) and dark-plumaged (D) nesting birds determined in ground estimates in south–southwestern Louisiana, USA, during May 2005. Dashed line represents slope equal to one.

ground and aerial estimates was so weak that it was not possible to evaluate bias through regression.

Probability of Detection

For ground-count comparisons, there was a significant difference in probability of detection among species ($F_{1,786} = 19.4$, $P < 0.001$; Table 5) and between observers ($F_{9,786} = 3.4$, $P < 0.001$). Average probability that the 2 ground observers would detect an individual nest was 0.796 and 0.706 for observers 1 and 2, respectively. Probability of detection for observer 1 was >0.75 for all species with the exception of snowy egrets. For observer 2, probability of detection was high (>0.70) for 6 of the 10 species but <0.60 for 3 species, little blue herons, snowy egrets, and *Plegadis* ibis. There was a difference in visibility bias among species ($F_{9,392} = 4.3$, $P < 0.001$). Post hoc comparisons revealed snowy egret had a mean visibility bias of 0.362 which was greater than 6 of the 10 species (Table 5). Use of marked-subsample method revealed that ground estimates conducted by one observer would result in an average underestimation of nesting pairs by 21.8%.

Unlike aerial surveys the marked-subsample approach we used with ground surveys provided an estimate of the error of the estimated number of breeding pairs. Coefficient of variation for estimates of total colony size varied between 0.0% and 6.1%; the average coefficient of variation was 2.1% (Table 5).

DISCUSSION

For both sampling periods, comparisons of colony size estimates revealed fixed-wing aircraft surveys overestimated total number of breeding pairs per colony. Using aerial simulations, Frederick et al. (2003) found the average observer underestimated total number of pairs per colony. The simulation of Frederick et al. (2003) assumed each bird model (white-painted alfalfa seed) placed on the scaled model of a colony represented an adult bird; hence, there were no juvenile or nonbreeding birds present in the scaled colony. As the breeding season progresses, actual colonies

Table 2. Regression assessing ability of helicopter counts (independent variable) to estimate number of nesting birds determined in ground counts (dependent variable) in south–southwestern Louisiana, USA, during May 2005 ($n = 17$).

Group or species[a]	R^2	P	Slope	SE	$P_{S=1}$	Intercept	SE	$P_{I=0}$
Overall	0.67[b]	<0.001[c]	1.00	0.12	0.978[d]	−9.96	27.37	0.721
White species	0.78	<0.001	1.02	0.08	0.782	−0.89	21.16	0.967
Dark species	0.70	<0.001	0.94	0.12	0.602	−5.12	9.17	0.584
Neotropic cormorant	0.82	<0.001	0.89	0.10	0.300	−0.92	6.82	0.894
Great blue heron	0.23	0.030						
Great egret	0.92	<0.001	1.09	0.10	0.418	12.14	12.34	0.340
Snowy egret	0.35	0.008	0.81	0.26	0.470	4.31	3.32	0.213
Cattle egret	0.00	0.753						
Roseate spoonbill	0.42	0.003	1.02	0.16	0.916	−2.21	3.91	0.580

[a] We do not show individual species found in ≤6 colonies (anhinga, little blue heron, tricolored heron, black-crowned night heron) due to small sample size.
[b] As R^2 approaches one, precision of the counts increases; P is associated with the test of the null hypothesis that $R^2 = 0$.
[c] In comparisons where $P < 0.05$, based on a sequential Bonferroni adjustment of alpha, slope and intercept values (and SEs) are based on ordinary least squares bisector regression.
[d] P-values, $P_{S=1}$ and $P_{I=0}$, are associated with tests of the null hypotheses that the slope and intercept were not significantly different from one and zero, respectively.

contain juveniles and potentially nonbreeding birds that may be difficult to distinguish from adult breeding birds from an airplane. Presence of juveniles and nonbreeders could presumably lead to overestimations of colony size during airplane surveys (Erwin 1982, Rodgers et al. 2005). However, presence of juveniles should not have been a problem for our comparisons made in May, when young birds are quite easily distinguished from adults. Also contrary to our findings, simulations by Frederick et al. (2003) suggested colony size did not influence estimation error within the range of 250–6,000 birds per colony. Our results showed, for certain species, estimates from fixed-wing surveys co-varied with colony size; we often overestimated larger colonies. Given differences in bias between our results and the model of Frederick et al. (2003), it would appear that biases might vary greatly depending on survey conditions.

Fixed-wing aircraft surveys tended to be biased and poorly reflected estimates made from the ground. Overestimates of snowy egrets by fixed-wing aircraft appeared to be the result of species misidentification. In several colonies, observers recorded little blue herons and cattle egrets from the ground that were identified as snowy egrets from the air, similar to results from other studies (Kushlan 1979, Rodgers et al. 2005). We also overestimated neotropic cormorants from fixed-wing surveys, presumably due to branching behavior by cormorants. In most surveys, including ours, active nests, rather than raw number of birds observed, are counted. Therefore, branching behavior makes it difficult, especially from fixed-wing surveys, to correctly assign birds to given nests (Rogers et al. 2005). Estimates of large, conspicuous species (e.g., great egret and roseate spoonbill) appeared to be the least biased and most precise estimates made from fixed-wing aircraft. With remaining species, fixed-wing aircraft estimates resulted in imprecise estimates of the actual number of breeding pairs as determined from ground estimates.

