

BIASES IN POPULATION ESTIMATION FOR COLONIALY NESTING GREAT EGRETS
(*Ardea alba*) AND WHITE IBISES (*Eudocimus albus*) IN THE FLORIDA EVERGLADES

By

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To my parents, Susan and Douglas Williams, for their unflagging love and support. You guys
are the best

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Abstract of Thesis Presented to the Graduate School
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Estimating avian breeding population sizes often involves extrapolations derived from estimates of related biological parameters, and may therefore fail to account for bias introduced from several sources. In colonialy breeding birds, estimation of breeding population size is complicated by visual biases and by asynchronous nest initiation and turnover. We used artificial landmarks to create quadrats in nesting colonies, and quantified visual biases by counting the number of nests in a quadrat via both walk-in survey and aerial photography. Visual bias due to vegetative occlusion caused aerial surveys of White Ibises (*Eudocimus albus*) to underestimate numbers of nests by an average of 12.37% ($\pm 20.65\%$) when compared with walk-in ground surveys. Misidentification of the species of nesting birds in mixed-species areas proved to be a problem in aerial surveys of Great Egrets (*Ardea alba*).

We examined asynchrony bias by applying a mark-recapture approach to nests. We individually identified nests from the air through the use of natural and artificial landmarks, and followed nest fates through subsequent aerial surveys to obtain presence-absence information over the course of a breeding season. We used the superpopulation approach (a variation on a Jolly-Seber open-population mark-recapture model) to model nest initiation and survival as if nests were animals in a marked population. The superpopulation approach allowed for the

estimation of the total number of nest starts throughout the survey period. We found that asynchrony in nest initiation dates caused one-time “snapshot” counts of nests at the peak of nesting to underestimate true numbers of nest starts by 47–382% for both species. Nest turnover rates were highly variable among years and between colony sites, suggesting that nesting asynchrony must be measured for each season and site of interest. These results indicate that, without bias-correction, peak counts do not allow for useful inter-year comparisons, because each peak count represents a different proportion of that season’s total nesting activity. Unless populations are highly synchronous, or this bias is measured on a seasonal basis, one-time “snapshot” surveys of avian breeding populations probably cannot be used effectively as indices of breeding population size.

Researcher disturbance may also bias estimates of population parameters for colonies. Walk-in censuses of White Ibis and Great Egret colonies (initiated after the onset of incubation for the majority of nests) found that while nest success was not significantly affected by researcher disturbance, disturbed areas demonstrated depressed rates of new nest initiation. These species may be sensitive to disturbance early in the nesting cycle, but be resilient to walk-in disturbance after the onset of incubation.

CHAPTER 1
VISUAL BIAS IN AERIAL ESTIMATES OF COLONIALY NESTING WHITE IBISES
AND GREAT EGRETS

Introduction

Birds are one of the most frequently used bioindicators (Temple and Wiens 1989, Stolen et al. 2004). Close monitoring of bird populations may improve our knowledge of the relationship between environmental conditions and demography and allow the populations to be used as indicators of ecological change. Estimates of population size also have value in their own right, by allowing for more informed management of birds. However, the estimation of avian breeding population size must often be an approximation derived from estimates of related biological parameters (Frederick et al. 2006, Bibby 2000, Bock and Jones 2004) and may therefore fail to account for bias introduced from several sources (Erwin and Custer 1982; e.g., Ogden 1994, Gratto-Trevor et al. 1998). In colonialy breeding birds, there may be several sources of bias involved in estimating breeding population size, especially for large breeding aggregations. These include species or groups of birds that nest asynchronously over the course of a breeding season, nest in multispecies colonies, and whose nests may be concealed by vegetation during aerial surveys.

A great amount of effort and scientific inquiry has been directed toward understanding bias in counts of animals (e.g., Prenzlown and Loworn 1996, Erwin 1982, Bart and Earnst 2002, Rosenstock et al. 2002, Tomialojc and Verner 1990, Dodd and Murphy 1995, Frederick et al. 2003, Frederick et al. 1996, Gibbs et al. 1988, Bayliss and Yeomans 1990, Rodgers et al. 1995). Detectability has been recognized as a problem in line transects (Bibby 2000, Dodd and Murphy 1996), perimeter counts (Dodd and Murphy 1996), point counts (Bibby 2000, Nichols et al. 2000), and other types of population surveys using vocal or visual counts. Detectability can be a

source of bias for several reasons, including individual heterogeneity in behavior (such as frequency of song) and visual bias caused by the varying distances of birds from the observer.

Although estimates of the size of bird aggregations taken from aircraft or other aerial platforms have many advantages, they introduce detectability concerns related to variation in visibility of nests (Gibbs et al. 1988, Frederick et al. 2003, Bayliss and Yeomans 1990) and species misidentification (Rodgers et al. 2005, Barbraud and Gélinaud 2005, King 1976). Visual occlusion of nests as seen from the air may be due to several factors, including vegetative occlusion and miscounting because of high nest densities (Dodd and Murphy 1995, Prater 1979, Bayliss and Yeomans 1990). For example, while Great Egrets (*Ardea alba*) and American Wood Storks (*Mycteria americana*) often nest at or near the top of the tree canopy, where the nests are generally highly visible from the air, White Ibises (*Eudocimus albus*) and small herons (*Egretta* spp.) usually nest in both canopy and midstory, where their nests may be occluded from above. Additionally, high nest density in species such as White Ibises may make it difficult to differentiate between individual nests. Misidentification of species in aerial surveys of mixed-species colonies has also been found to be a problem in at least one study, although this problem has not been well explored in the literature. Rodgers et al. (1995) found that observers' difficulty in distinguishing Great Egret and Wood Stork nests from the air led to large and highly variable estimates of aerial bias in wading bird counts (Order Ciconiiformes).

When estimating regional breeding populations it is vital that accurate estimates be obtained for large colonies, as they contain a large percentage of the total breeding population and errors in population estimation for large colonies will disproportionately affect total estimates. We studied visual bias in estimates of Great Egret (*Ardea alba*) and White Ibis (*Eudocimus albus*) population sizes because they are conspicuous colonial nesters that nest in

large colonies, and because the two species have different nesting habits and potentially different nest visibilities. In this chapter we compare counts taken from both the ground and the air in the same large marked quadrats. Resulting estimates of visibility bias were used to adjust colony counts for encounter probability. We predicted that, for both species, visual bias would result in an underestimation of numbers of nests. We also expected that degree of error would increase with higher vegetative density and nest density.

Methods

We studied Great Egrets and White Ibises in the Water Conservation Areas (WCAs) of the Florida Everglades (Broward and Palm Beach Counties, FL) in March through May of 2005 and 2006. WCA-3A and WCA-1 are large areas of primarily sawgrass and wet prairie in the central Everglades that are controlled by, respectively, the South Florida Water Management District and the U.S. Fish and Wildlife Service. Colony counts during this time ranged up to 1,193 Great Egret nests and 13,566 White Ibis nests in a single colony; these counts were derived from monthly aerial surveys conducted from January-June of 2005 and 2006. We conducted surveys in a Cessna Skyhawk (172) high wing aircraft flying at approximately 177 kph and 244 meters above ground level. We took photographs from the copilot's seat through an open window, using a Canon EOS 20D with a 28–135mm image stabilizing lens. We accepted the largest single-month count of the breeding season from these aerial photographs as the maximum or “peak” seasonal count for each colony and species. This type of count has been commonly used in the past as a minimum breeding population estimate for wading birds in the Everglades. We present data here from five colonies for one or both species and years.

For visual bias studies, we worked in the mixed-species colony at Alley North (WCA-3A; N 26° 11.179', W -80° 31.431'), which included both Great Egrets and White Ibises in different areas of the single large tree island. We also worked in the White Ibis colony New Colony 3 in

WCA-1 (N 26° 32.013', W -80° 17.879'), which consisted of over twenty smaller tree islands in close proximity. The emergent vegetation in both colonies was composed primarily of willow (*Salix caroliniana*) with small numbers of pond apples (*Anona glabra*). White Ibises at Alley North also nested in lower vegetation on the outskirts of the tree island, primarily in cattail (*Typha latifolia*).

Sample Areas

We created rectangular quadrats in Great Egret and White Ibis colonies to compare aerial and ground counts of nests within these areas. White Ibis quadrats varied in size from 100 m² to roughly 200 m², and Great Egret quadrats were either 400 m² or 900 m². Each quadrat consisted of four artificial physical landmarks that were large and conspicuous enough to be seen from aircraft at 100–200 meters above ground level. Markers were of three types:

- A roughly 1–2 meter wide area of vegetation painted with a dilute white latex paint (1:3 water:paint) dispensed from a backpack sprayer of the type common in landscaping. These markers were only utilized during the 2005 season.
- A 3-meter tall, 10-cm diameter white vertically mounted PVC pipe with a 1.5-meter horizontal X on the top. These markers were primarily utilized during the 2006 season.
- A 1x1-meter piece of white or pale-colored cotton cloth, tied at the corners to vegetation in a horizontal position (Figure 1-1). This type of marker was used exclusively during the 2006 breeding season.

We delineated the edges of quadrats with plastic flagging tied to vegetation at regular intervals between corner markers, except in cases at New Colony 3 where the sample area consisted of an entire, well-defined tree island. The creation of a quadrat and the counting of all nests within it required approximately 30 minutes to 1.5 hours, depending upon size of quadrat, ease of movement, and nest density.

We marked a total of 21 rectangular quadrats in Great Egret and White Ibis colonies in order to compare aerial and ground counts of nests within these areas. In 2005 we erected

markers for four quadrats in the White Ibis colony at Alley North. In 2006, we erected markers for ten quadrats in Alley North (four Great Egret quadrats and six White Ibis quadrats). We also erected markers for seven White Ibis quadrats in New Colony 3.

Counts and Photographic Analyses

On the date that markers for a quadrat were erected, we counted the number of nests in the quadrat on the ground, and marked each nest with flagging when it was counted in order to avoid double counting. Within 24–36 hours of the ground count, we photographed the quadrat from the air in a Cessna Skyhawk (172) at an altitude of approximately 152 meters. Photographs were taken from the copilot's seat with the door removed, so as to take photos as close to vertically as possible, using a Canon EOS 20D with a 28–135mm image stabilizing lens. Photographs were analyzed using either Adobe Photoshop Elements version 2.0 or the shareware program Paint.Net version 2.0, using the same general procedure as for colony-wide counts. On the computer screen we delineated quadrat edges using colored lines (Figure 1-1), and marked nests with colored dots as they were counted.

Error Calculations and Tests for Covariates

For most of the figures in this paper, we present aerial bias in nest counts as

$$\text{Percent bias in aerial count} = ((\text{aerial count}/\text{ground count}) - 1) \times 100$$

A –12% error, for instance, indicates that the aerial count of a quadrat underestimated the true number of nests found during the ground count by 12%. Note that in Table 2, estimates are presented in the slightly less intuitive format of (ground count/aerial count) in order to form a ratio with maximum colony counts.

During the ground count for each quadrat, we subjectively ranked the level of tall occlusive vegetative cover present as low (more than 50% cattails or tall grass cover and less than 50% willows and other tree cover), medium (between 10% and 50% cattails or grass cover,

50–90% small willows and other tree cover) or high (more than 90% willow and other tall tree cover). We compared White Ibis quadrats for statistically significant differences between vegetation groups, using a nonparametric Kruskal-Wallis test for k independent samples, since the ratio data were sufficiently non-normal that transformation did not produce a normal or symmetric distribution for the data. We also used nonparametric tests to determine if date of quadrat creation or colony location affected aerial estimation bias in 2006. We examined effect of colony location (Alley North or New Colony 3) using a 2-tailed Mann-Whitney U-test, and examined the effect of Julian date of quadrat creation using a 2-tailed Spearman rank correlation.

The four Great Egret quadrats were all located in an area where other species also nested, including Snowy Egrets (*Egretta thula*), Little Blue Herons (*Egretta caerulea*), Tricolored Herons (*Egretta tricolor*), and Black-crowned Night Herons (*Nycticorax nycticorax*). Adult Snowy Egrets and Great Egrets can be difficult to differentiate from the air, as they are both white and the difference in body size may not be obvious from a distance. Small heron nests can be reliably differentiated from Great Egret nests by sight on the ground, but small heron nests in the genus *Egretta* cannot be readily differentiated from each other until the chicks are 10–14 days old. For this reason, the true number of Snowy Egret nests present in the quadrats was unknown.

We averaged the information from all quadrats for a given species to derive visual bias estimates for that species in any colony, by taking the ratio between the ground and aerial count for each quadrat, summing the ratios for all quadrats for that species, and dividing by the number of quadrats, as in the equation below:

$$\text{Visual bias} = \Sigma(\text{ground count}_i / \text{aerial count}_i) / n$$

where i is a given quadrat and n is the sample size of quadrats for the species of interest. For each species, we used the resulting bias estimate for the left side of the ratio equation

$$(\text{quadrat ground count})/(\text{quadrat aerial count}) = (\text{bias-corrected count})/(\text{colony count})$$

to correct colony peak counts for visibility bias. We compared the new bias-corrected counts and associated confidence intervals to original colony-wide aerial counts to determine the significance of the results. We calculated the associated confidence intervals (CIs) for each species' visibility bias as follows: $\text{CIs} = \mu \pm (z^*(\text{sd}/\sqrt{n}))$. For 95% confidence intervals, $z=1.96$; μ was the sample mean error rate for the species; sd was the sample standard error for each species; and n was the number of quadrats observed for each species. The mean error and confidence intervals from the samples were then multiplied by the maximum total count for each colony for the season, in order to obtain a new bias-adjusted colony count and 95% CIs.

Results

Great Egrets

Numbers of nests identified from the air were greater than the ground counts for two out of four Great Egret quadrats, and we strongly suspect that some percentage of Snowy Egrets were mistaken for Great Egrets in aerial photos (Table 1-1). This source of bias was apparently larger on average than any bias due to vegetative occlusion, which would have caused aerial underestimates rather than overestimates. Aerial counts ranged from -14% to 260% of ground counts, with a mean of 70.28% (sd 131.20%). Due to the small sample size, statistical analyses were not conducted on the Great Egret quadrats. The common nest location preferences of this species meant that all four quadrats were placed in areas of high vegetative cover.

