



SOURCES OF VARIATION IN DETECTION OF WADING BIRDS FROM AERIAL SURVEYS IN THE FLORIDA EVERGLADES

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ABSTRACT.—We conducted dual-observer trials to estimate detection probabilities (probability that a group that is present and available is detected) for fixed-wing aerial surveys of wading birds in the Everglades system, Florida. Detection probability ranged from <0.2 to ~0.75 and varied according to species, group size, observer, and the observer's position in the aircraft (front or rear seat). Aerial-survey simulations indicated that incomplete detection can have a substantial effect on assessment of population trends, particularly over relatively short intervals (≤ 3 years) and small annual changes in population size ($\leq 3\%$). We conclude that detection bias is an important consideration for interpreting observations from aerial surveys of wading birds, potentially limiting the use of these data for comparative purposes and trend analyses. We recommend that workers conducting aerial surveys for wading birds endeavor to reduce observer and other controllable sources of detection bias and account for uncontrollable sources through incorporation of dual-observer or other calibration methods as part of survey design (e.g., using double sampling). Received 6 August 2007, accepted 18 February 2008.

Key words: aerial surveys, bias, detection, estimation, Everglades, Florida, wading birds.

Fuentes de Variación en la Detección de Aves Vadeadoras mediante Censos desde el Aire en los Everglades de Florida

RESUMEN.—Realizamos ensayos con dos observadores para estimar las probabilidades de detección (la probabilidad de que un grupo que está presente y disponible sea detectado) para censos de aves vadeadoras realizados desde el aire utilizando aeronaves con alas fijas en el sistema de los Everglades, Florida. La probabilidad de detección estuvo en un rango de entre <0.2 y ~0.75, y varió de acuerdo a la especie, al tamaño del grupo, al observador y a la posición del observador en la aeronave (en el asiento de adelante o en el de atrás). Las simulaciones de censos aéreos indicaron que la detección incompleta puede tener un efecto sustancial sobre la evaluación de las tendencias poblacionales, particularmente a lo largo de intervalos relativamente cortos (≤ 3 años) y en relación con cambios pequeños en el tamaño de las poblaciones ($\leq 3\%$). Concluimos que los sesgos en la detección son una consideración importante para interpretar las observaciones realizadas a partir de censos de aves vadeadoras realizados desde el aire, que potencialmente limitan el uso de estos datos para propósitos comparativos y de análisis de tendencias. Recomendamos que los investigadores que realizan censos de aves vadeadoras desde el aire se propongan reducir los sesgos en la detección causados por el observador y por otras fuentes controlables. Además, recomendamos que se consideren las fuentes no controlables mediante la realización de censos con dos observadores y la incorporación de otros métodos de calibración (e.g., el uso de muestreos dobles) como parte del diseño de los censos.

AERIAL COUNTS OF bird populations are typically incomplete because some fraction of the population is not detected during surveys (Johnson et al. 1989, Bromley et al. 1995, Dodd and Murphy 1995, Rodgers et al. 1995, Smith et al. 1995, Frederick et al. 1996,

Kingsford 1999). Although the sources of undercounting are varied, they can be roughly grouped into two categories: observer variability and visibility biases. Observers differ in their ability to detect and identify individuals, with differences often related to

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observer experience (Kendall et al. 1996) or visual acuity (Sauer et al. 1994). Observer variability can be reduced through the use of well-trained and experienced observers; however, even the most experienced observers will be unable to detect all individuals because of imperfect visibility, so counts may still be biased low. "Visibility bias" is defined here as over- or undercounting of populations because of variation in the ability to detect and identify individuals. Survey-induced bias is a source of bias that is inherent in the design of sampling protocols. For example, height and speed of the survey aircraft and transect width introduce certain biases (Pollock and Kendall 1987). Variability in detection rates can be reduced through the use of standardized survey protocols, but it is difficult to eliminate bias completely from this source.

Detection can vary among bird species (Pollock and Kendall 1987). Body size or coloration may influence the ability to detect birds. For example, larger and more colorful wading birds are generally more conspicuous and, therefore, are detected more frequently (Kingsford 1999). Species-specific behaviors, such as aggregative foraging behaviors, can also influence the ability to obtain accurate counts. Birds typically found in large (>5,000) or small (<10) aggregations are more difficult to count or detect, respectively, which results in inaccurate counts for these species (Kingsford 1999, Frederick et al. 2003). The habitat characteristics of survey areas also can affect detection (Bibby and Buckland 1987, Smith et al. 1995); for example, physical structures, such as tall grasses and tree canopies, can impair visibility.

Failure to account for incomplete detection results in biased estimators of abundance or other population parameters. Likewise, heterogeneous visibility induces variation in data that can confound inferences, such as comparisons between species or over time and space (Williams et al. 2002). Thus, our objectives in the present study were to (1) estimate detection rates for wading birds from aerial surveys of the Everglades system, (2) investigate sources of variation in detection rates among species and in relation to operational aspects of the surveys, and (3) examine the potential influence of incomplete detection on the evaluation of bird population trends.

METHODS

Our primary goals were to quantify the effects of various factors on detection of wading birds during aerial surveys and to evaluate the influence of these factors on interpretation of population trends. Thus, our analysis consisted of two parts: (1) we developed empirical models relating wading-bird detection to habitat, species, and observer effects; and (2) we used these models to evaluate the influence of incomplete detection on the detection and estimation of trends in wading-bird abundance via simulation.

Study area.—The Everglades basin is one of the world's largest wetland systems (11,640 km²; Fig. 1); the basin has undergone dramatic anthropogenic alterations, starting in the early 1900s. Concomitantly, there were large reductions in the number of wading birds using the system, though other factors, including changes external to the Everglades system, may have contributed to their declines (Walters et al. 1992).

Systematic Reconnaissance Flights survey.—The Systematic Reconnaissance Flights (SRF) survey is intended to record the relative abundance, flock composition, and spatiotemporal distribution

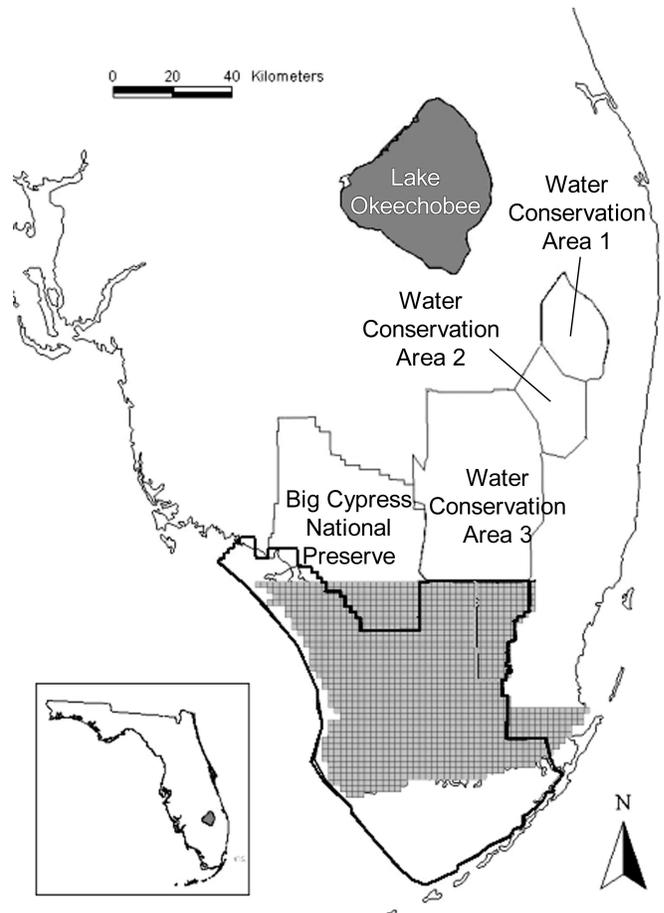


FIG. 1. Location of Everglades study areas and Systematic Reconnaissance Flights (SRF), with areas covered by the SRF indicated by cross-hatching in the Everglades National Park (bold outline).

of foraging wading birds across the entire Everglades system (Hoffman et al. 1990, Bancroft and Sawicki 1995, Sawicki et al. 1995, G. J. Russell and K. M. Portier unpubl. data). The surveys are conducted monthly during the historically drier part of the year (December–June), which includes the nesting season, but at least one survey is usually conducted in August, at the height of the wet season. The survey is also used to assess general surface-water conditions throughout the survey area and, in some survey areas, to assess vegetation conditions.