Because we could compare higher numbers of estimates from the ground to those from fixed-wing surveys in our expanded analysis, we could see if the poor performance of

Table 3. Regression assessing ability of fixed-wing counts (independent variable) to estimate number of nesting birds determined in helicopter counts (dependent variable) in south–southwestern Louisiana, USA, during May 2005 ($n = 27$).

Group or species[a]	R^2	P	Slope	SE	$P_{S=1}$	Intercept	SE	$P_{I=0}$
Overall	0.49[b]	<0.001[c]	0.52	0.16	0.006[d]	225.84	114.21	0.058
White species	0.31	0.001	1.10	0.30	0.720	3.14	80.67	0.969
Dark species	0.33	<0.001	1.06	0.20	0.761	−39.59	35.73	0.278
Neotropic cormorant	0.51	<0.001	0.87	0.21	0.539	−17.75	22.38	0.435
Great blue heron	0.56	<0.001	0.86	0.15	0.349	−2.45	6.69	0.717
Great egret	0.90	<0.001	0.75	0.04	<0.001	−3.76	11.65	0.749
Snowy egret	0.19	0.015	1.55	0.68	0.425	58.01	46.08	0.212
Little blue heron	0.88	<0.001	1.12	0.02	<0.001	2.39	6.27	0.705
Cattle egret	0.01	0.827						
Roseate spoonbill	0.38	<0.001	0.80	0.25	0.422	5.20	4.60	0.269

[a] We do not show individual species found in ≤6 colonies (anhinga, little blue heron, tricolored heron, black-crowned night heron) due to small sample size.
[b] As R^2 approaches one, precision of the counts increases; P is associated with the test of the null hypothesis that $R^2 = 0$.
[c] In comparisons where $P < 0.05$, based on a sequential Bonferroni adjustment of alpha, slope and intercept values (and SEs) are based on ordinary least squares bisector regression.
[d] P-values, $P_{S=1}$ and $P_{I=0}$, are associated with tests of the null hypotheses that the slope and intercept were not significantly different from one and zero, respectively.

Table 4. Regression assessing ability of fixed-wing aircraft counts (independent variable) to estimate number of nesting birds determined in ground counts (dependent variable) in south–southwestern Louisiana, USA, during May–June 2004–2005 ($n = 58$).

Group or species	R^2	P	Slope	SE	$P_{S=1}$	Intercept	SE	$P_{I=0}$
Overall	0.14[a]	0.002[b]	0.34	0.08	<0.001[c]	48.46	30.08	0.113
White species	0.34	<0.001	0.48	0.11	<0.001	33.92	20.59	0.105
Dark species	0.02	0.175						
Neotropic cormorant	0.29	<0.001	0.39	0.10	<0.001	−2.42	6.13	0.695
Anhinga	0.02	0.154						
Great blue heron	0.03	0.089						
Great egret	0.63	<0.001	0.94	0.13	0.64	−12.49	11.94	0.30
Snowy egret	0.14	0.002	0.31	0.14	<0.001	1.34	2.14	0.535
Little blue heron	0.12	0.005	1.15	0.31	0.626	0.70	2.72	0.80
Tricolored heron	0.00	0.678						
Cattle egret	0.12	0.005	0.47	0.17	0.002	5.92	11.87	0.620
Black-crowned night heron	0.02	0.162						
Roseate spoonbill	0.44	<0.001	0.97	0.11	0.81	0.11	1.51	0.948

[a] As R^2 approaches one, precision of the counts increases; P is associated with the test of the null hypothesis that $R^2 = 0$.
[b] In comparisons where $P < 0.05$, based on a sequential Bonferroni adjustment of alpha, slope and intercept values (and SEs) are based on ordinary least squares bisector regression.
[c] P-values, $P_{S=1}$ and $P_{I=0}$, are associated with tests of the null hypotheses that the slope and intercept were not significantly different from one and zero, respectively.

fixed-wing surveys in the TMC was due to sample size. In the expanded dataset, our analysis did not result in fixed-wing surveys explaining more variation in ground estimates than we observed in our more limited analysis. Increased sample sizes did result in an increased detection of biases in fixed-wing surveys; these biases went undetected at the sample sizes in the TMC because of weak relationships between most estimates made with fixed-wing aircraft compared to those made with ground estimates. However, our nonrandom sampling design, conducted for feasibility issues, constrained the inferences of our results.