White Ibises

White Ibis nest numbers were generally underestimated in aerial surveys (Figure 1-2). Although the severity of this underestimation varied, the mean bias in aerial surveys was

approximately -12.37% (sd=20.65%; n=17). Visual bias did not increase with density of nests (Figure 1-2), and in 2006 also did not vary by colony ($Z=-0.714$, $p=0.475$, $n=13$) or by date of quadrat initiation ($\rho=-0.275$, $p=0.363$, $n=13$). Visual bias for White Ibises did not significantly increase with increased vegetative cover (Figure 1-3; $\chi^2=0.163$, $p=0.922$, $n=17$, $df=2$) although the direction of the difference in median error values between the low and medium cover groups suggests that with a larger sample size for the high vegetative cover, we might see a progression in median error rate from low to high canopy cover (Figure 1-3). Median visual error for quadrats in low vegetative cover was -11.07% (IQR -14.97% to -5.40%, $n=6$); for quadrats in medium cover, -16.50% (IQR -18.71% to 8.96%, $n=9$); and for quadrats in high vegetative cover, -6.98% (IQR -15.47% to 1.51%).

Correction for Visibility Bias in Colony Counts

Uncorrected maximum colony counts for White Ibis colonies lay outside the 95% confidence intervals for the new bias-corrected estimates in both 2005 and 2006 (Table 1-2). These uncorrected peak counts may thus be judged to be statistically significant underestimates of the true numbers of nests present. The uncorrected counts for Great Egret colonies were not statistically significantly different from the bias-corrected estimates, as the 95% confidence interval for the bias-corrected counts overlapped with the original counts (Table 1-2). However, the sample size of quadrats and colonies was small, and there was large variation in degree of bias among quadrats. Visibility bias seemed to be quite substantial in some locations, if not on average.

Discussion

There is evidence that visual bias in animals varies by species (Short and Bayliss 1985), ground cover (Short and Bayliss 1985), observer quality (Erwin 1982), and other factors. However, several studies have found a consistent underestimation of true numbers of birds using

aerial surveys (Pollock and Kendall 1987; e.g., Gibbs et al. 1988, Dodd and Murphy 1995). Our results reinforce the conclusion that visual bias can be an important source of error in estimates of avian breeding population size, and that the evaluation of detection probability is essential for sampling efforts that use counts as population indices (Pollock and Kendall 1987). While the degree of visual bias seems likely to vary with colony site and species, the amount of variation we found in aerial bias among quadrats was similar to that found in other studies (Rodgers et al. 1995, Gibbs et al. 1988, Dodd and Murphy 1995). For ibises, the degree of bias (-12%) was similar to that for other estimates for wading birds (-15% for Squacco Herons *Ardeola ralloides*, Barbraud et al. 2004; -16%, -10% and -11%, respectively, for Great Egrets, Snowy Egrets, and White Ibises, Kushlan 1979). The bias for ibises did not appear to increase with greater nest density, in contrast to Great Blue Herons (*Ardea herodias*; Gibbs et al. 1988). This may be due in part to the fact that many of the White Ibis quadrats were located in areas of relatively low vegetative cover, which limited the number of potential nest strata and allowed individual nests to be relatively easily distinguished.

There is little evidence in support of the vegetative cover prediction. The locations in which quadrats could be placed were unfortunately limited by the necessity for ground access, and thus a disproportionate percentage of the quadrats at Alley North colony were located in areas of low and medium vegetative cover. An increased sample size for White Ibis quadrats in high vegetative cover is needed before level of vegetative cover can be ruled out as an important covariate for survey bias in White Ibises, but in our study the variation in aerial bias was much larger within vegetative cover groups than between groups. Initial evidence for this species does not support the hypothesis that visual bias due to vegetative occlusion increases with vegetative complexity. For Great Egrets, a larger sample size is also needed, as well as a finer-scale

stratification of vegetative cover level. Great Egrets nest almost exclusively in areas that, according to the criteria used in this study, would be classified as high cover (K. Williams pers. obs.). However, Great Egrets nest largely above the canopy, and it may be (as Rodgers et al. found for Wood Storks; 1995), that Great Egret visibility bias is likewise not significantly affected by level of vegetative cover.

The uncorrected maximum colony counts for Great Egret colonies were not statistically significantly different from the bias-corrected estimates, as the 95% confidence intervals for the bias-corrected counts overlapped with the original colony counts. However, the sample size of quadrats and colonies was small, and there was clearly a large amount of variation in bias for this species in mixed-species groups, due to both visual occlusion and to difficulty in distinguishing Great Egrets from other white species during aerial counts. The resulting bias-corrected peak count of Great Egrets for Alley North in 2006 (with the associated confidence intervals) reflects these dual sources of bias (Table 1-2).

The quadrat method of quantifying bias due to visual occlusion is necessary for situations in which nests are located on multilayered substrates. Vegetation is often the cause of this sort of visual bias (Frederick et al. 2003), but similar problems could be evident in colonies in which nests are occluded by rock crevices or artificial structures. However, our results indicate that ground truthing may not always be a gold standard for correcting visibility bias. It has been suggested that ground counts may be inaccurate in highly vegetated areas where movement within the colony is difficult, and canopy nests are difficult to see or count (Prater 1979, Frederick et al. 2003). Additionally, if ground counts and aerial surveys are not conducted within a very short time span, some nest turnover may occur and cause increased bias between the two estimates (Frederick et al. 2003). In our study, we believe that ground counts were not

hampered by nest location or difficulty of movement, and aerial counts were conducted within as short a time span as possible after ground counts. Nevertheless, ground/aerial comparisons could not adequately address bias due to species misidentification (see also Rodgers 1995). Even the ground surveys could not distinguish the non-target species (Snowy Egrets) from other small herons, which meant that we were unable to correct for aerial bias due to species misidentification. Since the two types of error (visual occlusion and misidentification) may be inseparable in multispecies colonies (King 1976), it is important that such estimates be applied to single-species colonies with extreme caution. In the future, separation of vegetative occlusion from species misidentification bias could be achieved by comparing bias estimates from single- and mixed-species areas. Alternatively, surveys could be conducted using helicopters, which allow species to be more easily differentiated.

Our results indicate that White Ibis aerial surveys are likely to be significantly biased due to vegetative occlusion. However, this bias did not increase significantly with vegetative complexity or nest density. Our small sample size for Great Egret aerial surveys did not indicate systematic bias due to vegetative occlusion, but species misidentification appears to be a significant problem for this species. We suggest that visual bias due to both vegetative occlusion and species misidentification should be explicitly measured in aerial surveys of colonies, as both of these sources of error can affect estimates of breeding population size.

Table 1-1. Quadrats from 2005 and 2006 seasons from the Everglades of southern Florida. White Ibis quadrats were 100 m² (or in one case 200 m²) and Great Egret quadrats were either 400 or 900 m². White Ibis nest densities varied from 0.08 to 4.45 nests per m².

Year	Species ^a	Ground count ^b	Aerial count ^b	% error in aerial count ^c	Vegetative cover ^d	Location
2005	WHIB	23	20	-13	Low	Alley North
2005	WHIB	54	21	-61	Medium	Alley North
2005	WHIB	10	11	9	High	Alley North
2005	WHIB	8	4	-50	Low	Alley North
2006	WHIB	205	173	-16	Low	Alley North
2006	GREG/mixed	GREG 14 SH 35	GREG 12 SNEG 19	-14	High	Alley North
2006	GREG/mixed	GREG 24 SH 7, SNEG 1	GREG 19 SNEG 6	-21	High	Alley North
2006	GREG/mixed	GREG 5 SH 19	GREG 18 SNEG 6	260	High	Alley North
2006	GREG/mixed	GREG 16 SH 18	GREG 25 SNEG 10	56	High	Alley North
2006	WHIB	72	69	-4	Low	Alley North
2006	WHIB	33	30	-9	Low	Alley North
2006	WHIB	30	24	-20	Medium	Alley North
2006	WHIB	18	20	10	Medium	Alley North
2006	WHIB	67	73	-8	Medium	Alley North
2006	WHIB	414	467	11	Medium	New Colony 3
2006	WHIB	445	491	9	Low	New Colony 3
2006	WHIB	139	113	-19	Medium	New Colony 3
2006	WHIB	303	253	-17	Medium	New Colony 3
2006	WHIB	96	73	-24	High	New Colony 3
2006	WHIB	390	319	-19	Medium	New Colony 3
2006	WHIB	114	99	-13	Medium	New Colony 3

a. WHIB= White Ibis; GREG= Great Egret; SNEG= Snowy Egret; SH= unidentified small heron.

b. Ground counts and aerial counts are estimated numbers of nests present in the quadrat.

c. Values in “% error” column are ((aerial count/ground count)-1)x100.

d. Vegetative cover values are subjective measurements (low = more than 50% cattails or tall grass cover and less than 50% tree cover; medium = between 10% and 50% cattails or grass cover and 50–90% small willows and other tree cover; high = more than 90% willow and other tall tree cover).

Table 1-2. Visibility bias-corrected peak counts for five Great Egret and White Ibis colonies from the 2005 and 2006 breeding seasons.

Colony (species) ^a	Year	Peak count	Visibility error ^b (sd)	New estimate (LCI-UCI) ^c
Vulture (GREG)	2005	121	0.84 (0.46)	101 (46–156)
Vulture (GREG)	2006	458	0.84 (0.46)	383 (176–591)
Vacation Island (GREG)	2005	79	0.84 (0.46)	66 (30–102)
Vacation Island (GREG)	2006	155	0.84 (0.46)	130 (59–200)
Cypress City (GREG)	2005	107	0.84 (0.46)	90 (41–138)
Cypress City (GREG)	2006	173	0.84 (0.46)	145 (66–223)
Alley North (GREG)	2005	850	0.84 (0.46)	711 (326–1,097)
Alley North (GREG)	2006	1193	0.84 (0.46)	998 (458–1,539)
Alley North (WHIB)	2005	12750	1.23 (0.43)	15,702 (13,078–18,327)
Alley North (WHIB)	2006	13566	1.23 (0.43)	16,707 (13,915–19,499)
New Colony 3 (WHIB)	2006	4800	1.23 (0.43)	5,911 (4,924–6,899)

a. GREG=Great Egret; WHIB=White Ibis.

b. Error calculated for each species as $(\sum(\text{ground count}_i/\text{aerial count}_i))/n$, where i is a given quadrat and n =number of quadrats.

c. Confidence intervals for visibility error were calculated as $CI = \mu \pm (z * (sd/\sqrt{n}))$, where μ is the sample mean error, $z=1.96$ for 95% confidence limits, sd =sample standard deviation, and n =sample size (number of quadrats for the species). New bias-corrected estimates and confidence intervals were derived from multiplying mean proportion visibility error and error CIs by the peak count for each colony.

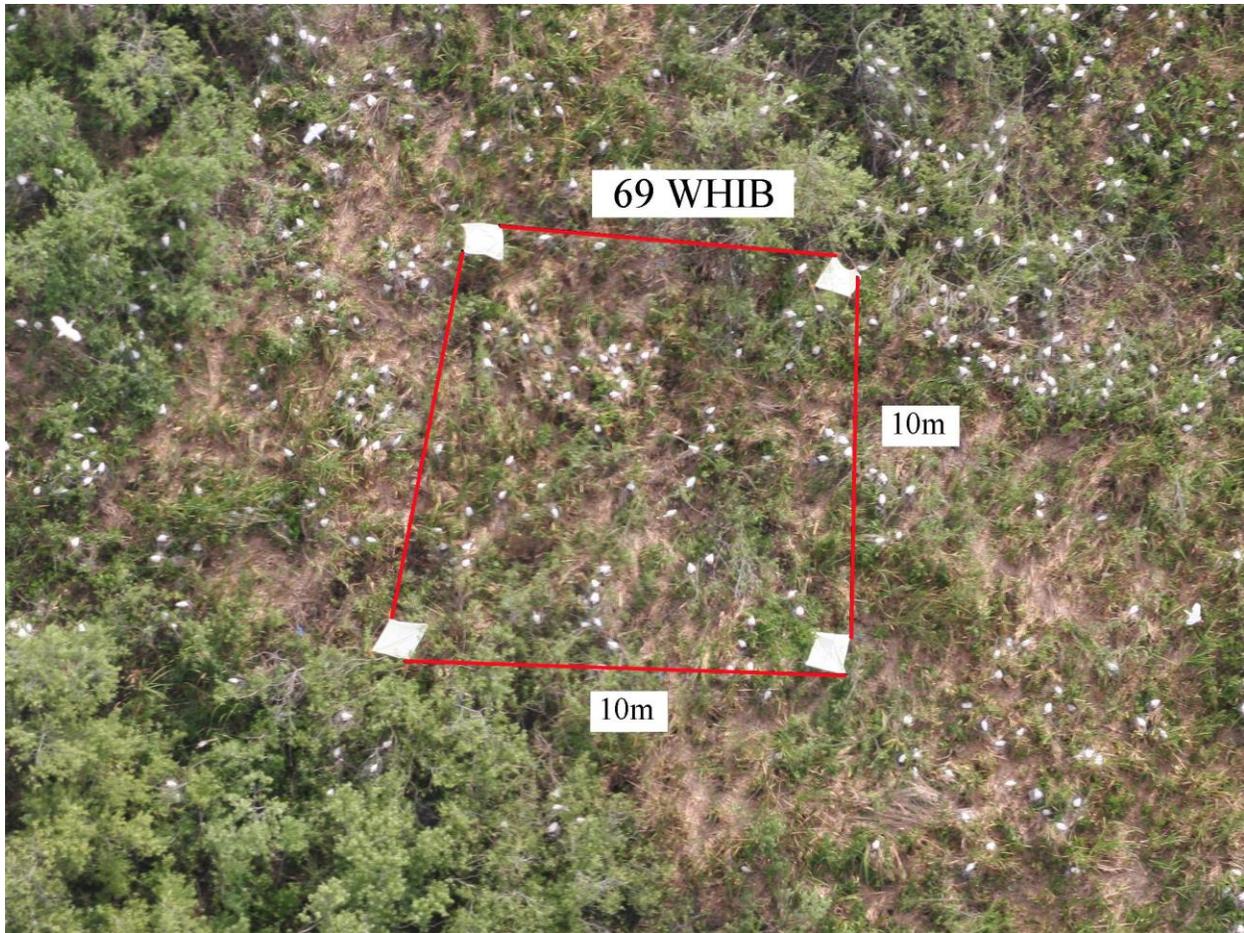


Figure 1-1. A 10x10 meter White Ibis quadrat at Alley North colony in WCA-3A (04/07/06). The ground count for this quadrat was 72 nests; the aerial count from this photograph was 69 nests. Written labels and lines between the four artificial markers were inserted into the photograph using Adobe Photoshop Elements v. 2.0.