Aerial surveys were initiated in 1985, following a one-year pilot study (Portier and Smith 1984). The survey area comprised the water conservation areas (WCA) of the northern and central Everglades, Everglades National Park (ENP) and southern Big Cypress National Preserve (BCNP) in the south, and BCNP proper in the west. Surveys in the northern and central Everglades (hereafter "northern survey area") were initially conducted by the National Audubon Society (NAS) through a contract with the South Florida Water Management District (SFWMD) (Hoffman et al. 1990, Bancroft and Sawicki 1995, Sawicki et al. 1995). Surveys in the BCNP (hereafter "western survey area") were initially conducted by the Florida Fish and Wildlife Conservation Commission (FWC)

(J. Schortemeyer, Florida Fish and Wildlife Conservation Commission, pers. comm.). However, the U.S. Army Corps of Engineers (USACE) now surveys both the northern and western survey areas (USACE, Vicksburg, Mississippi, unpubl. data), having assumed survey responsibilities from the NAS in 1996 and from the FWC in 1998. The southern survey area has been continually surveyed by ENP personnel since 1985 (G. J. Russell and K. M. Portier unpubl. data).

Transects oriented east–west were spaced 2 km apart throughout the surveyed region. For purposes of data organization and reporting, transects were subdivided longitudinally into 2-km segments. Georeferencing equipment (LORAN C or GPS) was used to assure consistency in line and segment location among surveys. A fixed-wing aircraft flying at 148 km h⁻¹ ground speed follows the transects in alternating directions. Surveys are flown at a height of 61 m and strip width of 150 m per observer (left and right) for a total of 300 m. Aircraft altitude was variously identified as 45 m (D. M. Fleming et al. unpubl. data), 61 m (Hoffman et al. 1990, Bancroft and Sawicki 1995, Sawicki et al. 1995), and 90 m (G. J. Russell and K. M. Portier unpubl. data).

Survey aircraft generally contained the pilot, two observers of wading birds, and a front-seat observer, whose responsibilities were to record water surface conditions and other ancillary data and to monitor the location of the aircraft in relation to the transect. However, both the crew complement and individuals' roles have varied through time and among survey areas. Observers recorded species, number, and location (longitude) of all wading birds sighted within the transect strips. Counts of Great Egret (*Ardea alba*), Great Blue Heron (*A. herodias*), White Ibis (*Eudocimus albus*), Glossy Ibis (*Plegadis falcinellus*), and Wood Stork (*Mycteria americana*) were recorded. In the southern survey area, counts of Great White Heron (white morph of Great Blue Heron) and Roseate Spoonbill (*Platalea ajaja*) were also recorded. Individuals of smaller-bodied, dark-plumaged species were counted collectively in a "Small Dark Herons" class that included (depending on survey area) Tricolored Heron (*Egretta tricolor*), adult Little Blue Heron (*E. caerulea*), Green Heron (*Butorides virescens*), Black-crowned Night-Heron (*Nycticorax nycticorax*), Yellow-crowned Night-Heron (*Nyctanassa violacea*), and the dark phase of Reddish Egret (*E. rufescens*). Depending on the survey area, a class of "Small Light Herons" were counted that included Snowy Egret (*E. thula*), Cattle Egret (*Bubulcus ibis*), immature Little Blue Heron, and the light phase of Reddish Egret. During the surveys, observers also visually categorized the types of foraging habitats within the transect strips on the basis of estimated water depth and coverage. These surface water conditions were recorded in five categories—dry (DD), dry transitional (DT), wet–dry (WD), wet–transitional (WT), and wet (WW)—and used as covariates for modeling detection.

Components of detection.—Before describing our dual-observer trials, we note that detection in the SRF (or other survey) has three components: (1) groups of birds are present in the sampling unit and available for detection, (2) present and available groups are detected by an observer, and (3) the number of birds present in each group detected is accurately counted. Let $y_i = 1$ be the event that a group of birds present on sampling unit i is detected, $y_i = 0$ be the complementary event that the group is missed, and $p_i = \text{Prob}(y_i = 1)$ be the probability that the group is detected; as we will

show, p_i may depend on the number of birds actually present in the group, as well as other factors. Now, let C_i be the observed count of birds and N_i the number of birds actually present on the i^{th} sampling unit. Naive estimation of N_i using unadjusted counts C_i requires the assumptions (1) that 100% of groups are detected (i.e., $p_i = 1$) and (2) that groups detected are accurately counted ($E(C_i) = N_i$). We note that (assuming no species misidentification or misassignment of species to class) the number of groups detected is some fraction of the available groups ($p_i \leq 1$), but, in principle, it is possible to overcount ($E(C_i) > N_i$) as well as undercount ($E(C_i) < N_i$) groups. Our study design was directed at the second of these components (p_i), group detection, but considers the group counts to the extent that the numbers of birds present in a group can potentially influence group detection. We discuss the third component when we consider the implications of our findings, below.

Dual-observer trials.—To evaluate visibility (detection) rates on the SRF, we designed dual-observer trials, which were flown by biologists from Everglades National Park during February and March 2004, in conjunction with the operational SRF (Fig. 1). We initially considered employing distance-sampling methods (Buckland et al. 2001) to estimate detection but rejected this approach as infeasible because of logistical difficulties of accurately classifying groups into more than two distance categories in flight. As with the SRF, 300-m (150 m per observer) fixed-width strip plots were flown; all flights were conducted at an altitude of 61 m. During these trials, one observer was seated in the right front seat (RF) and the other in the right rear seat (RR). Three observers (labeled observer E, L, or M) rotated between the front and back seat positions over the course of eight survey days. Training flights were conducted to familiarize the observers with survey protocol, species identification, and estimation of numbers. Observers independently recorded the number of birds detected by species via electronic recorders and did not communicate or otherwise provide cues to one another. We matched observations of species groups between observers by synchronization of observation times, assuming that observations of the same species taken within 10 s (~400 m at aircraft speed) by two observers were of the same group of birds. Generally, observers agreed on the species identity for each group, but in cases where identity differed, we assumed that the observers saw different groups. Most flocks were of a single species, but in cases where mixed flocks occurred, observers assigned identity to the predominant species, excluding groups that could not clearly be assigned to a species. Observers generally agreed closely on group size, especially for small (<10 individuals) groups, but in cases of major discrepancy (>25% disagreement in count), we assumed that different groups were detected. As noted below, group size was also used as a covariate to predict detection rates. The observations were used to construct group detection histories for nine species or species classes: Great Egrets (GREG), White Ibis (WHIB), Great Blue Herons (GBH), small dark herons (SDH), small white herons (SWH), Wood Storks (WS), Glossy Ibis (GI), Roseate Spoonbills (RS), and Great White Herons (GWH). A detection history contained an indicator digit for each observer-position, "11" denoting detection by both observers, "10" by RF but not RR, and "01" by RR but not RF. A detection history of "00" occurred if no groups for the species of interest were detected over a 10-s interval; however, as discussed below, these observations were not included in the analysis.