Helicopters generally cost 2–3 times more per hour than fixed-wing aircraft, but colonies can generally be surveyed faster in helicopters. For example, we surveyed 31 colonies with fixed-wing aircraft and helicopter using 15 hours and 6.5 hours of flight time, respectively. This difference in flight time meant that the actual costs of each survey flight were fairly similar (fixed-wing: 15 hr at US$275/hr for total of US$4,125.00; helicopter: 6.5 hr at $700/hr for total of $4,550.00). When considering costs, it is important to note that the estimated costs include only charges for use of the aircraft, not the salaries of the observers. Because the helicopter survey required 1 day to complete the survey, versus 2 days for the fixed-wing survey, use of the helicopter might be less expensive than the fixed-wing aircraft in some situations. Given the advantages of reduced survey time and improved estimates in colony size obtained with helicopter surveys relative to those from fixed-wing aircraft, any small increase in cost associated with the former is probably justified.

Our results suggest probabilities of detection may differ significantly between observers conducting ground surveys of waterbird colonies. Although dark-plumaged species appeared to decrease probability of detection, relative size of the bird also was important, as all species with probabilities of detection <0.60 were small heron or ibis species. Surprisingly, snowy egrets, an all white bird, had the highest visibility bias of any species, which was unexpected due to the perception that white plumage enhances a bird's visibility to human observers (Martin and Lester 1990).

Table 5. Observer probability of detection, mean visibility bias, single-count underestimation, and coefficient of variation for ground counts of wading bird colonies in south–southwestern Louisiana, USA, during May–June, 2004–2005. Species with the same letter had estimates of mean visibility bias or coefficient of variation that were not significantly different at $\alpha = 0.05$ based on multiple comparison tests.[a]

Group or species	n[b]	P_1	P_2	Mean visibility bias	Single-count underestimation	Median CV	Mean CV
Neotropic cormorant	50	0.764	0.736	0.250 B	19.7	2.3	2.9AB
Anhinga	22	0.837	0.666	0.249 AB	25.7	0.0	5.1BCD
Great blue heron	49	0.831	0.784	0.192 B	15.6	0.0	1.4D
Great egret	75	0.841	0.749	0.208 B	14.2	1.8	3.6A
Snowy egret	48	0.687	0.599	0.362 A	32.5	3.2	8.0A
Little blue heron	27	0.833	0.587	0.290 AB	19.0	0.0	2.0D
Tricolored heron	26	0.757	0.834	0.204 B	23.8	0.0	4.2CD
Cattle egret	50	0.774	0.712	0.257 B	21.3	1.7	5.2A
Plegadis ibis	10	0.859	0.588	0.277 AB	24.9	0.0	1.3CD
Roseate spoonbill	51	0.780	0.774	0.213 B	21.0	0.0	4.4BC

[a] We used Tukey's and Dunn's multiple comparison tests for comparing mean visibility bias and CV, respectively.
[b] No. of different estimates for nesting pairs of a species; we obtained each estimate from a colony occupied by a species with no colonies being sampled more than once in a 30-day period.

However, based on comparisons of the notes of observers, high visibility bias associated with snowy egrets was mostly due to its relatively small stature and misidentification with other white species, namely cattle egrets and juvenile little blue herons. Differences in probabilities of detection between observers demonstrate the importance of using multiple observers in conducting colony estimates. Single observers are likely to underestimate number of nesting birds in ground estimates, resulting in a biased count.

Use of the marked-subsample approach resulted in estimates that had small associated errors. The average coefficients of variation for all of the species were <9%, with medians of estimates considerably smaller. Typically, population estimates with coefficients of variation <10% are considered to be fairly precise (White et al. 1982). Although small, uncertainty associated with estimates was higher for white-plumaged species than for those with less conspicuous plumage, again suggesting that high visibility of white-plumaged species does not necessarily result in better estimates of their numbers based on ground counts.

MANAGEMENT IMPLICATIONS

Whenever feasible, we recommend managers conduct ground surveys to estimate colony size and increase probability of detection of rarer species (e.g., black-crowned night herons). We strongly recommend that managers incorporate the use of double observers for ground estimates and preferably use the marked-subsample method, especially for smaller sized colonies (e.g., <500 breeding pairs). When a survey involves many colonies, or includes some colonies that are either inaccessible or impractical for ground surveys, we recommend managers use a combination of ground and aerial surveys to estimate colony size. For larger or irregularly shaped colonies that are accessible from the ground, we recommend employing the mark–recapture method in sample plots to account for problems with detection. For aerial methods, helicopter surveys appeared to be the least biased and most precise method (Buckley and Buckley 1979, Kushlan 1979). If examination of spatial and temporal dynamics of colonies is the goal, helicopter surveys would provide considerably better estimates of nesting pairs than those possible with fixed-wing aircraft. Given the high bias and low precision of surveys from fixed-wing aircraft, it is difficult to recommend this method for surveys attempting to estimate the number of birds of each species in colonies (Frederick et al. 2003, Rodgers et al. 2005). However, fixed-wing aircraft surveys can estimate whether colonies are active; such surveys rarely (<10%) failed to identify whether a colony was active as determined from ground surveys. Furthermore, fixed-wing aircraft surveys appeared to correctly identify most of the common species within a colony; however, as already noted, number of nesting pairs was often poorly estimated.

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