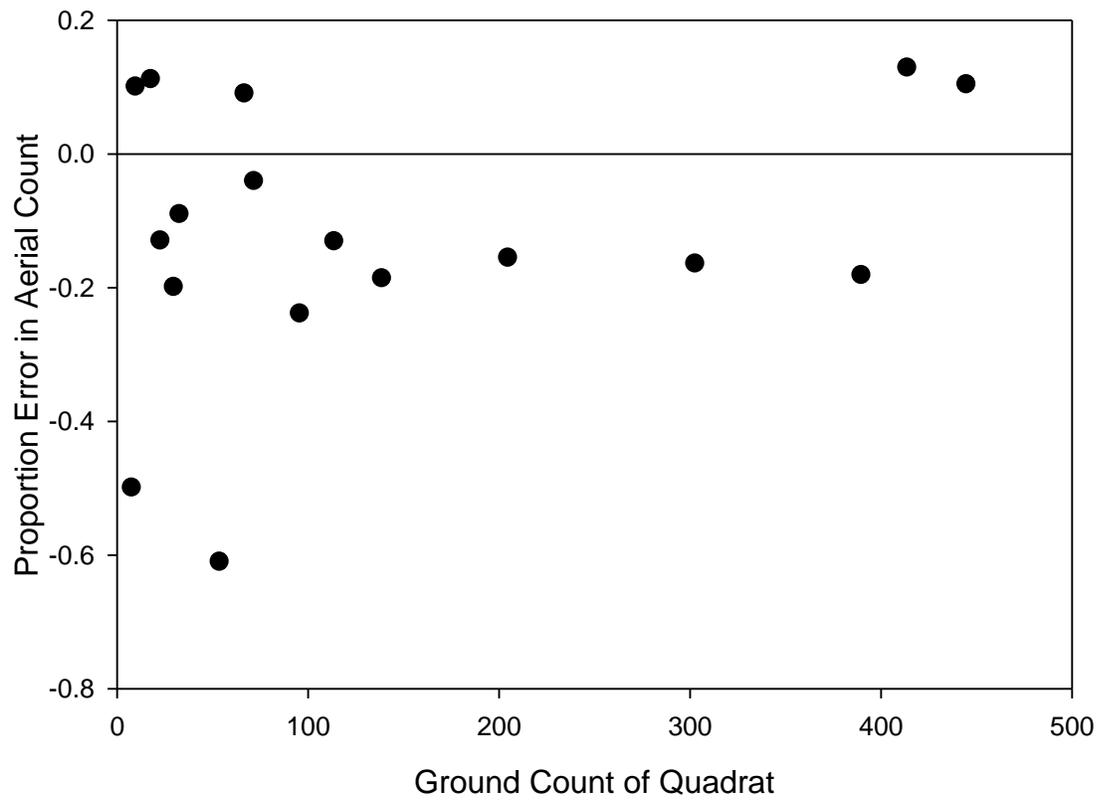


Figure 1-2. Proportional error in aerial counts of White Ibis quadrats. Proportion error is calculated as (aerial count/ground count)-1, where the ground count of number of nests was conducted during a walk-in survey of the quadrat and the aerial count was obtained via digital photography of the quadrat site from small aircraft.

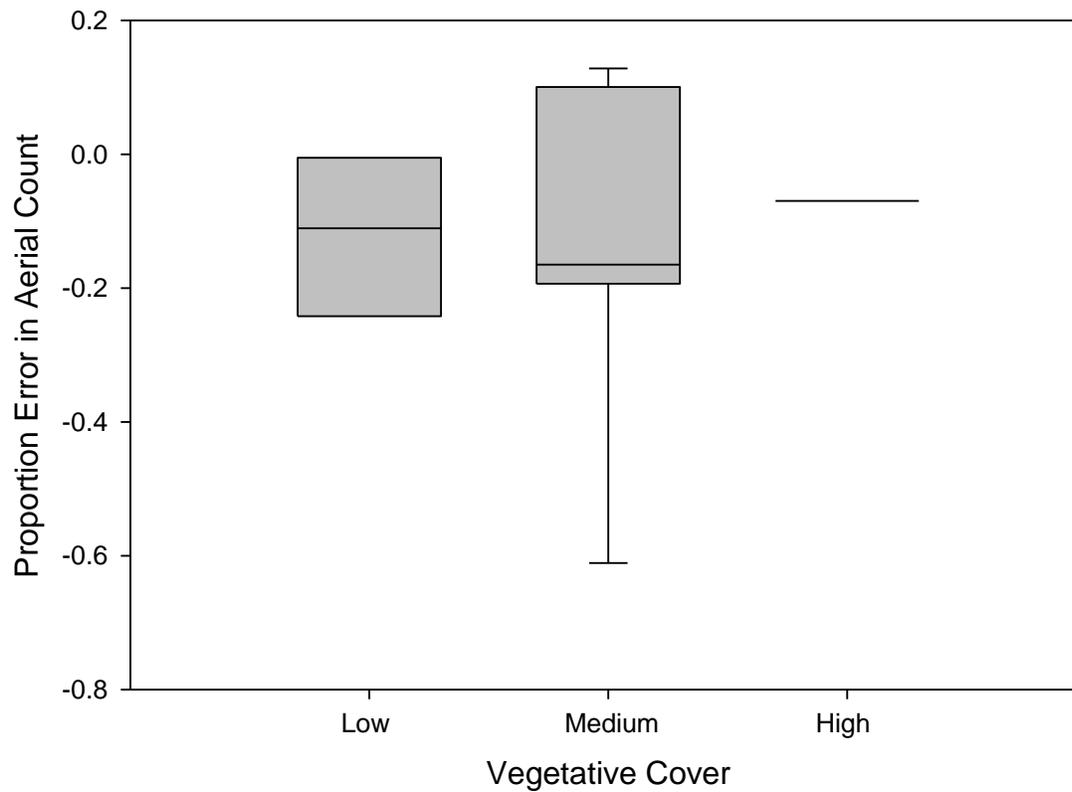


Figure 1-3. Proportion error in aerial estimates of White Ibis quadrats by vegetative cover. Vegetative cover values are subjective measurements (low = more than 50% cattails or tall grass cover and less than 50% tree cover; medium = between 10% and 50% cattails or grass cover and 50–90% small willows and other tree cover; high = more than 90% willow and other tall tree cover).

CHAPTER 2 ESTIMATING BREEDING POPULATION SIZE FOR ASYNCHRONOUSLY NESTING COLONIAL WADING BIRDS

Introduction

The need for reliable avian demographic information has increased as scientists attempt to use attributes of birds to measure both ecological degradation and restoration (Thompson 2002, Rosenstock et al. 2002, Stolen et al. 2004). Birds are one of the most frequently suggested bioindicators (Temple and Wiens 1989, Stolen et al. 2004), but accurate estimates of population parameters can be hampered by a number of different kinds of bias. It is rare that entire breeding populations can be counted, for instance, and most attempts at estimating population size are approximations derived from estimates of related biological parameters, such as numbers of nests (Bibby 2000, Williams et al. 2002, Bock and Jones 2004, Frederick et al. 2006). However, there is a large amount of uncertainty in survey counts of nests and in the relation of those nest counts to population size (Thompson 2002, Bock and Jones 2004, Frederick et al. 2006). Inter-observer error, visibility bias, and species that nest asynchronously over the course of a breeding season or nest in multispecies groups can present significant problems when trying to estimate breeding population size. In the case of colonially breeding birds, large aggregation size may also cause difficulties when attempting to estimate population size. However, it is vital that accurate estimates be obtained for large colonies, as they may contain a large percentage of a species' breeding population, and errors in population estimation for large colonies will disproportionately affect total estimates.

Estimation Error

A huge amount of effort and scientific inquiry has been directed toward understanding bias in nest counts (e.g., Erwin 1982, Gibbs et al. 1988, Tomialojc and Verner 1990, Dodd and Murphy 1995, Frederick et al. 1996, Prenzlów and Loworn 1996, Bart and Earnst 2002,

Rosenstock et al. 2002, Frederick et al. 2003). Aerial estimates of the population sizes of colonial nesters have been found to be biased due to visibility problems, interobserver variation in estimation error, and misidentification of species (Bayliss and Yeomans 1990, Frederick et al. 2003, Rodgers et al. 1995). In addition, most studies of estimation error to date have focused on estimating nests that are present at the time of survey, and have rarely recognized the problem of estimating nests that occur during the breeding period of interest but are not present at the time of survey (Frederick et al. 2006, Cherenkov 1998).

Asynchronous breeding, even within a defined breeding season, is common in colonially nesting birds, including terns (Hernandez-Matias et al. 2003), prions (Liddle 1994), martins (Magrath 1999), and wading birds (Ciconiiformes; Piazza and Wright 2004). In many species, nesting may therefore occur before surveys begin during a season, after they end, or in between consecutive surveys. Estimates of unmarked nests on any given date are inherently underestimating the true numbers of nests, partly because nests may be occurring outside the dates of survey, and partly because novel nests on any given survey may be confused with nests that were present on a previous survey date. This is true even if the counts on each date are highly accurate. In such a situation, where nests cannot be individually distinguished, the best guess for the population size is often the largest or “peak” count of concurrent nests on a single survey date. These circumstances occur in several taxa, including wading birds, seabirds, loons, and shorebirds (Frederick et al. 2006; e.g., Sagar and Stahl 2005, Earnst et al. 2005, Morrison et al. 1994). While the resulting bias may be negligible when nesting is highly synchronous and little re-nesting occurs, the degree of error in less synchronous birds can be substantial (e.g., 47% in wading birds; Frederick et al. 2006).

In addition to problems with nesting asynchrony, using numbers of nests as a proxy for breeding population size can be complicated by the degree of occurrence of renesting or multiple nesting (Thompson et al. 2001, Nagy and Holmes 2004). Renesting and multiple brooding are rare in many populations of high-latitude nesting birds, but they can be common among temperate and tropical species. We wish to make clear in this chapter that we are addressing the problem of estimating numbers of nests, and make no assumptions about degree of renesting or double brooding.

A New Strategy For Estimating Breeding Population Size For Unmarked Populations

The problems described above illustrate a need for the development of new methods for estimating the size of breeding bird populations (Figure 2-1). Visibility bias has been addressed elsewhere (Chapter 1) and has been well explored in the literature; therefore we will primarily focus here on methods to account for nesting asynchrony. This problem may be approached by estimating the turnover of individually marked nests and incorporating this information into a population estimate using a mark-resight method. We have used the superpopulation approach (Schwarz and Arnason 1996), a variation on a Jolly-Seber open-population capture-recapture model. In this case nests are treated as individuals in an animal population, where the population is equivalent to the estimated total numbers of nest starts during a period of interest such as a breeding season. We chose to study bias derived from nesting asynchrony in Great Egrets (*Ardea alba*) and White Ibises (*Eudocimus albus*) because these two birds are conspicuous colonial nesters with very different life histories and temporal nesting patterns. We believe that the methods outlined here provide a new and much improved technique for the monitoring and estimation of large unmarked populations of nesting birds.

Methods

Survey Methodology

We conducted monthly aerial surveys between January and June of 2005 and 2006 in which we searched for and counted colonies of wading birds in the central and northern Everglades (Broward, Dade and Palm Beach counties, FL). We conducted surveys in a Cessna Skyhawk (172) high wing aircraft flying at approximately 177 kph and 304 meters altitude, with one observer on each side of the aircraft. When we located colonies we circled them for aerial visual estimates and aerial photography at 244 meters above ground level. We took photographs from the copilot's seat through an open window, using a Canon EOS 20D high-resolution digital camera with a 28–135mm image stabilizing lens. We edited photographs and counted nests using either Adobe Photoshop Elements version 2.0 or the shareware program Paint.Net version 2.0, using colored dots to mark nests as they were counted and delineating overlapping photograph edges using colored lines. We accepted the largest single-month count of the breeding season from these aerial photographs as the peak seasonal count for each species.

In addition to these “peak count” aerial surveys, we also took photographs on a roughly semiweekly basis of groups of individually identifiable nests. This allowed us to estimate turnover (losses of nests and new entries to the colony). Groups of birds were identified through proximity to natural or artificial landmarks (see below). We took photographs at an altitude of approximately 152 meters from the copilot's seat with the door removed, so as to take photos as close to vertically as possible. We generally conducted survey flights between 08:00 and 10:30 am or 16:00 to 18:00 pm, but flight times varied with weather, plane availability, and other factors. Midday light was better for survey photographs, but turbulence, wind and poor weather also tended to be more severe in the heat of the day. We conducted these surveys in three small Great Egret colonies and one large mixed-species colony (Table 2-1) in Water Conservation

Area 3A (Figure 2-2) in one or both of the 2005 and 2006 breeding seasons. The mixed-species colony, Alley North (Figure 2-3) was too large to conduct a complete survey. We therefore concentrated on photographing certain landmarks that could be reliably located from the air.