Statistical analyses.—Our statistical model is a special case of modeling detection via multiple independent observers (Williams et al. 2002). To model detection probability, we conditioned on detection by at least one observer. Thus, we modeled the effects of species, observer, and seat position via a conditional, single-trial multinomial, with event probabilities as

$$P(x_i = 10 | o_1, o_2) = \frac{p_i(o_1, 0)[1 - p_i(o_2, 1)]}{p_i(\cdot)}$$

and $P(x_i = 01 | o_1, o_2) = \frac{[1 - p_i(o_1, 0)]p_i(o_2, 1)}{p_i(\cdot)}$

and $P(x_i = 11 | o_1, o_2) = \frac{p_i(o_1, 0)p_i(o_2, 1)}{p_i(\cdot)}$

where $p_i(j, k)$ is the probability of encounter of species i by observers $j = o_1, o_2$ in the front ($k = 0$) and rear ($k = 1$) seat positions, respectively, and

$$p_i(\cdot) = p_i(o_1, 0)[1 - p_i(o_2, 1)] + [1 - p_i(o_1, 0)]p_i(o_2, 1) + p_i(o_1, 0)p_i(o_2, 1).$$

Additionally, we considered models in which probability of detection was influenced by group size and water conditions. Of course, we did not know actual group size N_p , but instead took as our covariate predictor observed size, C_p , as follows. First, we calculated C_i as the average of RF and RR observers' counts when $x_i = 11$, and as the count for the observer that detected the group otherwise. We then summarized the data by five group-size categories: $C_i = 1$; $1 < C_i \leq 5$; $5 < C_i \leq 10$; $10 < C_i \leq 50$; and $C_i > 50$. Finally, we used recorded water conditions (five categories described earlier) as predictors potentially explaining variability in detection attributable to physical characteristics of the habitat.

Our basic statistical model for detection probability was

$$\text{logit}(p_{spp, obs, pos, group, water}) = \underline{\beta}X$$

$$\text{where } \text{logit}(p) = \ln\left(\frac{p}{1-p}\right)$$

and where $\underline{\beta}$ is a vector of parameters to be estimated and X a design matrix representing main effects and interactions among factors considered. For example, the model "species + observer + position" specifying main effects of species identity, observer, and seat position would be expressed as

$$\text{logit}(p_{spp, obs, pos}) = \beta_0 + \sum_{j=1}^8 \beta_{spp, j} I(spp = j) + \sum_{m=1}^2 \beta_{obs, m} I(obs = m) + \beta_{pos} I(pos = front)$$

where β_0 is an intercept, and β_{spp} , β_{obs} , β_{pos} are the $k - 1$ coefficients corresponding to the k levels of each categorical variable. A fully interactive model for the above three factors (species*observer*position) would be specified by the above model plus all second- and third-order interactions. Both water conditions and group counts were recorded in five categories, and we initially treated these factors as categorical variables in the models, as above.

However, this treatment produced models with excessive numbers of parameters and poor convergence, and we therefore recast both factors as continuous variables, with water conditions on the original scale (1–5) and using the medians for each of the group-size categories. We initially attempted to model these data using continuous counts but encountered problems with model convergence and excessive computing time because of the large number of observations (>4,000 individual encounter histories vs. 411 histories summarized by categories). We used this approach to construct models incorporating each of these factors in combination with the categorical factors. For instance, a model incorporating fully interactive species*observer*position factors with an additive group-size effect would be

$$\text{logit}(p_{spp, obs, pos}) = \text{logit}(p_{spp, obs, pos}) + \beta_{count} \times count$$

where $\text{logit}(p_{spp, obs, pos})$ is the fully interactive (main effects and all interactions) model described above and $count$ is the median value for a group-size category. The global model was specified as the fully interactive model together with the main effects of group count and water conditions and the interactions of these two factors with all main effects and interactions of the species*observer*position model.

The nature of our data precluded the use of existing capture–recapture software (e.g., MARK) for fitting models relating bird detection to species and observation-specific characteristics (e.g., observer). Therefore, we fitted alternative models of wading-bird detection with Markov-chain Monte Carlo (MCMC; Gilks et al. 1996), using information-theoretic criteria (Akaike 1973, Spiegelhalter et al. 2002) to compare alternative models. Models were implemented using PyMC, a module for the Python programming language (see Acknowledgments) that implements a random-walk Metropolis–Hastings sampler. Models were run for 20,000 iterations and the initial 10,000 iterations were discarded as burn-in before analysis.

We used uniform prior distributions for all model parameters (Lambert et al. 2005, Gelman 2006). Because none of our models contained random effects, effective parameter size (Spiegelhalter et al. 2002) was not an issue. Therefore, for model selection, we used posterior mean deviances adjusted by the parameter count to compute Akaike's information criterion (AIC) values and corresponding model weights (Burnham and Anderson 2002). Akaike's information criterion is an entropy-based measure used to compare candidate models that describe the same data (Burnham and Anderson 2002), the best-fitting model having the lowest AIC.

The goal of our modeling was to identify the most parsimonious predictive models, given our data. We began by constructing a global model based on previous investigations of bird detection (Bibby and Buckland 1987, Smith et al. 1995, Kendall et al. 1996, Kingsford 1999). We then fitted 12 candidate models (subsets of the global model) representing hypothesized effects of combinations of factors on detection of wading birds. The relative plausibility of each candidate model was assessed by calculating Akaike weights (w) as described in Burnham and Anderson (2002), the most plausible model having the greatest Akaike weight (range: 0–1). Goodness-of-fit for the global model was evaluated using a Bayesian goodness-of-fit procedure proposed by Gelman et al. (1995). This measure computes the proportion of observations for

which the deviance of the observed data exceeds the deviance of data simulated under the assumed model; under perfect model fit, this value is expected to be 0.5.

Because of the relative performance of the competing models (see below), we based all inferences and predictions on the model with the highest Akaike weight. The precision of each predictor was estimated by computing 95% credibility intervals, which are analogous to 95% confidence intervals. To facilitate interpretation of model parameters, we used the posterior distributions of parameter values from the best-fitting model to generate predictions of wading-bird detection probabilities, as follows. First, for each combination of predictors (e.g., species, observer, position, group size, and water conditions), we drew parameter values from normal distributions, with mean and standard deviation specified by the posterior distribution of the parameter estimates. We then generated posterior predictions of wading-bird detection probabilities for the best-fitting model by running an additional 10,000 simulation iterations.

Evaluation of effect of visibility bias on bird abundance trends.—We were concerned that incomplete and heterogeneous detection of birds during sampling might affect models of wading-bird abundance and distribution and, hence, statistical inferences regarding population trends and bird distribution patterns. We evaluated the influence of incomplete detection by conducting relatively simple simulations of SRF sampling protocols using specified abundances and population growth rates for Great Egret and White Ibis. Each simulation began with a specified initial number of birds in the surveyed population, different for the two species. The simulated sampling crew consisted of two observers who counted during the entire sampling period, never changing from their randomly assigned rear seats with each observer counting only birds on his side of the aircraft. The number of groups (flocks) of birds foraging during the survey was modeled as a function of the total number of birds in the population using an empirical model parameterized using SRF survey data (Table 1). The number of birds per flock was randomly generated assuming (1) a negative binomial distribution with a mean equal to the population size divided by the number of groups and (2) variance that was modeled as a function of the mean (Table 1). During sampling, individual groups of birds were randomly assigned to an observer. Then, detection of individual groups was randomly determined using a Bernoulli distribution with probability of success estimated as a function of the observer, location (rear seat), species,

group size, and water conditions, using the best-fitting model estimated above. If a group was detected, we assumed that all members were counted accurately. Abundance was then estimated as the sum of all birds detected by both observers. During the next time-step, the abundance changed, assuming a fixed population growth rate (λ) that varied with simulation scenario (Table 1). This population was then sampled using the same protocol with two randomly assigned observers. The process was repeated until the specified time-frame was reached (Table 1). We assume that trends in wading-bird populations through time are generally evaluated via linear (or similar) regression. Thus, the simulated actual and observed population trends were estimated by fitting a linear regression model of the simulated actual and observed population size, respectively, versus survey year. The assessment of a trend was assumed when the P value for the regression slope was ≤ 0.10 .

We evaluated the relative influence of population size, rate of population change, and number of years surveyed on the detection of population change by evaluating all possible combinations of three initial population sizes, nine population growth rates, and five survey durations (Table 1). For each scenario and species, we ran 1,000 replicate simulations and estimated (1) the trend assessment rate, defined as correctly finding an actual positive or negative trend in population change; (2) the trend assessment error rate, defined as falsely finding a trend when none was present or incorrectly determining the direction of an actual trend; and (3) the relative bias in the slope of the regression, which was estimated as the actual slope minus the observed slope.

RESULTS

Detection estimation.—We successfully completed eight survey days with dual observers during February and March 2004. Surveys generally commenced at ~0730 hours and were completed by ~1500 hours (EST). Front and back observers were paired throughout, rotating as previously described; however, in the first (morning) portion of the 3 March survey, data for the back seat were lost because of a recording error, and the front-seat observations were, therefore, excluded from analysis. We obtained 4,152 detections (occasions where one or more birds were counted) by at least one observer, with frequencies of 1,373, 1,984, and 795 among the 01, 10, and 11 observer-position histories, respectively (Table 2). The most frequently detected species were Great Egret (2,424 detections), and White Ibis (1,001), whereas the remaining seven

TABLE 1. Parameters used during simulation of SRF sampling protocols. The coefficients of determination (r^2) values are for models fit to SRF data of observed bird counts and group sizes.

Simulation component	Great Egret	White Ibis
Initial population size	5,000, 7,000, 10,000	5,000, 10,000, 15,000
Population growth per year	No change ($\lambda = 1$), increase or decrease of 0.01, 0.03, 0.05, or 0.07	
Number of years sampled	3, 5, 7, 9, 11	
Number of groups ^a	$0.478 + 0.818 \cdot \ln(\text{population size})$, $r^2 = 0.81$	$199.82 + 0.050 \cdot (\text{population size})$, $r^2 = 0.71$
Variation in group size ^b	$0.420 + 1.461 \cdot \ln(\text{mean group size})$, $r^2 = 0.71$	$0.323 + 1.208 \cdot \ln(\text{mean group size})$, $r^2 = 0.88$

^aEstimate for number of Great Egret groups required exponential transformation.

^bVariation is expressed as a standard deviation and required exponential transformation for both species.

TABLE 2. Summarized detection histories by species for dual-observer detection trials.

Species	Detection history ^a			Total detections	Group size		
	01	10	11		Mean	Standard error	Range
Great Egret	745	1,093	586	2,424	1.77	2.34	1–75
White Ibis	348	485	168	1,001	6.88	18.87	1–275
Great Blue Heron	83	95	17	195	1.04	0.19	1–2
Small dark herons	40	49	5	94	1.57	1.08	1–6
Small white herons	77	145	2	224	1.49	1.50	1–15
Wood Stork	53	85	11	149	2.32	3.13	1–28
Glossy Ibis	12	13	2	27	4.24	5.05	1–20
Roseate Spoonbill	12	17	4	33	1.84	1.80	1–10
Great White Heron	3	2	0	5	1.00	0	1–1
Total	1,373	1,984	795	4,152			

^a01 = detected by second observer and not first; 10 = detected by first and not second; 11 = detected by both.

species or species groups accounted for 727 detections. Estimated size of detected groups ranged from 1 to 275, and average group sizes were greatest for Great Egret and Glossy Ibis.

Examination of the MCMC goodness-of-fit measure indicated that the global model adequately fit the data (Table 3). The top-ranked model of wading-bird detection included species, observer, and seat-position interactive effects, with additive group-size effects (Table 3); this model accrued virtually 100% of the total AIC weight. We present the parameter estimates for the species \times observer \times position effects back-transformed to the original probability scale (Table 4); these estimates represent the intercept for the fully interactive model before the addition of the group-size effect (Table 4). Parameter estimates and posterior predictions indicated substantial variation in detection among species, with Great Egret and White Ibis having higher predicted detection probabilities than other species (Fig. 2A). Detection probability also varied across observers and seemed to depend on position in the aircraft; detection of small flocks of Great Egrets was higher for observer M and in the front-seat position (Fig. 2B). Finally, predicted detection varied with group size, with increasing detection with increasing group sizes;

however, we note that this analysis does not take counting inaccuracies into account but, rather, assumes that observers perfectly counted a group if it was detected (Fig. 2C).

Evaluation of effect of visibility bias on assessment of bird abundance trends.—Simulations of the effect of incomplete detection on the evaluation of wading-bird population trends indicated that the effects were similar among different initial population sizes and between species but differed depending on the rate of population change and numbers of years surveyed; correct assessment of trends was positively related to the rate of population change and numbers of years surveyed (Fig. 3). Correct assessment rates were lowest for three survey years and were generally <60%, on average, across species and growth rates (Fig. 3). After seven years, correct assessment was 100% when population growth rates were relatively high ($\pm 5\%$ and 7% per year), but assessments were much lower for smaller growth rates. By contrast, false assessment rates were highest when population growth rate and number of survey years were low, and greatest under no population change (Fig. 4). The simulations suggest that false trend rates are as high as 10% even after 11 survey years for both species, under no population change.

TABLE 3. Akaike's information criterion (AIC) values, AIC difference (ΔAIC_c), Akaike weights (w_i), and number of parameters (K) for predicting wading-bird detection probabilities during Systematic Reconnaissance Flights (SRF) surveys. Akaike weights are interpreted as relative plausibility of each model (i).

Model	AIC	ΔAIC_c	w_i	K
Species*observer*seat position + group size	8,366.63	0.00	>0.999	55
Species*observer*seat position	8,381.79	15.16	<0.001	54
Species + group size	8,408.54	41.91	<0.001	10
Species*observer*group size	8,414.77	48.15	<0.001	38
Species + observer + count + water + seat position	8,419.35	52.72	<0.001	17
Species*observer	8,423.61	56.98	<0.001	27
Species + observer + seat position	8,425.87	59.24	<0.001	12
Species*seat position*group size	8,453.94	87.32	<0.001	28
Species + observer	8,514.61	147.98	<0.001	11
Species	8,564.47	197.84	<0.001	9
Species*observer*seat position*group size	8,597.44	230.81	<0.001	109
Null (constant detection)	8,715.75	349.12	<0.001	1
Species*observer*group size*water*seat position ^a	10,931.95	2,565.32	<0.001	539

^aGlobal model (Bayesian goodness-of-fit, $P = 0.16$).