Artificial Geographic Markers

The repeated identification of individual nests in aerial surveys required some kind of identifying landmarks. We used natural landmarks such as clearings within the tree island, but we also erected artificial markers in areas of colonies that were both accessible on the ground and where birds nested in substantial numbers. These markers were of three types, all of which were easily identifiable from 100-300 meters above ground level:

- A roughly 1–2 meter wide area of vegetation painted with a dilute white latex paint (1:3 water:paint) dispensed from a backpack sprayer of the type common in landscaping. These markers were only utilized during the 2005 season.
- A 3-meter tall, 10-cm diameter white vertically mounted PVC pipe with a 1.5-meter horizontal X on the top (Figure 2-4A). These markers were primarily utilized during the 2006 season.
- A 1x1-meter piece of white or pale-colored cotton cloth, tied at the corners to vegetation in a horizontal position (Figure 2-4B). This type of marker was used exclusively during the 2006 breeding season.

Photographic Analysis

We used printed photographs of the same areas from different dates to identify individual nests and obtain presence-absence data for each nest on each subsequent survey date. We uniquely numbered nests consecutively from the earliest date, and entered presence-absence information into the database using the following format:

- Nest inactive (0)- this included cases in which nest and parent/chicks were not visible; nest was visible but empty (no sign of parents/chicks); or there was no photo of the nest area available on that date
- Nest active (1)- parent and/or chicks were visible

Since some nests were temporarily inactive or not visible in photos from a particular date, we only assumed that a nest had failed if it was found to be inactive on four consecutive survey dates. After that time, we treated any nest in that location as a new nest start. Although we used the presence of a large white bird as an initial indication of nesting, these could have been roosting birds or birds temporarily away from their nests. Before we analyzed each presence-absence database, we therefore eliminated first observations of all nests from the database, and so deleted from the database all “nests” that were seen only once. In actuality, we believe that some small proportion of these single-appearance nests were indeed nests. In addition, the use of the four consecutive zero rule (as above) may have missed some nests that failed, restarted, and failed again within the period of four visits. However, both these types of possible errors seem unlikely given the relatively long courtship and egg-laying periods of these birds (4–10 days for Great Egrets, according to McCrimmon et al. 2001; 9–10 days for White Ibises, as cited in Kushlan and Bildstein 1992) and the semiweekly frequency of aerial surveys. In any case, if either of these assumptions is incorrect, the effect is in the same direction, to underestimate the true numbers of nests. We eliminated the first sighting of nests that were seen on multiple dates, in addition to those nests seen only once, in order to avoid artificially inflating survival estimates.

Independent observers. Three independent observers analyzed the same set of photographs for one colony (Vacation Island) from the 2006 breeding season. This allowed for a comparison of photo analysis methods between observers, and served as a test of the repeatability of the method. We used Observer 3’s results (the median estimate from the three observers) as the final superpopulation estimate for the 2006 Vacation Island colony, as that observer also conducted the analyses for all other colonies.

The Superpopulation Modeling Approach to Population Estimation

The superpopulation approach (Schwarz and Arnason 1996) is a variation on a Jolly-Seber open-population capture-recapture model that includes as a derived parameter the gross births within the population. This parameter includes all animals that enter the population during the sample period and either survive until the next survey, or emigrate or die before they are available to be sampled (Schwarz and Arnason 1996, Schwarz et al. 1993). In our study, nests were equivalent to individuals in a population; the number of new nests present at each survey represented immigration into the population, and the number of “marked,” or individually identifiable, nests that failed between consecutive surveys indicated the level of emigration from the population. The model’s calculated gross superpopulation size represented the total number of nest starts over the entire sampling period. Detectability of nests is included in the model as an encounter probability term for each survey.

We fit regression models to the capture-recapture data from colonies using Program MARK version 4.3 (White and Burnham 1999). We used the POPAN data type (Arnason and Schwarz 1995), which utilizes a robust parameterization of the Jolly-Seber model (Schwarz and Arnason 1996). We set time intervals to fractions of weeks between each set of consecutive surveys, and allowed the four parameters (survival ϕ , encounter probability p , entry probability p_{ent} , and superpopulation size N) to vary with time, depending upon the model. For example, for a database with six survey dates, there were a total of seventeen possible parameters (five survival interval probabilities, five entry interval probabilities, six encounter probabilities, and one superpopulation size). For each database, we tested a set of four candidate models: a general (fully time-dependent) model, a so-called “dot model,” in which survival and entry variables were held constant through time, and two models in which either encounter probability or survival probability was allowed to vary with time while the other was held constant (Cooch and

White 2007). Probability of entry into the population would not be expected to hold constant throughout the season, since for both species there tends to be a surge of initial nesting in an area followed by lower levels of nest initiation thereafter (McCrimmon et al. 2001, Kushlan and Bildstein 1992). Thus, entry probabilities were allowed to be time-dependent in all models. For models in which survival probability ϕ and encounter probability p varied with time, not all parameters in the model were estimable (Schwarz and Arnason 1996). We set $p_1=p_2$ and $p_k=p_{k-1}$ so that all survival parameters were estimable in the model (J. Nichols pers. comm.). In the model in which survival was held constant and encounter probability varied, the initial p value was still inestimable, so for this model we set $p_1=p_2$ and allowed all other encounter probabilities to vary. We used a sin link function to estimate survival and encounter parameters, a mlogit(1) function to estimate entry parameters, and a log link function to estimate superpopulation size N .

The gross superpopulation size N^* is a derived parameter of the POPAN model. It includes the net superpopulation size (all animals that enter the population between two consecutive surveys and are available to be captured during the second survey) as well as animals that enter and leave the population between consecutive surveys and thus are never available to be sampled. We used MARK's model averaging capability to find the weighted average values for all parameters across all models. Using the counts from each survey date and the estimated encounter and survival probabilities from each survey date or interval (adjusted for time elapsed between surveys), the number of new entries ("births") into the population between each consecutive set of surveys could be calculated (Schwarz et al. 1993, Schwarz and Arnason 1996). The gross superpopulation size in MARK is derived from summing these gross entries between each consecutive set of survey dates, and adding the sum to the estimated number of nests present during the first survey (after Schwarz and Arnason 1996, Schwarz et al. 1993):

$$N_i = n_i/p_i$$

$$B_i = N_{i+1} - N_i (\varphi_i)^{t_i}$$

$$B_i^* = B_i \frac{\ln(\varphi_i^{t_i})}{(\varphi_i^{t_i})-1}$$

$$N^* = N_1 + \sum^{k-1} B_i^*$$

where N_i is the estimated total number of individuals in population at occasion i ; n_i is the number of individuals seen at occasion i ; p_i is the encounter prob. at occasion i ; B_i is the estimated number of individuals entering the population between sampling occasions i and $i+1$; φ_i is the survival probability at occasion i ; t_i is the time between surveys i and $i+1$ (as a proportion of a week); B_i^* is the estimated gross number of individuals entering population between i and $i+1$; N^* is the estimated gross superpopulation size; and k is the total number of surveys.

We fit the four models to the data from each colony's presence-absence database (Appendix A). We used an information-theoretic approach to model selection, and considered that a model with a $\Delta AICc$ value of less than 2 was relatively well supported by the data, while a model with a $\Delta AICc$ value of greater than 10 was not supported by the data (Williams et al. 2002). We quantified the goodness of fit (GOF) of the most general model using chi-square tests for each survey interval to see if observed values varied from the expected number of surviving and encountered nests. These tests evaluated the following assumptions inherent in Jolly-Seber models (Cooch and White 2007, Pollock et al. 1990):

- There is no heterogeneity in capture probability, either among individuals or among cohorts (cohorts in this case meaning all nests that were seen for the first time on the same date).
- There is no heterogeneity in survival probability among individuals or cohorts.

We calculated chi-square values using Program RELEASE (Burnham et al. 1987), available within MARK. The chi-square values generated for each survey interval were summed for the entire sampling period, and were divided by the degrees of freedom to obtain a variance inflation factor, $c\text{-hat}$ (a measure of overdispersion in the data). Following Cooch and White (2007), we accepted that a $c\text{-hat}$ value of 1 indicated good model fit, values of 1–3 indicated moderately good fit, and >3 indicated probable violation of model assumptions—that is, that none of the models in the tested model suite may be a good fit for the data. A $c\text{-hat}$ value of less than 1 essentially means that the data are underdispersed, and there is little agreement in the literature about what this means or what to do about it (Cooch and White 2007). Following the recommendation of Cooch and White (2007), we used a $c\text{-hat}$ value of 1 when the $c\text{-hat}$ calculated in RELEASE was less than that. Otherwise, we multiplied the calculated $c\text{-hat}$ values presented in the tables in Appendix A ($c\text{-hat}$ values of less than 1 are not presented) by the model-based variance and covariance estimates for each model suite. This adjusted model weights to compensate for the overestimation of precision caused by overdispersion.

Subsampling Alley North Colony

For the smaller Great Egret colonies (tree island lengths of approximately 120–200 meters), all or most of the colony could be covered in one or two photographic passes. For the very large colony (length of tree island approximately 1900 meters; Figure 2-3), we subsampled the colony during aerial photography, resulting in a collection of geographically distinct year- and species-specific estimates of superpopulations with standard errors. Samples were surveyed for different lengths of time during the breeding season, depending upon nesting patterns and the availability of good-quality photographs for each area. We calculated a superpopulation estimate for each sample, and compared it to the raw count for each sample, which was the number of nests seen in the sample on the survey date closest to the colony's peak count date. This raw

count was assumed to be the number of nests in the sample unit that would have been seen and included in the peak count on the peak count date. We assumed that the ratio between the samples' superpopulation estimates and raw counts also held for the entire colony, and used that proportional difference in a ratio with the entire colony's peak count to find an extrapolated superpopulation size for the entire colony. For example, if on average 70% of nests present during the season in the sample areas were not present at the survey date closest to the peak count (when the raw counts were taken), then the colony peak count likewise would be assumed to be about a 70% underestimate of the total number of nest starts.

We found the proportional difference between the superpopulation estimate and the raw count for each sample, and then took the average of these proportions across all samples. We took the ratio between each sample's values and averaged the individual ratios, rather than obtaining an overall ratio between the two types of estimates for all samples (e.g., calculating the difference between the summed raw counts and superpopulation estimates across all samples), as it is unlikely that there is one underlying level of nest turnover within the colony; different nesting cohorts within the colony are likely to have different levels of nest turnover at different times within the breeding season. The ratio of averages (summed value), while in some cases shown to be less biased and have a smaller variance estimator than the average of ratios (Rao 2005), weights all nests in all samples equally and assumes that there is one underlying ratio between raw counts and superpopulation estimates for the colony. The average of ratios recognizes that each sample may represent an area with a different ratio between the raw count and superpopulation estimate (due to date of cohort initiation, nest density, or other factors), and thus takes natural variation in turnover rate into account when estimating an overall proportion for the colony.

The average ratio of this proportional error across all samples was our estimated colony-wide proportional difference between the peak count and extrapolated superpopulation count, as follows:

$$(\sum(N^*_i/RC_i))/n = (N^*_{colony}/PC_{colony})$$

N^*_i is the superpopulation estimate for sample i ; RC_i is the raw count for sample i ; n is the number of samples in the colony for that year and species. Cumulatively, $(\sum(N^*_i/RC_i))/n$ is the average proportion of the total number of nest starts that were seen in the raw counts. PC_{colony} is the peak count for the colony. We solved for “ N^*_{colony} ,” the entire colony’s extrapolated superpopulation estimate. We also calculated the variance of the ratio estimate, in order to calculate 95% confidence intervals for the colony-wide superpopulation estimate (Appendix B). These superpopulations were compared to colony peak counts to determine the level of bias introduced into peak counts by 1) asynchronous nesting activity, expressed through changes in the identities and numbers of nests present over the course of the season due to changes in survival and entry probabilities; and 2) imperfect detectability of nests in aerial surveys, expressed for each survey term as an encounter probability.

Subsampling to Determine Necessary Survey Frequency

We subsampled the 2006 Cypress City dataset, a very complete survey dataset with 17 surveys over the course of two months, to determine if flying approximately twice a week as we did for this research is necessary for the success of the technique. We subsampled the dataset to manipulate both the number of surveys conducted within a specified time period and the regularity of the survey intervals. We calculated a superpopulation estimate for each subsampled dataset and compared these estimates to the inclusive superpopulation estimate for the colony, in order to examine the loss of estimation accuracy associated with reduced flight frequency.

Results

Interobserver Error in Tallying Individual Nest Histories From Photographs

Three independent observers analyzed the same photographic library from surveys of the Vacation Island Great Egret colony during the 2006 breeding season (Figure 2-5). The peak count for this colony in 2006 was 155 nests. Observer 1's presence-absence database resulted in a superpopulation estimate of 509 nests (± 4.45 nests); Observer 2's estimate was 409 nests (± 2.65); and Observer 3's estimate was 480 nests (± 3.28). Average interobserver error rate was roughly 13%. Colony information presented in the superpopulation and combined results (below) is from Observer 3's analysis, as this observer also conducted analyses for all other colonies.

Superpopulation Estimates

Superpopulation estimates for the smaller Great Egret colonies were 147% to 482% of the associated peak counts for the same colonies (Figure 2-6), suggesting that asynchrony in nest initiation has a large effect upon the likely number of nest starts. The extrapolated superpopulation estimates for Alley North White Ibis colonies in 2005 and 2006 and the Great Egret colony in 2006 were 213% to 300% of peak counts for the same breeding populations (Figure 2-7). In all eight cases, the peak counts for colonies were well outside the 95% confidence intervals for the superpopulation estimates (Table 2-2).

The superpopulation estimates and raw counts for Great Egret and White Ibis samples in the very large Alley North colony are shown in Table 2-3. The peak count for 2005 was 12,750 White Ibis nests on March 20th; the closest superpopulation survey was also on the 20th, so the raw counts for each sample were taken from this date. Using the superpopulation estimates and raw counts for each sample as described above and in Appendix B, we estimated the superpopulation size for the entire White Ibis colony to be 38,275 nests ($\pm 1,941$ nests). In 2006,

the peak count for White Ibises was 13,566 nests on April 19th. The two closest superpopulation survey dates were on April 17th and 21st, so we used the average of the two raw counts from these dates. We estimated the superpopulation size for the entire colony to be 29,287 nests (± 306 nests). The peak count for Great Egrets in 2006 was 1,193 nests on March 16th. The closest superpopulation survey date for four samples was the 17th. Two samples were only partially surveyed during the season (surveys of these areas were initiated later in the season, as a new cohort of nests entered the area), and for these samples the closest survey date was the 21st. We estimated the superpopulation size for the entire colony to be 2,538 nests (± 32 nests).