TABLE 4. Parameter estimates (mean ± SE) and 95% credibility intervals (CI) for best-fitting model of wading-bird detection during Systematic Reconnaissance Flights (SRF) surveys.

Parameter ^a	Species	Observer	Seat position	Parameter estimate ^{b, c}	95% CI
Group size (β)				0.024 ± 0.006	0.012–0.036
p^b	Great Egret	E	Front	0.407 ± 0.024	0.360–0.449
			Rear	0.398 ± 0.019	0.361–0.436
		L	Front	0.384 ± 0.025	0.337–0.435
			Rear	0.280 ± 0.017	0.246–0.311
		M	Front	0.465 ± 0.021	0.426–0.511
			Rear	0.318 ± 0.022	0.272–0.358
	White Ibis	E	Front	0.243 ± 0.032	0.177–0.301
			Rear	0.244 ± 0.025	0.186–0.291
		L	Front	0.230 ± 0.027	0.171–0.274
			Rear	0.176 ± 0.026	0.127–0.222
		M	Front	0.375 ± 0.036	0.294–0.442
			Rear	0.278 ± 0.034	0.186–0.336
	Great Blue Heron	E	Front	0.210 ± 0.064	0.106–0.338
			Rear	0.201 ± 0.056	0.112–0.368
		L	Front	0.130 ± 0.059	0.035–0.254
			Rear	0.230 ± 0.062	0.128–0.338
		M	Front	0.246 ± 0.052	0.137–0.329
			Rear	0.093 ± 0.045	0.024–0.219
	Small dark herons	E	Front	0.176 ± 0.070	0.066–0.321
			Rear	0.139 ± 0.045	0.063–0.229
		L	Front	0.085 ± 0.056	0.013–0.219
			Rear	0.362 ± 0.078	0.242–0.508
		M	Front	0.236 ± 0.070	0.095–0.358
			Rear	0.110 ± 0.073	0.017–0.261
	Small white herons	E	Front	0.082 ± 0.044	0.016–0.177
			Rear	0.030 ± 0.011	0.013–0.054
		L	Front	0.027 ± 0.018	0.003–0.072
			Rear	0.188 ± 0.076	0.041–0.321
		M	Front	0.284 ± 0.065	0.162–0.412
			Rear	0.069 ± 0.044	0.009–0.180
	Wood Stork	E	Front	0.143 ± 0.081	0.032–0.301
			Rear	0.109 ± 0.035	0.054–0.185
		L	Front	0.178 ± 0.072	0.059–0.302
			Rear	0.162 ± 0.082	0.043–0.304
		M	Front	0.270 ± 0.064	0.150–0.404
			Rear	0.094 ± 0.036	0.031–0.163
	Glossy Ibis	E	Front	0.405 ± 0.201	0.039–0.699
			Rear	0.272 ± 0.083	0.153–0.436
		L	Front	0.084 ± 0.059	0.005–0.205
			Rear	0.514 ± 0.115	0.342–0.707
		M	Front	0.521 ± 0.093	0.372–0.679
			Rear	0.161 ± 0.068	0.030–0.326
	Roseate Spoonbill	E	Front	0.526 ± 0.183	0.248–0.838
			Rear	0.131 ± 0.049	0.028–0.246
		L	Front	0.459 ± 0.093	0.292–0.684
			Rear	0.501 ± 0.060	0.398–0.636
		M	Front	0.190 ± 0.068	0.045–0.303
			Rear	0.454 ± 0.201	0.138–0.699
Great White Heron	E	Front	0.448 ± 0.106	0.303–0.644	
		Rear	0.234 ± 0.123	0.029–0.441	
	L	Front	0.116 ± 0.081	0.005–0.299	
		Rear	0.610 ± 0.162	0.335–0.808	
	M	Front	0.583 ± 0.171	0.191–0.813	
		Rear	0.341 ± 0.123	0.135–0.541	

^aModel predicts detection as $\text{logit}(p) = \text{logit}(p_{\text{spp, obs, pos}}) + \beta \times \text{count}$, where *count* is median group size in each of five categories: $C = 1$; $1 < C_{ij} \leq 5$; $5 < C \leq 10$; $10 < C \leq 50$; and $C > 50$ and $\text{logit}(p_{\text{spp, obs, pos}})$, a fully interactive species × observer × seat-position model.

^bParameter estimate is intercept of fully interactive (species × observer × position) model back-transformed to probability scale.

^cMean, SE, and 0.025 and 0.975 quantiles of posterior distribution for each parameter.