Although peak counts consistently underestimated numbers of nest starts, the degree of underestimation varied widely among colonies and years (Figure 2-8); the Cypress City Great Egret colony, for instance, was more asynchronous in 2005 than 2006, and thus the peak count in 2005 represented a much smaller proportion of the superpopulation-derived estimate than did the peak count for 2006. However, at Vacation Island colony, only 25 kilometers away, the level of nesting asynchrony actually increased slightly from 2005 to 2006. Interestingly, although levels of nest turnover varied by season and location, turnover did not appear to vary consistently by species (Figure 2-8).

Subsampling to Determine Necessary Survey Frequency

There was a clear tradeoff between frequency of survey and accuracy of superpopulation estimate (Table 2-4). Although conducting survey flights 17 times over the course of a 3-month period provided the highest superpopulation estimates for the Cypress City colony in 2006, each survey flight cost roughly \$180, and this frequency was expensive to sustain. Of the frequencies tested in Table 2-4, flying every five days provided the best combination of accuracy and number of nests added to the superpopulation estimate per additional survey flight. Superpopulation estimates (including the costs of weekly surveys and the labor costs involved in photographic

analysis) appear to be around five times as expensive as peak count estimates to produce (Appendix C).

Discussion

The estimates of numbers of nest starts that incorporated asynchrony and detectability bias were significantly different from the peak counts in all eight colonies and years. Asynchrony in nest initiation and failure, rather than problems with nest detectability, is the major source of bias in our peak count estimates. In Chapter 1, we compared ground and aerial counts of nests and indicated that visual bias alone may cause errors on the order of 12% underestimates and 70% overestimates for White Ibises and Great Egrets, respectively. Kushlan (1979), using apparently similar methods, found underestimates of 11% for White Ibises and 16% for Great Egrets. In general, such independent visual bias estimates are at least an order of magnitude smaller than our estimates of combined asynchrony and visual bias in this chapter, which ranged from 47% to 382%. Moreover, the detectability term in the superpopulation model, although functionally equivalent to an independent visual bias estimate, is actually smaller than such an independent estimate would be. The detectability term is based solely upon those types of visual bias that may be detected from repeated aerial surveys (e.g., adult birds temporarily off of nests, vegetative occlusion due to the angle of a particular photograph), and does not include sources of bias that may only be detected through a comparison of aerial and ground counts. Nests that are so heavily occluded by vegetation that they are never seen during any aerial survey, for instance, are not included in our superpopulation modeling, and species misidentification in aerial surveys may only be recognized through the comparison of aerial to ground counts. Thus, if the estimates were truly equivalent, the difference between simple visual bias estimates and our combined estimates would probably be larger than is represented here. Regardless, visibility bias appears to affect estimates of nest numbers to a relatively small degree. The vast majority

of error in our combined estimates appears to be from the effects of asynchronous nesting and nest failure (together taken as “turnover”), as the numbers of individually identifiable nests were several times the peak count values for all colonies. We therefore address the importance of superpopulation modeling below solely in regard to the problem of turnover and asynchrony in nest initiation.

Our results indicate that there was not a large difference between White Ibis and Great Egret nest turnover rates. This was surprising, since the two typically have different reproductive phenologies, timing of nesting, and nest failure rates (Frederick and Collopy 1989a, Kushlan and Bildstein 1992, McCrimmon et al. 2001). However, the inter-year comparisons (Figure 2-8) illustrated that the degree of turnover varied widely between years and, moreover, between colonies during the same year (see also Frederick et al. 2006). This suggests that nest turnover rates are not constant and will have to be estimated on an individual colony basis for each season of interest. This is unfortunate, since it makes measuring nest turnover much more difficult and costly.

However, it is apparent from these results that the amount of bias introduced through the failure to incorporate nesting asynchrony into estimates is also unacceptably large. Estimates of total number of nest starts at a colony over the course of a season are a vast improvement over peak counts for two reasons. First, we believe that our estimates of total number of nest starts are much closer to the actual breeding population size for these colonies than are peak count estimates. Peak counts have been accepted as minimum breeding population size estimates for the purposes of developing an index of breeding activity between seasons, but (with good reason) they have never been presented as estimates of actual breeding population size. Second, some authors have claimed that peak counts and related methods may be of use as indices of

population growth (James et al. 1996, Link and Sauer 1998), even if they are not reliable estimates of true population size (Link and Sauer 1998, Link and Sauer 2002). Indices are useful indicators only if they reliably reflect true relative differences between periods of interest. In the case of wading birds, we have shown that peak counts are not reliable indicators of relative differences between annual numbers of nests, and are reflecting different proportions of the actual breeding population size in different seasons. Given the variability in turnover between seasons, it appears likely that monitoring schemes using peak counts may be failing to serve their intended purpose of providing even a reliable index of population size.

Superpopulation estimates of numbers of nests, in contrast, are comparable between years and may be used as an index of breeding activity. Since renesting may occur, the total number of nest starts is still not an accurate estimate of actual breeding population size; however, by examining the total number of nest starts each season (along with an estimate of nest success), one can obtain a fairly good idea of reproductive conditions for wading birds in a given season. At Vulture colony in 2005, for instance, the estimate of total number of nest starts was almost five times the peak count. This colony was completely destroyed by a mammalian predator early in the season, and was repopulated with new nests five weeks later. The peak count does not provide an accurate depiction of breeding conditions within Vulture colony for this season, but our estimate of total number of nest starts, along with a rough estimate of nest failure rate, was more informative. We therefore feel that despite any shortcomings of the methods used (see below), the superpopulation technique of estimating nest effort in colonies is likely to be more accurate than the peak count method.

Limitations and Assumptions

There are several apparent biases and limitations that we have noted in the use of these estimation techniques. First, detectability estimates in superpopulation modeling do not include

nests that were so heavily occluded by vegetation that they are impossible to see from the air (and thus are never included in any survey counts). The relative frequency of these completely occluded nests may only be estimated by comparing ground and aerial counts of the same areas in colonies (Chapter 1). This inherent bias in the superpopulation-aerial photographic method probably leads to a slight underestimation of true number of nest starts. This is particularly true for birds that typically nest subcanopy (e.g., White Ibises), as opposed to those nesting predominantly in the canopy (Great Egrets). In addition, the total number of nest starts in each colony was also probably underestimated because the first sightings of all nests were removed from a database before it was analyzed. Although most of the one-sighting “nests” probably were not true nest starts, the small proportion that were could cause a bias of unknown magnitude and lead to an underestimate of true nest starts. We believe, however, that this error is likely to have been small in comparison to other sources.

Not all of the colonies or samples within colonies were surveyed for the same period of time, due to photo quality and survey restraints. For example, many of the sample superpopulation estimates for the very large Alley North colony are likely to be underestimates of true numbers of nest starts, since only about 20% of samples were surveyed for the entirety of the breeding season. Surveys of a particular area were usually initiated when markers were placed in the area, except in cases where the survey area was identifiable in one or multiple survey photographs before the markers were erected, and surveys were halted when there were very few or no visible birds remaining in the area. Since there are often different nesting cohorts in a colony of this size, and nest initiation rates varied during the season, we did not feel that it was biologically justified to attempt to extrapolate superpopulation sizes for the entire survey period for samples that were partially surveyed. However, it must be noted that a more thorough

colony-wide, pre-season marking methodology would enable more accurate estimates of superpopulation size (see below), and likely further increase superpopulation estimates for this large colony.

Model fit

The calculated \hat{c} values for several of the model sets were larger than 3, indicating problems with model fit and possible violations of model assumptions. Survival probability is probably temporally heterogeneous in colonies, because nest survival varies among stages of nesting (Mayfield 1975, Frederick and Collopy 1989b, Torres and Mangeaud 2006) and as a result of environmental variability within the season (Frederick and Collopy 1989a). Likewise, encounter probability is unlikely to be the same for all nests, because nests that are located in taller vegetation are more highly visible from the air and more likely to be seen on every survey. Many of the violations of model assumptions appeared to be related to the test for homogeneity in capture probability. If this heterogeneity was the result of visibility, as above, it might help in the future to categorize nests according to visibility and conduct analysis in MARK with visibility as a grouping variable. Fortunately, however, both survival and encounter probability estimates in Jolly-Seber models tend to be robust to this type of heterogeneity, so long as average encounter probability is high (>0.5 ; Pollock et al. 1990), which it was for all colonies and samples we examined.

It is also possible that our models fit better in reality than was indicated by the calculated \hat{c} values in RELEASE. Due to the large sample sizes in our study, we had very good power for our goodness-of-fit tests to resolve even small differences between observed and expected values. We examined the chi-square tables in RELEASE and suggest that the differences found, while in some cases statistically significant, were probably not biologically significant in terms of numbers of surviving or encountered nests.

Refinements of the superpopulation technique

We recommend that the first two flights of the season be close together (within 2–4 days), as the first survey flight will be dropped from the database before analysis. This maximizes the usable period of observation. Aerial photographic surveys should also be initiated as soon as incubation begins for the majority of the colony. For wading birds, the end of breeding and onset of incubation corresponds to a decrease in noise and movement within the colony. From an aerial view, birds in incubation seem settled and sitting still; few are flapping around or displaying with any frequency (Frederick 2006). After the second survey flight, our analysis suggests that survey interval can be reduced to once every five to seven days without large loss of information. While some information can be obtained from less frequent surveys, it becomes increasingly difficult to accurately identify nests with greater time elapsed between sequential photographs.

Very large colonies will require random or stratified random sampling designs in order to capture the full heterogeneity in nest turnover among cohorts within the colony. Since landmarks must be used to identify nests, our sampling areas were not located randomly. Even for areas where we used artificial markers, the difficulty of moving through high-density vegetation restricted our choice of sites. By comparing the ratio of superpopulation estimates to raw counts for all samples, we examined the relative proportion of nests missed in the peak count, rather than absolute numbers missed. However, nest turnover rate may vary with nest density, a possibility that has not been examined in wading birds. If true, in order for the average sample ratio of superpopulation estimate to raw count to hold true for the entire colony, our samples would have to be representative of the range and relative proportions of different nest densities within the colony. The ideal solution would be to distribute markers throughout the colony site prior to the beginning of the nesting season, in order to allow for random placement of samples.

The design of such a marker must be 1) small enough to fit into small aircraft, 2) small enough to be deployed from the aircraft safely, 3) large and conspicuous enough to be easily visible from the air, 4) biodegradable, and 5) of a nature such that it will rest on the canopy of nesting substrate. The colonies we studied were densely vegetated, remote, and very difficult to place markers in, and may represent a worse case scenario. For colonies that are more readily accessible, artificial landmarks might be more readily placed by hand.

We consider the large sample sizes of nests obtainable through the use of the aerial photographic technique to be central to encompassing the inherently large variation in nest success and synchrony that exists in large colonies. It is clear that the repeated photo technique represents a significant increase in manpower and cost by comparison with the peak count method (Appendix C), but we would suggest that there is no bargain to be had in using a cheaper method that yields uninterpretable results. If funds are limited, a potential strategy may be to survey intensively every two to three years, rather than on an annual basis.

Incorporation of renesting

We have focused in this paper on providing estimates of total numbers of nest starts occurring throughout a nesting season. Since nest failure is common (Frederick and Collopy 1989c), and the nesting season is long (3–4 months), renesting may be frequent. For this reason, the nesting population (numbers of pairs or breeding females) would be smaller than the numbers of nest starts (Piazza and Wright 2004). Since this difference could be substantial, we strongly recommend that this technique be used in conjunction with studies of renesting frequency.

Implications of Results

The results of this study indicate that breeding population sizes for colonially breeding birds may be considerably larger than previously supposed. However, actual numbers of breeding pairs are probably somewhat smaller than suggested by the estimated numbers of nest

starts in this study, because of the probability of renesting (see above). Likewise, it should be clear that the larger estimates resulting from the methodology we used do not represent an actual increase in population, but rather an increase in our ability to measure the population. The combined estimates of breeding population size allow us to more accurately measure inter-annual and inter-site variation, and thus to see variation in breeding effort that was previously masked by bias associated with peak counts or similar surveys. These new estimates are therefore both more accurate and offer associated confidence estimates, which peak counts and related one-time surveys lack.

We suggest that peak or snapshot counts can be useful as indices in situations where the study species has high nest synchrony, or alternatively where sources of bias are measured on a seasonal basis and incorporated into estimates. However, our research indicates that unless demonstrated otherwise, snapshot surveys of avian breeding populations probably cannot be used effectively as indices of breeding population size. Moreover, there is no way to tell from snapshot counts alone just how biased these estimates of population size may be. In this study we have examined an extreme case (long nesting period, highly variable nest failure, potential for poor nest visibility), but many avian species probably show similar characteristics, if to a smaller degree. Given the strong biases that have now been demonstrated (this study, Frederick et al. 2006) even lesser degrees of asynchrony are likely to alter estimates of breeding population size by a considerable amount.

Table 2-1. Names and locations of study sites. WCA-3A is Water Conservation Area 3A, a large area of primarily sawgrass and wet prairie in the Everglades controlled by the South Florida Water Management District. The city of Homestead lies south and slightly east of the majority of WCA-3A.

Colony	Location	Latitude	Longitude
Alley North	WCA-3A	N 26° 11.179	W -80° 31.431
Cypress City	WCA-3A	N 26° 07.468	W -80° 30.283
Vacation Island	WCA-3A	N 25° 54.939	W -80° 37.813
Vulture	WCA-3A	N 26° 01.470	W -80° 32.240
Homestead General Airport (KX-51)	Homestead	N 25° 30.0	W -80° 33.3

Table 2-2. All colonies for which we followed nest fate through time in aerial survey photographs and calculated a superpopulation estimate. For smaller Great Egret colonies, number of aerial surveys conducted during the season and the final number of individually identified nests (database size) are listed. For Alley North colonies, surveys were conducted of samples within the colony rather than of the colony in its entirety; data from all samples is in Table 2-3. Peak counts are the maximum one-time counts of number of nests in colonies, taken from a series of monthly aerial surveys during the breeding season. Superpopulation estimates for the same colonies incorporate detectability bias and bias due to nesting asynchrony, and thus are much higher estimates of nest numbers than peak counts. Superpopulation estimates also have measures of uncertainty associated with them, which peak counts lack.