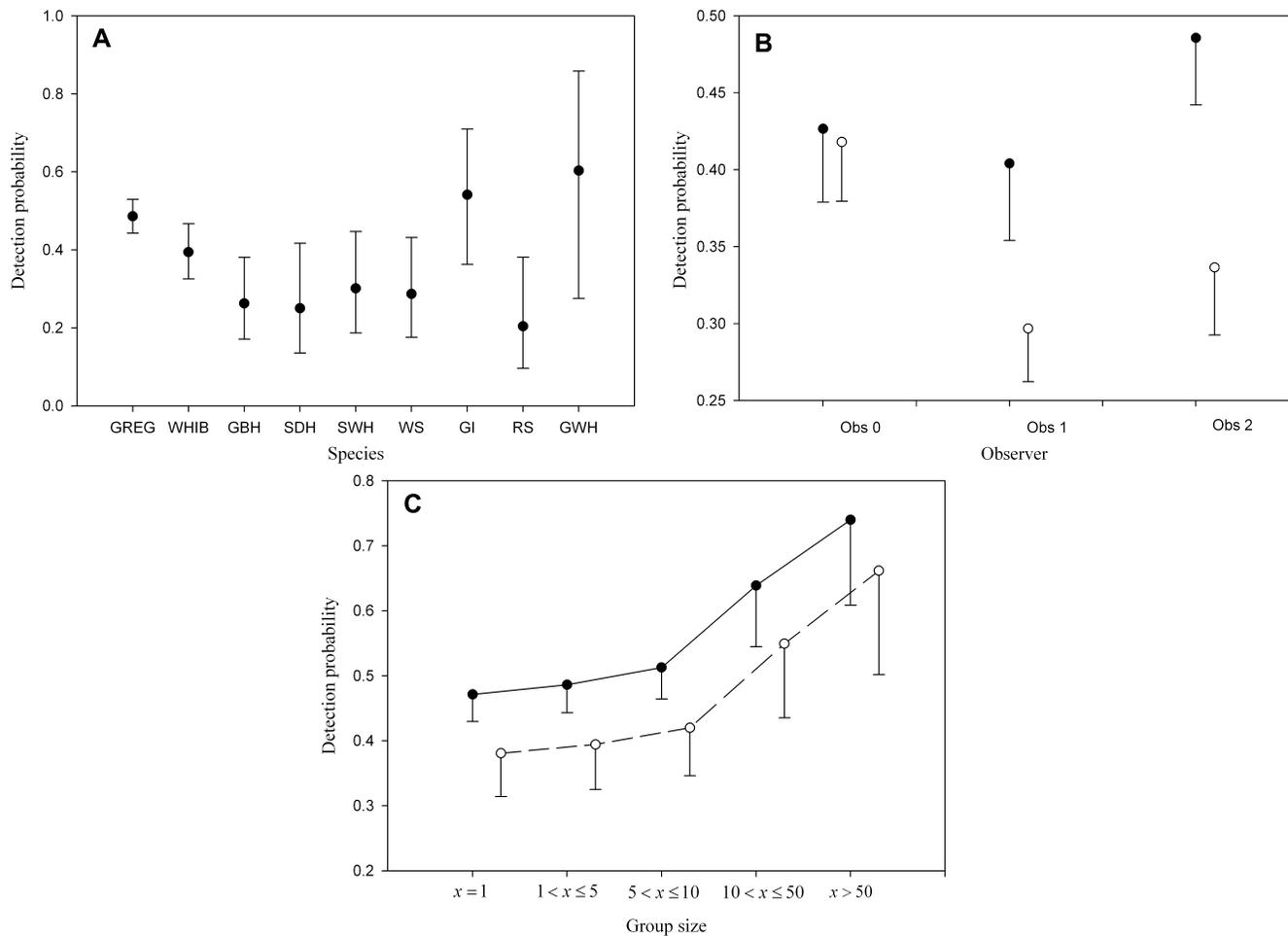


FIG. 2. Predicted detection probabilities (95% credibility intervals) in relation to selected combination of species, observer, position of observer in aircraft, and group size from dual-observer trials. (A) Detection in relation to species or species group, conditioned on observer M, front position t , and $1 < \text{flock size} \leq 5$. (B) Detection in relation to observer and position in aircraft, conditioned on species = Great Egret and $1 < \text{flock size} \leq 5$. (C) Detection in relation to group size for Great Egret and White Ibis, conditioned on observer M and front position.

An evaluation of the bias in the parameter estimates indicated little variability with initial population size (<10%) and number of survey years (Fig. 5). Observed estimates of the magnitude of the population change (i.e., the slope) were always lower than the true change, and the magnitude of the bias varied with population growth rate. When annual changes in population size were greatest ($\lambda = 0.93$ and 1.07), the observed slope underestimated the true rate of change, on average, by 0.035 and 0.021 for Great Egret and White Ibis, respectively. This represented 50% and 30% underestimates of the true population trends, respectively. In addition, the bias in slope estimates tended to increase with increased number of simulation years under scenarios with large changes in population growth rate.

DISCUSSION

Our dual-observer trials indicated that detection probabilities for aerial surveys of wading birds that follow procedures similar to the SRF may be lower than previously suggested. Hoffman et al. (1990) estimated that detection rates for wading birds in the SRF were

~ 0.85 . However, Russell and Portier (unpubl. data) estimated detection rates of 0.54 for “large dark birds” and 0.26 for “large white birds.” Our data indicate rates of 0.4–0.6, or even much lower, depending on species and other factors, and are certainly more in agreement with the estimates of Russell and Portier (unpubl. data).

With few exceptions, previous estimates of detection of birds from aerial surveys have been based on indirect evidence, such as comparison of aerial counts to other methods (e.g., ground observers) of unknown accuracy. Johnson et al. (1989) used independent observer trials and distance sampling to estimate detection probabilities as low as 0.16 for surveys of Mottled Ducks (*Anas fulvigula*) from fixed-wing aircraft. Smith et al. (1995), using experiments involving Mallard (*A. platyrhynchos*) decoys, inferred that detection probabilities varied from <0.3 to >0.7, principally because of differences in canopy cover. Bromley et al. (1995), Dodd and Murphy (1995), Rodgers et al. (1995), Kingsford (1995), and Frederick et al. (2003) used comparison of aerial to ground counts to infer detection probabilities ranging from 0.20 to 0.98, with wide variation attributable to species, group size, specific survey techniques, habitat, and bird behavior. However, Rodgers et al.

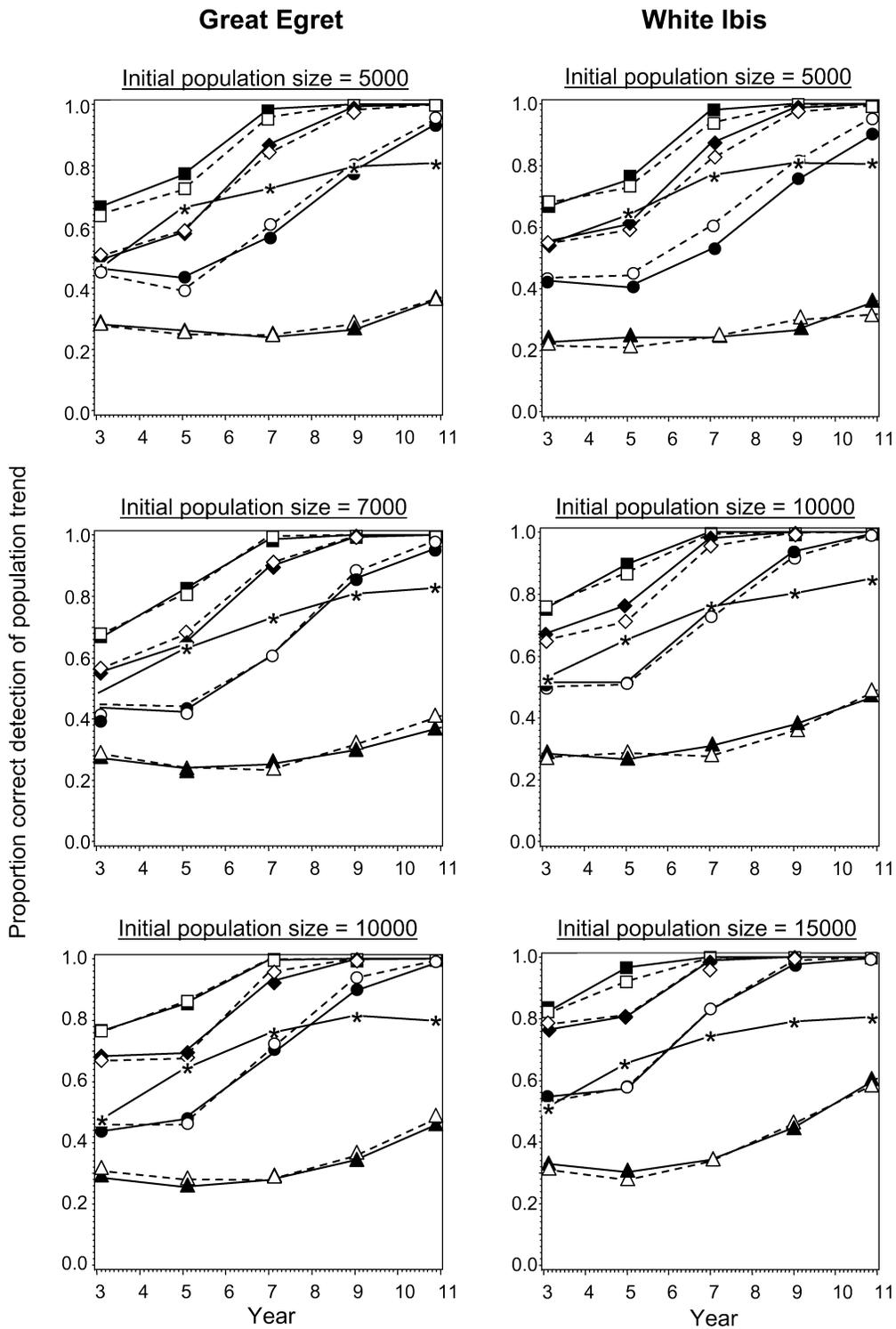


FIG. 3. Proportion of simulations that assessed the correct population trend by number of simulated sampling years, using linear regression and $\lambda = 0.10$ for simulated positive (solid line and symbols) and negative (broken line, open symbols) changes in annual population growth of 0.07 (square), 0.05 (diamond), 0.03 (circle), and 0.01 (triangle), and for no change (asterisk) and three initial population sizes for Great Egret (left) and White Ibis (right). Proportion based on 1,000 simulations of two randomly assigned rear observers during Systematic Reconnaissance Flights surveys.

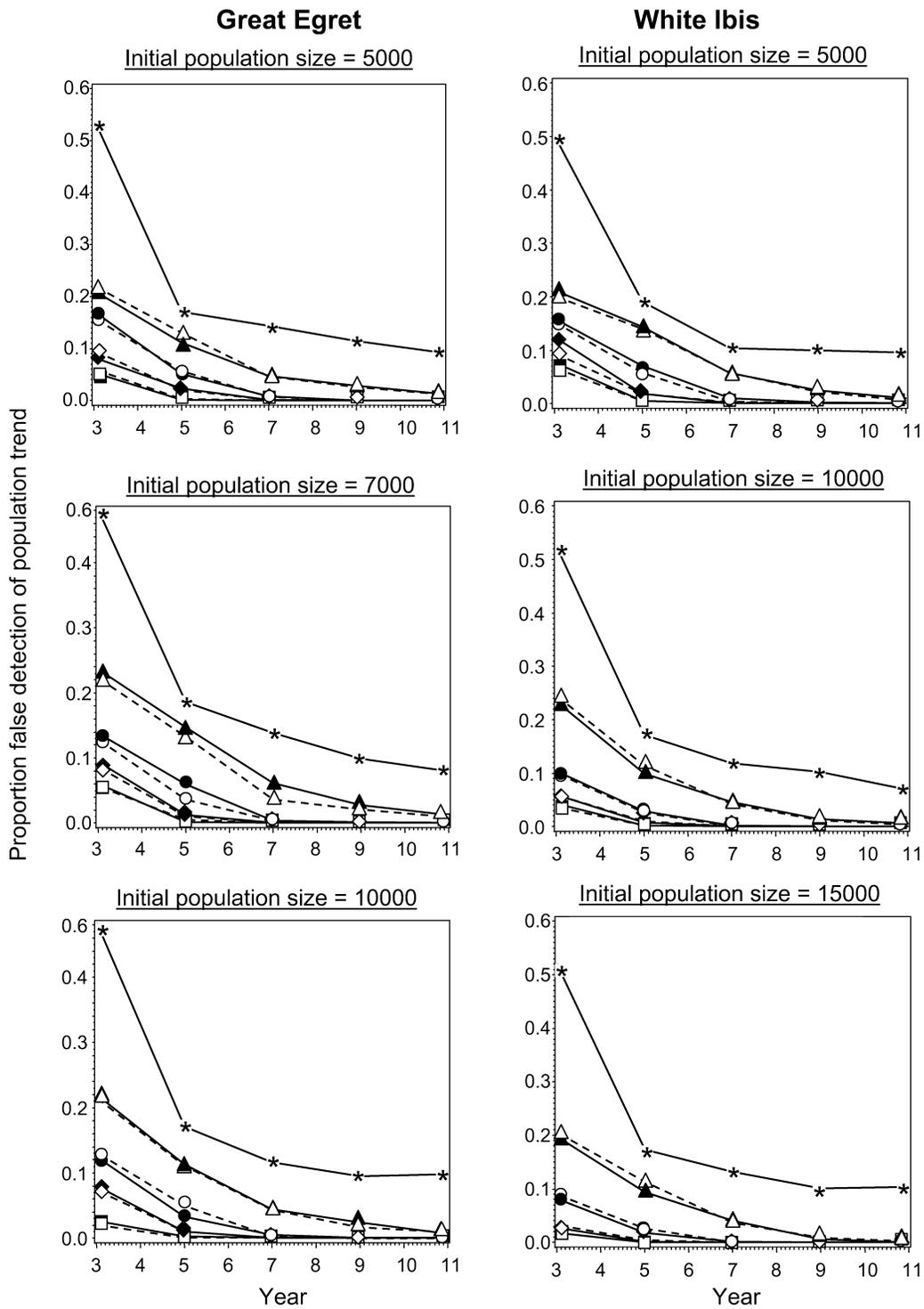


FIG. 4. Proportion of simulations that falsely assessed a population trend by number of simulated sampling years using linear regression and $\lambda = 0.10$ for simulated positive (solid line and symbols) and negative (broken line, open symbols) changes in annual population growth of 0.07 (square), 0.05 (diamond), 0.03 (circle), 0.01 (triangle), and no change (asterisk) and three initial population sizes for Great Egret (left) and White Ibis (right). Proportion based on 1,000 simulations of two randomly assigned rear observers during Systematic Reconnaissance Flights surveys. False assessments were defined as determining a significant decrease in population size ($\alpha = 0.10$) when there was a simulated increase and vice versa.

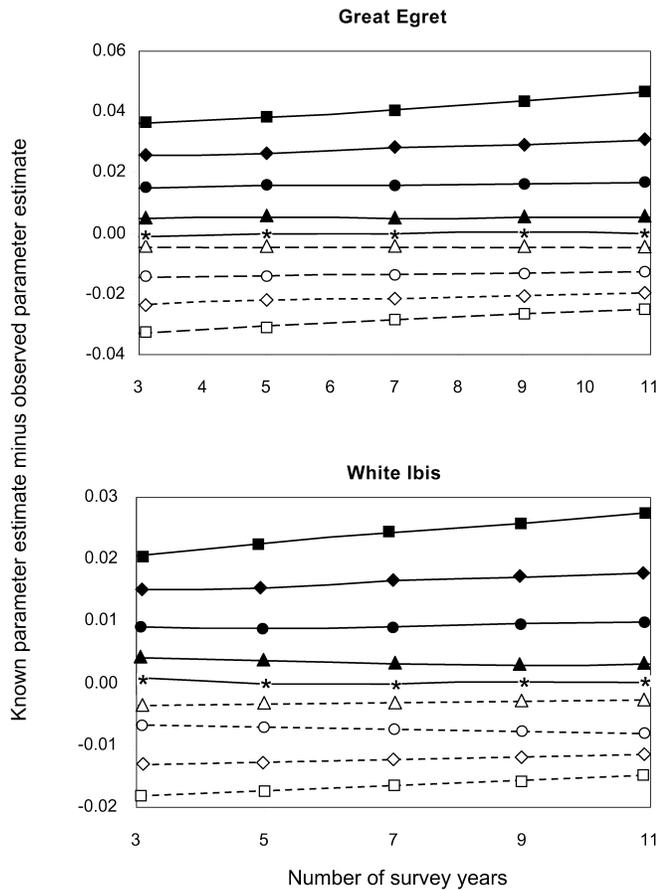


FIG. 5. Estimated bias in population trend (averages across initial population sizes) using linear regression by number of simulated sampling years for simulated positive (solid line and symbols) and negative (broken line, open symbols) changes in annual population growth of 0.07 (square), 0.05 (diamond), 0.03 (circle), and 0.01 (triangle) and for no change (asterisk) and three initial population sizes for Great Egret (top) and White Ibis (bottom). Bias is estimated as known parameter estimate (population growth rate) minus simulated observed estimate. Proportion based on 1,000 simulations of two randomly assigned rear observers during Systematic Reconnaissance Flights surveys.