Year	Colony	Species ^a	Peak count	Number of surveys in database ^b	Database size (# nests) ^c	Superpopulation estimate N* (LCI-UCI) ^d
2005	Vulture	GREG	121	7	499	583 (521–645)
2005	Vacation Island	GREG	79	7	215	233 (226–240)
2006	Vacation Island	GREG	155	21	474	480 (477–483)
2005	Cypress City	GREG	107	6	244	268 (259–277)
2006	Cypress City	GREG	173	17	249	254 (251–256)
2006	Alley North	GREG	1,193	-	-	2,538 (2,474–2,601)
2005	Alley North	WHIB	12,750	-	-	38,275 (34,392–42,157)
2006	Alley North	WHIB	13,566	-	-	29,287 (28,674–29,899)

a. GREG=Great Egrets; WHIB=White Ibises.

b. Number of surveys in database does not include first survey, as all first sightings of nests were eliminated from the database before analysis (see text).

c. The database size is the number of nests in the sample's presence-absence database after the first sightings were eliminated.

d. N*=weighted model-averaged superpopulation estimate, calculated in Program MARK. LCI-UCI are 95% confidence intervals.

Table 2-3. All samples of Great Egret and White Ibis populations from large colony (Alley North) for which we followed nest fate through time in aerial survey photographs and calculated a superpopulation estimate.

Year	Sample ^a	Species ^b	# surveys in database ^c	N* (LCI-UCI) ^d	Raw count for sample ^e	Proportional difference between N* and raw count ^f
2006	Q1	GREG	10	56 (54–59)	24	2.33 (2.25–2.46)
2006	Q2	GREG	9	59 (58–60)	28	2.11 (2.07–2.14)
2006	Q3	GREG	9	58 (56–60)	20	2.90 (2.80–3.00)
2006	GE SE 1	GREG	17	43 (43–44)	22	1.95 (1.95–2.00)
2006	GE SE 2	GREG	16	73 (73–74)	57	1.28 (1.28–1.30)
2006	GE SE 3	GREG	10	54 (51–58)	19	2.84 (2.68–3.05)
2005	IT 1	WHIB	5	51 (47–54)	28	1.82 (1.68–1.93)
2005	IT 3	WHIB	6	67 (63–70)	36	1.86 (1.75–1.94)
2005	GST 1	WHIB	8	19 (16–22)	3	6.33 (5.33–7.33)
2005	GST 2	WHIB	5	30 (25–34)	14	2.14 (1.79–2.43)
2005	GST 3	WHIB	8	12 (8–15)	4	3.00 (2.00–3.75)
2006	Q5-N	WHIB	5	94 (93–95)	54.5	1.72 (1.71–1.74)
2006	Q5-S	WHIB	5	69 (69–70)	38	1.82 (1.82–1.84)
2006	Q6	WHIB	9	118 (115–121)	41.5	2.84 (2.77–2.92)
2006	Q6-S	WHIB	8	124 (121–127)	33.5	3.70 (3.61–3.79)
2006	Q7	WHIB	3	34 (33–35)	25.5	1.33 (1.29–1.37)
2006	Q8	WHIB	5	35 (32–38)	22	1.59 (1.45–1.73)
2006	Q9	WHIB	12	31 (28–34)	13.5	2.30 (2.07–2.52)
2006	Q10	WHIB	12	98 (96–101)	50.5	1.94 (1.90–2.00)

a. Alley North samples are labeled for convenience by location and nearby landmarks.

b. GREG=Great Egrets; WHIB=White Ibises.

c. Number of surveys in database does not include first survey, as all first sightings of nests were eliminated from the database before analysis (see text).

d. N*=weighted model average superpopulation estimate, calculated in Program MARK. LCI-UCI are 95% confidence intervals.

e. Raw counts are the numbers of nests seen in sample areas during the survey closest to the colony peak count date. If two survey dates were equally close to the colony peak count date, the average of the two raw counts from these surveys is presented here.

f. Difference calculated as N*/Raw count. Proportion CIs calculated using CIs for N*.

Table 2-4. Subsampling of Cypress City 2006 database to determine minimum survey frequency for superpopulation method. Peak count for same colony during this period is 173 nests.

Database	Number of surveys in database (not including first; see text)	Database size (# nests)	N* (LCI-UCI) ^a
Inclusive (flights ~twice/week, irregular spacing)	17	249	253 (250–255)
Every third survey deleted after first two (irregular spacing)	12	229	235 (232–239)
Flights every 5 days	12	240	247 (243–251)
Every other survey deleted after first two (flights ~once/week, irregular spacing)	10	229	237 (233–241)
Weekly flights (after first two surveys)	10	223	232 (228–236)
Flights every ten days (after first two surveys)	7	214	224 (219–229)
Bimonthly flights (after first two surveys)	6	194	207 (201–213)

a. N*=superpopulation estimate. Superpopulation estimates and confidence intervals are weighted model averages.

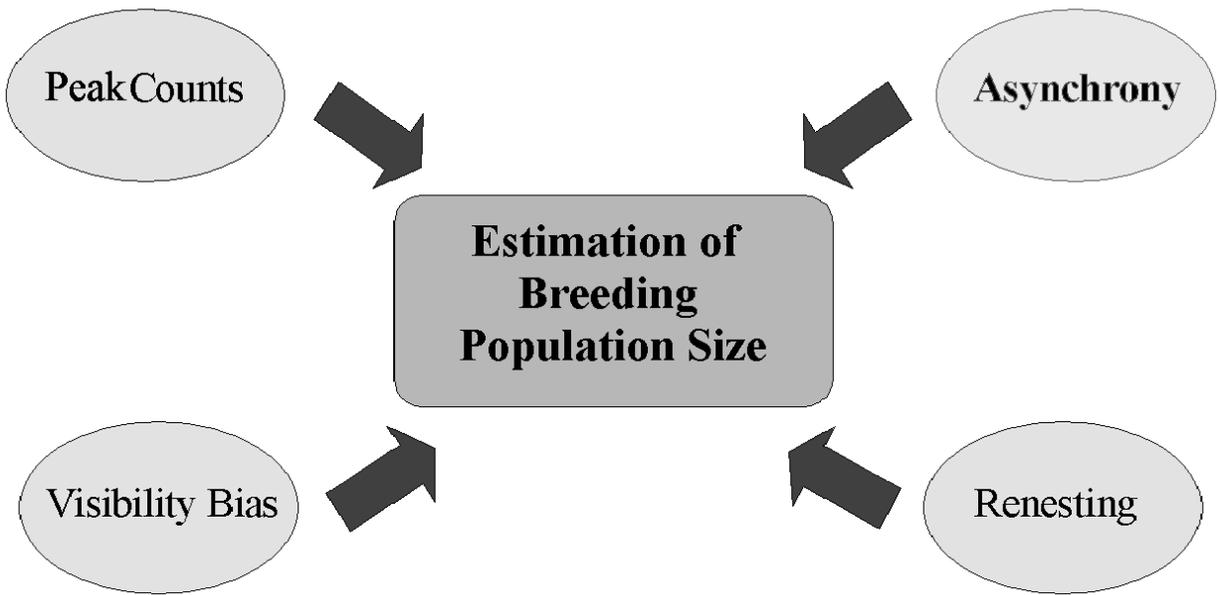


Figure 2-1. Types of data that should be incorporated into estimates of breeding population size.

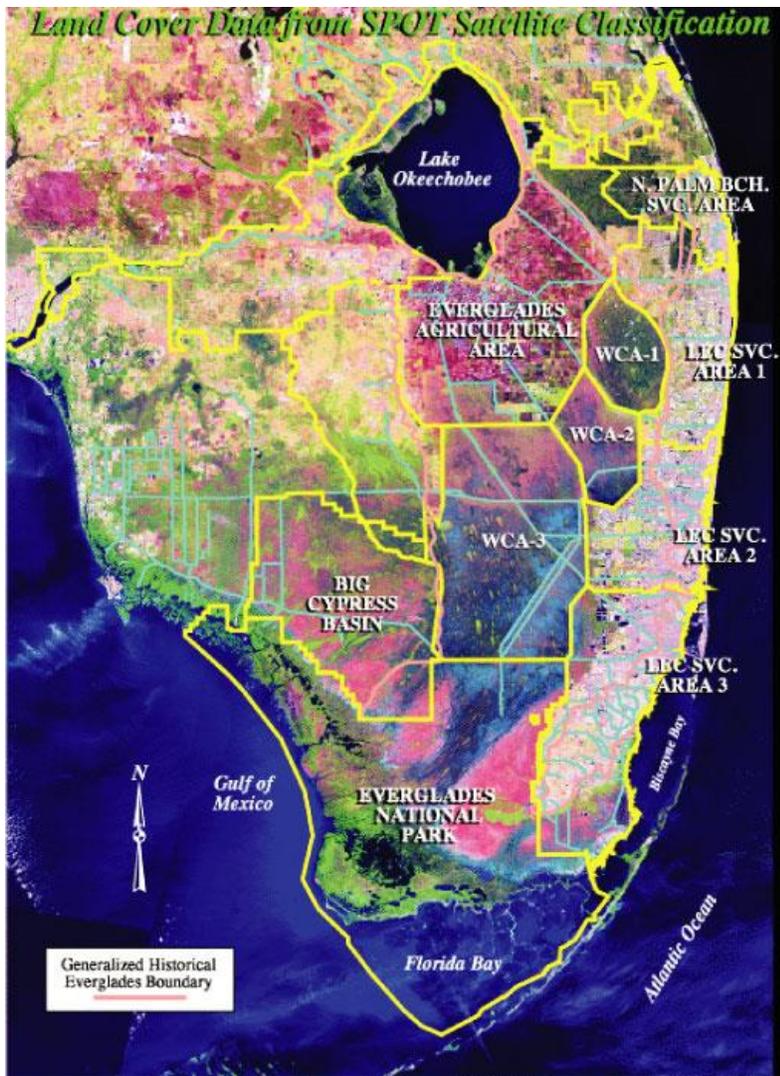


Figure 2-2. Satellite photograph of the modern Everglades, with major watershed regions outlined in yellow. All research presented in this paper was conducted in Water Conservation Area 3A (WCA-3A) in the central Everglades. Photo from <http://sofia.usgs.gov/>; available at <http://sofia.usgs.gov/publications/circular/1275/images/cover-landcvrdataspot.jpg>.

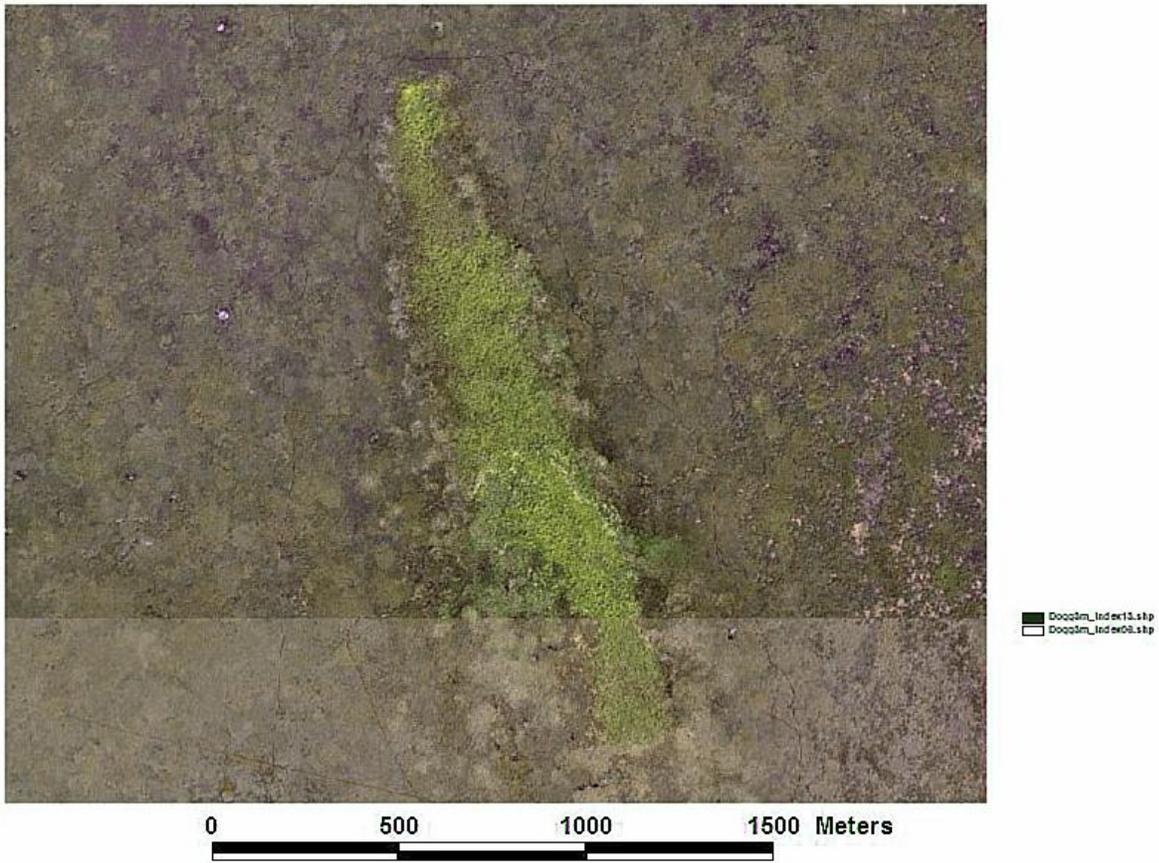


Figure 2-3. Satellite photograph of Alley North colony's tree island (WCA-3A). Alley North colony was subsampled in order to develop a superpopulation estimate, as it is too large to conduct photo analyses in its entirety.



A.



B.

Figure 2-4. Two types of artificial landmarks used in this study. A) Markers made of 10-cm diameter PVC pipe pounded into the ground and anchored with a steel fence post, topped with a 1.5-meter wide X. B) Markers made of 1x1 meter white cotton cloth, tied to vegetation.

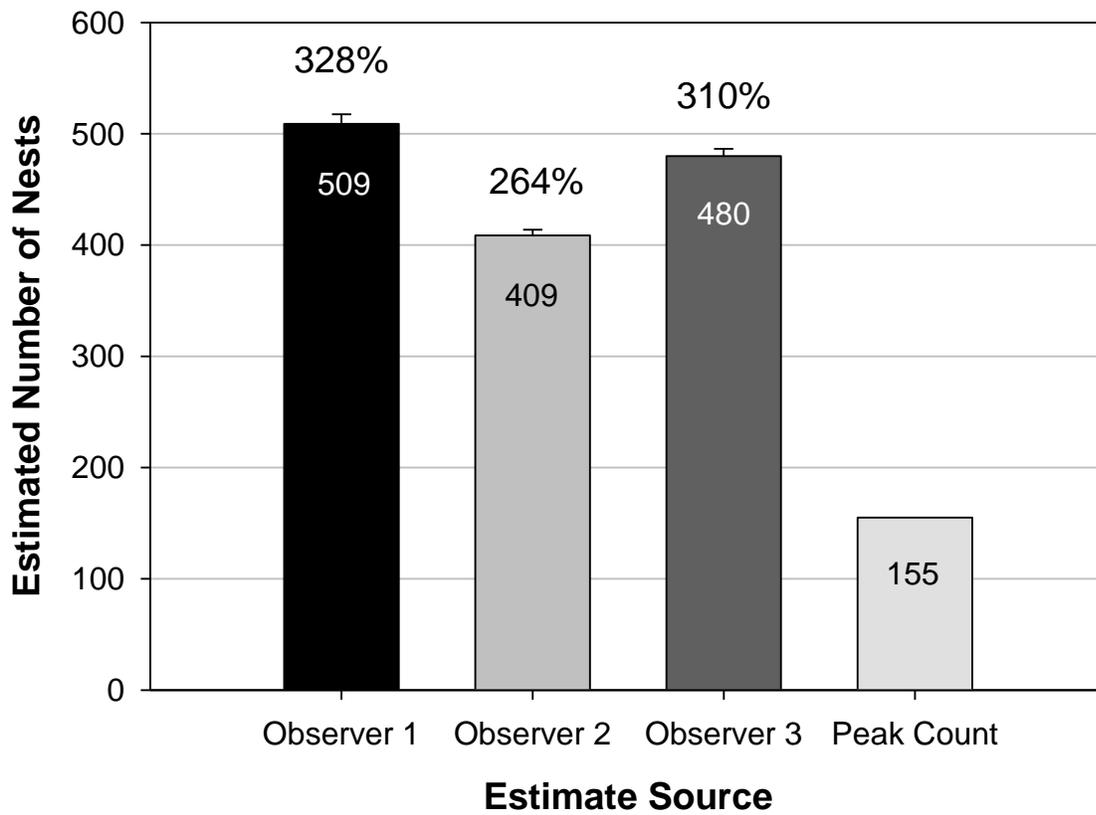


Figure 2-5. Multi-observer comparison of superpopulation estimates for Vacation Island 2006 colony, derived from photographic analyses by three independent observers. Percentage values are the percents by which each observer's superpopulation estimate is greater than the colony's peak count. Numbers inside the bars are labels of estimates.

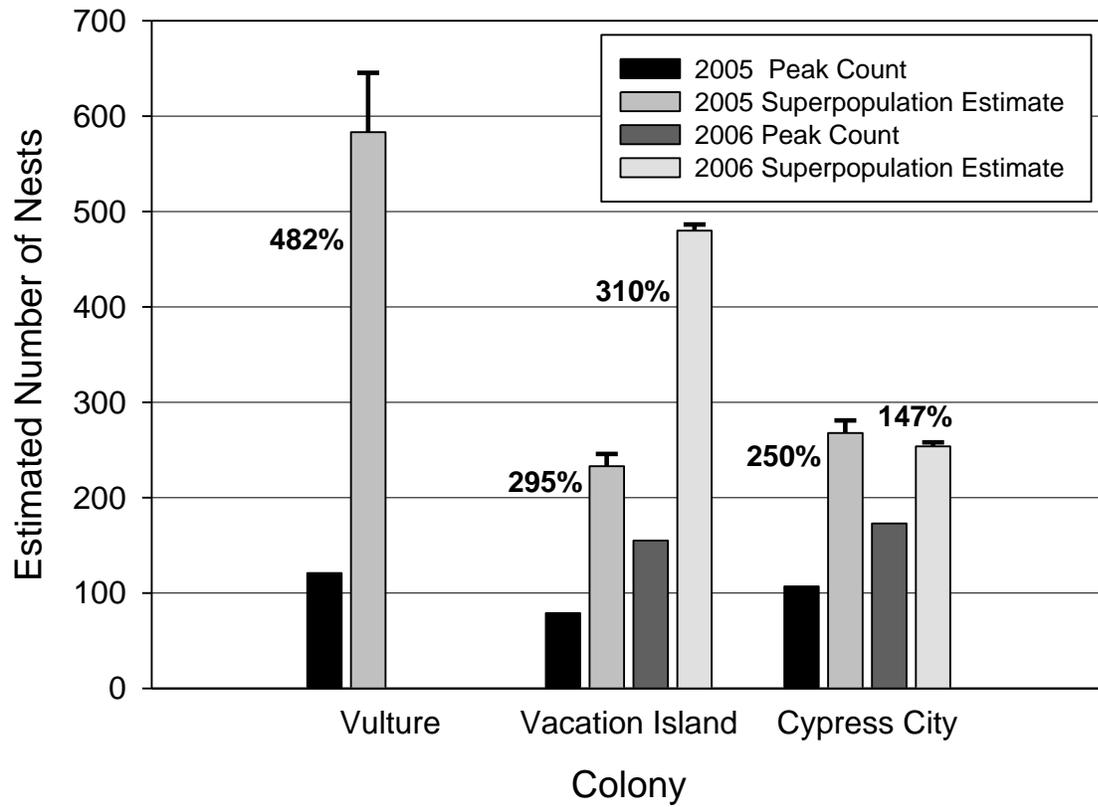


Figure 2-6. Peak counts and associated superpopulation estimates for three Great Egret colonies in WCA-3A (2005-2006). The percentage difference between the two estimates for each colony and year are located above the bars.

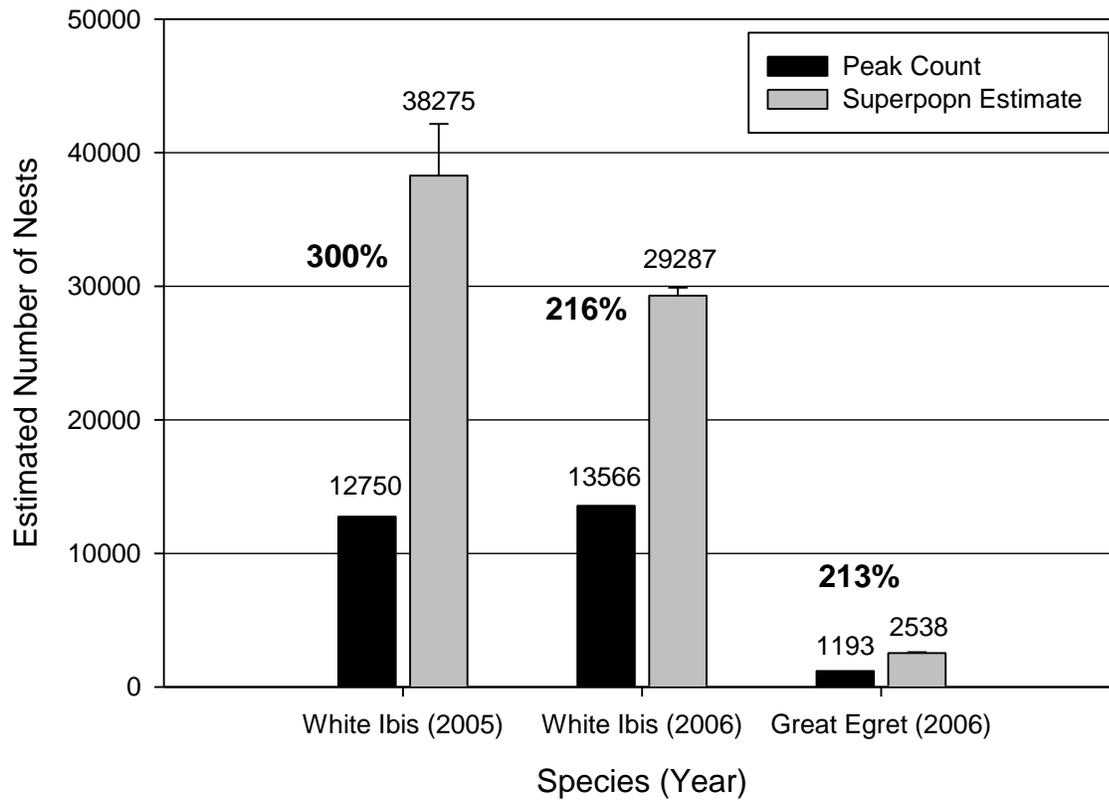


Figure 2-7. Peak counts and extrapolated superpopulation estimates for White Ibises in 2005 and 2006 and Great Egrets in 2006 at Alley North colony (WCA-3A). Each bar is labeled with the value (in estimated number of nests) it represents; the percentage difference between the two estimates for each colony and year are located above the bars.

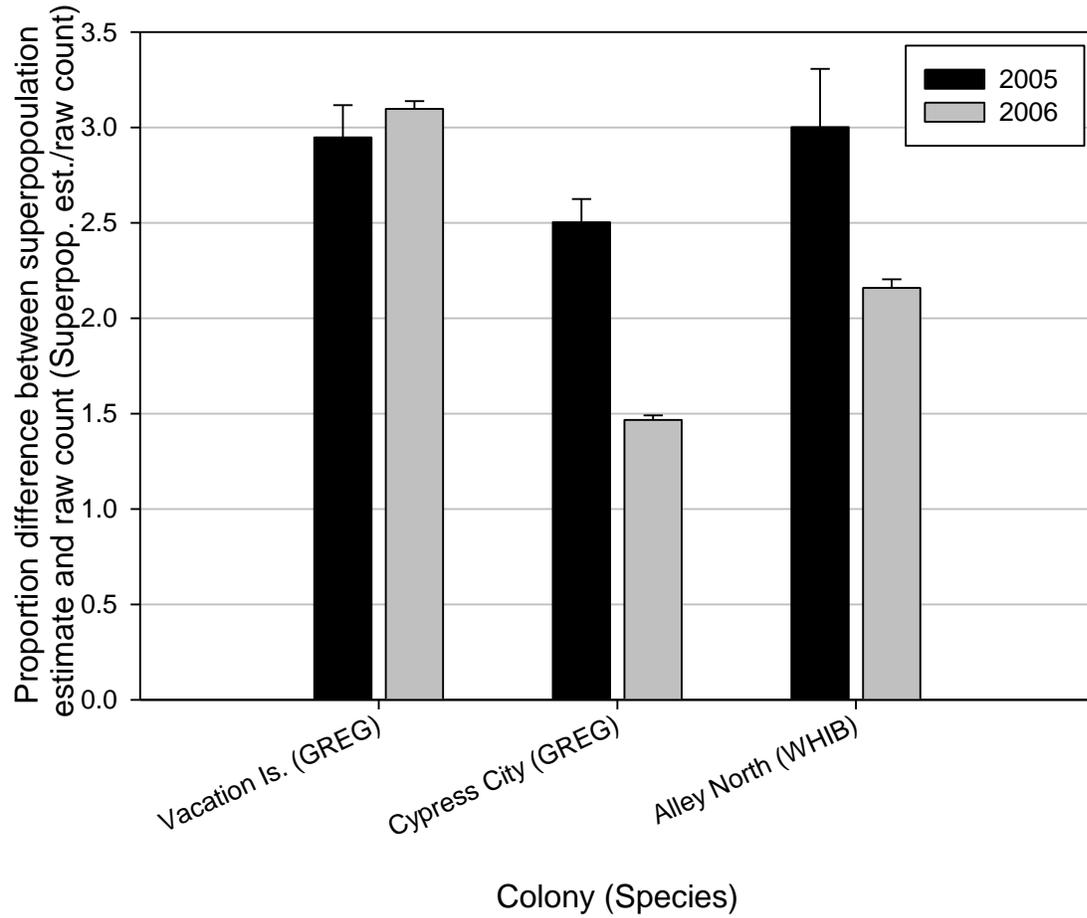


Figure 2-8. The proportional difference between superpopulation estimates and peak counts for 2005 and 2006. GREG=Great Egret colony; WHIB=White Ibis colony.