(1995) and Kingsford (1999) found aerial-to-ground count ratios >1, suggesting that in some cases ground counts may be less accurate than aerial counts. Our estimates, based on methods that do not depend on comparison to counts that are assumed to be accurate, are generally consistent with these previous estimates and confirm that detection of birds from aircraft is influenced by multiple factors, many beyond investigator control.

The dual-observer trials and accompanying statistical model required us to make several assumptions, violation of which could affect the validity of our results. First, the method requires the assumption that all observations were correctly classified into detection histories. At best, this was only approximately true, and classification errors could have arisen because of observer discrepancies in recording times, species identification, or group size. Because we considered a detection history to be “11” only if

these variables closely agreed for the two observers, it is possible that our analysis underestimates overall detection probability. We believe that errors in these factors would likely have only a small biasing effect and, in any case, we have no reason to suspect any systematic trends in errors; thus, inferences about factors influencing detection rate should be unaffected. Secondly, we must assume that the observers operated as independent detection trials, so that one observer’s detection did not influence the other’s. Because the observers were physically separated (front versus back seat), used separate recording devices, and were not in direct, voice communication during the trials, we believe that this assumption was met. Finally, we assumed that factors used as covariates to predict detection, such as species identity, observer identity, seat position, water conditions, and group size, were assessed and recorded accurately. Of these, the only factors for which non-negligible errors may have occurred were species identity and group size. However, because we used only data for which there was close agreement in these factors, we believe that these potential errors were also minimal.

We illustrate the effect of nondetection on naive estimation of abundance for White Ibis and Great Egret, using the mean posterior baseline value for P from Table 4, the mean posterior estimate for β_{group} , and two levels of group size: 7.3 birds per group (the average over the study for all species) and 50 birds per group (the median count in the highest group-size category) (Table 5). We assume that observers detect the 100 groups in the surveyed population at the predicted rate, and we apply the average group size to an estimate of abundance on the surveyed area. Naive estimation results in substantial (25–80%) underestimation, depending on species, survey conditions, and group size. A natural approach would be to obtain unbiased estimates of abundance; for example (Williams et al. 2002),

$$\hat{N}_i = \frac{C_i}{\hat{p}_i}$$

provides an approximately unbiased estimate of abundance on the i th sampling unit, given an uncorrected count (C_i) and an estimate of detection (\hat{p}_i). In practice, unbiased abundance estimation could be accomplished via direct incorporation of abundance as a posterior prediction, after accounting for appropriate sources of variation in detection.

Under-detection of birds from aerial surveys would be less of a concern if detection rates were constant (Williams et al. 2002). Unfortunately, our results strongly suggest that this assumption is invalid. We found that detection varied substantially among species, flock sizes, and observers. Use of aerial-survey data for comparative purposes and modeling must take into account that detection varies by species, in relation to group size (smaller groups tend to be missed more frequently) and operational issues (observer identity, position of observer in the aircraft). Many other controllable (e.g., aircraft altitude) and uncontrollable (e.g., year effects) factors that we were not able to examine may also affect detection rate. To the extent that these factors are unaccounted-for, caution should be exercised in interpreting comparisons based on raw counts from aerial surveys. In particular, comparing species with greatly different detection rates, combining data across species, and inferring habitat quality through comparisons of foraging-group size distributions are each likely to be biased by heterogeneous detection (Williams et al. 2002). Although, under certain conditions, uncorrected counts may be useful as indices

TABLE 5. Predicted effect of incomplete detection on naive estimation of abundance for Great Egrets and White Ibis.

Species	Observer	Seat position	\bar{x} group size = 7.3 $N = 730$		\bar{x} group size = 50 $N = 5,000$	
			n groups observed	Naive estimate of N^a	n groups observed	Naive estimate of N
Great Egret	E	Front	45	328.5	69	3,450
		Rear	44	321.2	68	3,400
	L	Front	43	313.9	67	3,350
		Rear	32	233.6	56	2,800
	M	Front	51	372.3	74	3,700
Rear		36	262.8	60	3,000	
White Ibis	E	Front	28	204.4	51	2,550
		Rear	28	204.4	51	2,550
	L	Front	26	189.8	49	2,450
		Rear	20	146	41	2,050
	M	Front	42	306.6	66	3,300
		Rear	31	226.3	56	2,800

^aDetected number of groups \times average group size.

(Williams et al. 2002), we suggest that those conditions are limited. For example, heterogeneity among species in detection rates might be unimportant in estimating trends for single species, if other sources of heterogeneity (e.g., those attributable to observer position and group size) could be controlled. However, managers are often interested in compositional variation in bird communities, in which case, heterogeneous detection among species, if uncorrected, would be totally confounded with even relative measures of species composition (Williams et al. 2002). Rather than imagining scenarios under which uncorrected counts could be valid indices, we prefer appropriate sampling and estimation procedures that avoid untestable assumptions.

Our simulation modeling also suggested that incomplete detection can lead to large biases in model parameter estimates using data that have not been corrected for detection. This was apparent in even simple models of population trends; the effects would be even more profound in models designed to estimate and predict the influence of physical and biotic factors on wading-bird abundance and distribution. Only under the most fortuitous circumstances would incomplete, heterogeneous detection have a neutral effect on model parameters and predictions. We can easily envisage situations in which detection rates could interact with physical or biotic predictors in a form of “demonic intrusion” (Hurlbert 1984) that either masks true relationships or creates apparent (but nonexistent) ones.

Our simulations were simplifications of the sampling process that did not include all the factors that are likely to affect population estimates. That is, our dual-observer experiments could address only factors that affect the detection of groups of birds and did not address the accuracy of counting for groups that are detected. Under- or over-counting of groups, obviously, would bias estimates of abundance, even if group detection were 100%; therefore, our estimates of detection may, in fact, be optimistic assessments of the accuracy of aerial-survey counts as abundance measures. For example, we assumed that all the birds in a group were counted if a group of birds was detected, whereas previous studies suggest that counts of birds can be off by as much as 70% (Frederick et al. 2003). Nonetheless, the simulations indicated that incomplete detection can have a substantial effect on the detection of population trends, particularly at

relatively short intervals (≤ 3 years) and small changes in population size. Given the effect of sampling error (i.e., random variation) on detection of population trends (Thompson 2002), we expect that detection of actual trends with data similar to the SRF counts would require longer intervals and larger changes in actual population sizes.

To minimize the influence of visibility bias on estimates of population change, methods for adjusting bird counts should be developed to ensure sound management decisions. One method of developing bias adjustments is through calibration of aerial surveys. This can be accomplished by comparing aerial counts with presumably more accurate counts, such as ground counts (Frederick et al. 1996, Kingsford 1999), boat counts (Conant et al. 1988), aerial photographs or videography (e.g., Dodd and Murphy 1995), and dual-observer sampling (present study) and through the use of known numbers of surrogates (e.g., duck decoys; Smith et al. 1995). Evaluations should be conducted under a variety of sampling conditions encountered in the study area and adjustments developed by relating the relative difference in counts to species traits and to sampling conditions such as water level.

Finally, technical limitations on the dual-observer experiments and data recording leave the possibility that some “detection histories” were misclassified, which, conceivably, could result in underestimation of detection. We doubt that such conditions were common enough to substantially influence our results, particularly our modeling of sources of variation in detection rates. Nevertheless, we suggest replication of these experiments, over a larger span of spatial and temporal conditions and with improved technology for classifying detection histories. Indeed, estimation of detection—by dual-observer experiments, ground calibration, or other means—could be incorporated into operational surveys via a double sampling design (Thompson 2002), in much the same way as is done for surveys of waterfowl (Pospahala et al. 1974, Smith 1995).

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