CHAPTER 3
REMOTELY MEASURED EFFECTS OF RESEARCHER DISTURBANCE ON GREAT
EGRETS (*Ardea alba*) AND WHITE IBISES (*Eudocimus albus*)

Introduction

For colonially breeding birds, the disturbance created by researchers walking very close to or within the colony may affect reproduction, especially early in the nesting cycle (Bouton et al. 2005, Giese 1996, Ellison and Cleary 1978, Tremblay and Ellison 1979). Indeed, the effects of disturbance on nest success may be more severe for colonially breeding bird species than for solitary nesters, due to the number of nests potentially affected by a single disturbance (Carney and Sydeman 1999, Burger 1981, Kadlec and Drury 1968, Vos et al. 1985). Potential effects of disturbance may include abandonment (Cairns 1980, Safina and Burger 1983, Carlson and Mclean 1996), reduced clutch or brood size (Ellison and Cleary 1978, Lock and Ross 1973), increased rate of predation (Ellison and Cleary 1978, Kury and Gochfeld 1975, Hunt 1972), reduced rate of new nest initiation (Tremblay and Ellison 1979, Safina and Burger 1983), and reduced hatching and fledging success due to exposure of eggs and chicks to extreme temperatures (Hunt 1972, Ellison and Cleary 1978, Cairns 1980). In Great Blue Herons (Vos et al. 1985, Carlson and Mclean 1996) and various species of Pelecaniformes, Ciconiiformes and Charadriiformes (Rodgers and Smith 1995), ground disturbances in which people walk through colonies have been found to have a more severe effect than boating or mechanical disturbances. However, walk-in surveys are often used to measure nest success (e.g., Cairns 1980, Frederick and Collopy 1989b, Hunt 1972) or to collect biological samples or other census information (Frederick et al. 1999, Rodgers et al. 2005, Lock and Ross 1973). If ground surveys themselves significantly decrease nest success or other reproductive parameters, it may defeat the purpose of the research (Rodgers and Burger 1981). However, at least in wading birds (Ciconiiformes), there is some debate as to what level of disturbance is biologically or demographically

significant, and what constitutes “acceptable” disturbance levels may vary widely by species (Carney and Sydeman 1999, Erwin 1989).

The effects of human disturbance are inherently difficult to measure, since measurement itself usually requires some level of human intrusion (Shields and Parnell 1986, Frederick and Collopy 1989b). While this has been addressed through the comparison of colonies with different rates of human disturbance (e.g., Frederick and Collopy 1989b, Piatt et al. 1990, Davis and Parsons 1991, Tremblay and Ellison 1979, Burger 1981), it is not clear that location effects can be entirely controlled in such studies. Comparison has also been made of areas within a single colony, but this has been limited to rare situations in which birds can be observed from distant vantage points (Pratt 1970, Hulka and Stirling 2000, Bouton 1999, Galbraith 1987). In this paper we describe a study of human disturbance effects as inferred by observations made from aircraft, comparing disturbed and undisturbed areas of the same colonies. As has been indicated by other studies on ciconiiform species, we predicted that areas with walk-in disturbance would experience increased nest failure rates and a decreased rate of new nest initiation.

Methods

Ground Transects

We monitored nesting in two breeding colonies located in Water Conservation Area 3A of the Everglades (Broward County, FL) in March-May of 2006. Both colonies were located in tree islands dominated by willow (*Salix* spp.) set within an emergent marsh of primarily sawgrass (*Cladium jamaicense*) and cattail (*Typha* spp). Vacation Island colony (approximately 1 ha, located at N25°54.939 by W-80°37.813) was composed of roughly 90% Great Egrets (*Ardea alba*), though a small number of Great Blue Herons (*Ardea herodias*) and Anhingas (*Anhinga anhinga*) nested in the taller trees. This colony was distant from other sources of human

disturbance (12.5 km to nearest road and 600 meters to nearest airboat trail) and we believe our visits to be the only form of human disturbance to which this colony was exposed. The second colony, Alley North (N25°11.179, W-80°31.431), was a much larger (45 ha) mixed-species colony that included Great Egrets, Snowy Egrets (*Egretta thula*), Little Blue Herons (*Egretta caerulea*), Black-crowned Night Herons (*Nycticorax nycticorax*), Tricolored Herons (*Egretta tricolor*), White Ibises (*Eudocimus albus*), and other species. The northern end of the colony (approximately 30 ha) was exclusively composed of White Ibis nests, and we studied two small areas within this single-species area of the colony (hereafter referred to as “Alley North colony”). The colony was distant from sources of non-researcher human disturbance (3.2 km to nearest road and 400 meters to nearest airboat trail). One other research team was also working in the colony during the time period in which we conducted surveys. The majority of this research was based on remotely monitoring radiotelemetry signals from outside the tree island, but researchers did occasionally enter the colony as well.

We used both aerial photography and repeated walk-in censuses of marked nests to monitor nesting. At Vacation Island, the “disturbed” area around the walk-in census trail encompassed the northern 40% of the nesting area. The southern 60% of the tree island (all nests >15m from the census trail) comprised the “undisturbed” sample area, and was never surveyed on foot during the breeding season. Walk-in censuses of Alley North were located in the northeastern portion of the colony, and encompassed less than 1% of the area of nesting. One 100-m² area was censused using walk-in methods only once, and then aerial methods thereafter; another 200 m² area was censused four times on the ground in addition to aerial surveys. The undisturbed (single-visit) area used in this study was located approximately 200 meters south of

the disturbed site; apart from the initial visit to erect markers to delineate the sample area, we did not come closer to this control site than 200 meters during the breeding season.

We began walk-in censuses after incubation was already underway for most nests. We approached the edge of the colony via airboat to within 15 meters (for Great Egrets) or 75 meters (for White Ibises) of the closest nest. Nest checks were conducted every 5–7 days, and each visit to a colony took roughly one hour with 2–5 people present on each visit. Each nest was briefly examined for nest contents, using a mirror pole if necessary, but the contents were not removed. If abandonment was suspected, the eggs were sometimes touched to determine temperature. Nests were monitored until abandonment (all eggs in nests were cold) or failure (eggs were broken or gone from nest, or chicks were dead or gone from nest before fledge date).

Aerial Survey Methodology

We conducted aerial photographic surveys of nests that were individually identifiable from the air in order to examine nest turnover rates. Surveys were conducted twice a week at irregular intervals during the breeding season in a Cessna Skyhawk (172) aircraft, and photographs were taken using a Canon EOS 20D high-resolution digital camera with a 28–135mm image-stabilizing zoom lens. Camera settings were primarily on auto. We took photographs from an altitude of approximately 152 meters out the copilot's door (right side of plane), and the door was removed for all survey flights so that photographs could be taken as close to vertically above nests as possible. We conducted survey flights between 08:00 to 10:30 am or 16:00 to 18:00 pm, but flight times varied with weather, plane availability, and other factors.

To allow for the identification of walking routes from the air, we erected artificial landmarks around the outer perimeter of each walk-in survey route. For Vacation Island, markers were placed within 1–3 meters of the edge of the transect path at roughly 15-meter intervals, and we considered all nests within 15 meters of a marker to be in the “disturbance

zone,” while nests outside this area were identified as “undisturbed.” We used the length of the X at the top of the PVC markers (below) in each photograph as a metric for scaling ground distances in the colony. For the Alley North colony, we placed a marker at the four corners of both the disturbed and undisturbed study sites. The “disturbed” site had regular walk-in surveys and the “undisturbed” site had no further ground disturbances after the markers were erected.

The markers were of two types:

- A 3-meter tall, four-inch PVC pipe with a 1.5-meter X made of PVC attached to the top of the pole (Figure 3-1A).
- A 1x1-meter piece of white or pale-colored cotton cloth tied at the corners to vegetation (Figure 3-1B). These were placed in sheltered areas where they would be less likely to flap in the wind.

Photographic Analysis

We edited photos in Adobe Photoshop Elements version 2.0. Printed copies of photos were used to identify individual nests and obtain presence-absence data for each nest on each subsequent survey date. Nests in the photos were individually numbered and presence-absence data for nests was entered into the database using the following format:

- Nest inactive (0)- this included cases in which nest and parent/chicks were not visible; nest was visible but empty (no sign of parents/chicks); or there was no photo of the nest area available on that date
- Nest active (1)- parent and/or chicks were visible

We compared photos of the date we were currently working on with photos of all previous dates to ensure that all nests were assigned unique and non-overlapping identities. We used a conservative definition for nest failure in the photographic censuses, due to visibility constraints and because some nests were temporarily unoccupied at the moment the picture was taken.

Nests that were apparently inactive for four consecutive survey dates were categorized as failed, and nests in the same location were thereafter treated as new nest starts. Although we used the

presence of a large white bird as an initial indication of nesting, these could have been roosting birds or birds temporarily away from their nests. Before we analyzed each presence-absence database, we therefore eliminated first observations of all nests from the database, and so deleted from the database all “nests” that were seen only once. Although it is possible that some proportion of these single-tally birds were actually short-lived nest starts, this was considered to be a rare occurrence given the amount of time required for breeding and nest-building in these species (4–10 days for Great Egrets, according to McCrimmon et al. 2001; 9–10 days for White Ibises, as cited in Kushlan and Bildstein 1992). We eliminated the first sighting of nests that were seen on multiple dates (in addition to those nests seen only once) in order to avoid artificially inflating survival estimates.

Analysis of Presence-Absence Databases: A Mark-Recapture Scenario

We used aerial photographs of individually identifiable nests and a variation on a Jolly-Seber (JS) open-population capture-recapture model called the superpopulation method (Schwarz and Arnason 1996) in order to estimate rates of nest initiation and abandonment in large colonies of nesting birds (see also Chapter 2). JS models estimate survival and encounter probabilities for marked animals, and the superpopulation approach also estimates the net immigration into a population. The application of the superpopulation method to nests allows for the monitoring of nests initiated in a colony during a period of interest, such as a breeding season. In our study, nests were equivalent to individuals in a population; the number of new nests present at each survey represented immigration into the population, and the number of “marked,” or individually identifiable, nests that failed between consecutive surveys indicated the level of emigration from the population. Encounter probabilities indicate the chance of seeing a nest on a particular survey date, given that it has survived and is actually present.

The first survey of the colony was deleted from the database, since due to the first-observation nest adjustment (described above), it contained only zeroes. The presence-absence database input into MARK thus started with the second survey date. We fit regression models to the capture-recapture data from colonies using the POPAN data type (Schwarz et al. 1993, Schwarz and Arnason 1996) in Program MARK version 4.3 (White and Burnham 1999). We set the time intervals to fractions of weeks between each set of consecutive surveys and assigned all nests to either the disturbed or undisturbed attribute group in the model. The four variables (survival, ϕ ; encounter probability, p ; entry probability, p_{ent} ; and superpopulation size, N) were allowed to vary with time, vary by attribute group, or some combination thereof, depending upon the model. The “null hypothesis” model was a so-called “dot” model, in which survival, encounter probability, and entry probability were not allowed to vary by group or to change through time. N , population size, was allowed to vary with group for all models, as the number of nests seen over the course of the season was different in each location ($n=279$ for disturbed area and $n=194$ for undisturbed area of Vacation Island colony; $n=163$ for disturbed area and $n=201$ for undisturbed area in Alley North colony). For alternative models in which survival probability ϕ and encounter probability p varied with time, not all parameters in the model were estimable (Schwarz and Arnason 1996). We set $p_1=p_2$ and $p_k=p_{k-1}$ for each group (if group was included in the model) so that all survival parameters were estimable (J. Nichols pers. comm.). In the models in which survival was held constant or varied by group and encounter probability was time-dependent, the initial p value is still inestimable, so for this model we set $p_1=p_2$ for each group and allowed all other encounter probabilities to vary. We used a sin link function to estimate survival and encounter parameters, mlogit functions to estimate entry parameters, and a log link function to estimate population size N of each group.

We used AIC (Akaike's Information Criterion) to distinguish among competing models when testing the validity of our predictions (Williams et al. 2002). Each model had an associated Δ AIC value (a measurement of the difference between it and the best model), and Akaike weights that expressed the relative probability of each model being the best fit for the data. We considered Δ AIC values of less than 2 to indicate relatively well-supported models, while a Δ AIC value of greater than 10 indicated that the data did not support the model (Williams et al. 2002). We also used MARK's model averaging capability to find the weighted average values for all parameters across all models.

Additionally, we quantified the model fit of the most general model in the tested suite, using chi-square tests for each survey interval, to see if observed values varied from the expected number of surviving or encountered nests. These tests evaluated the following two assumptions inherent in Jolly-Seber models (Pollock et al. 1990, Cooch and White 2007): that there is no heterogeneity in capture probability within groups, either among individuals or among cohorts (cohort in this case meaning all nests that were seen for the first time on the same date); and that there is no heterogeneity in survival probability within groups, either among individuals or cohorts. We calculated chi-square values using Program RELEASE (Burnham et al. 1987), available within Program MARK. The chi-square values generated for each survey interval were summed for the entire sampling period, and were divided by the degrees of freedom to obtain a variance inflation factor (\hat{c}). Following Cooch and White (2007), we interpreted a \hat{c} value of 1 to indicate good model fit, values of roughly 1–3 to indicate moderately good fit, and >3 to indicate probable violation of model assumptions. We adjusted model weights for the Great Egret colony using the calculated \hat{c} for the dataset, so the information criterion values presented for these models are thus quasilikelihood (QAICc) values. This modification adjusts

for the overestimated precision of parameter estimates caused by overdispersion in the data (Burnham et al. 1987; Burnham and Anderson 1998; Williams et al. 2002). The calculated \hat{c} value for the White Ibis colony was <1 , which essentially means the data were underdispersed. As there is little agreement in the scientific literature as to what this means or what to do about it, we followed the recommendation of Cooch and White (2007) in using a \hat{c} value of 1 for model weighting in this case.

Results

Vacation Island Great Egret Colony

After adjusting the model selection used in MARK for the calculated \hat{c} value ($\hat{c}=3.21$), two models were equally supported by the data (Table 3-1). All other models in the model-testing suite had less than 1% support (Appendix D for full list). Due to this relatively high \hat{c} value, models with fewer parameters were much more highly supported; in the two best models, both encounter probability and survival probability were held constant over time.

Time had an important effect on probability of entry into the population (new nests being initiated) in both models. Disturbance category was also retained as an important covariate in one model, though its effect was additive rather than multiplicative. The undisturbed group had slightly higher probability of entry into the population across all time periods than did the disturbed nest group (Figure 3-2). According to the most parsimonious model, this difference did not vary appreciably with the survey interval, regardless of how the entry probabilities themselves changed. Although it appears that there may have been an interaction with time on a linear scale (Figure 3-2), the interaction was not included in the best models, either because the interaction was examined on a logit scale or because including an interaction term would have added an additional 19 parameters to the model, and consequently was not supported by the QAICc model selection criteria.

Alley North White Ibis Colony

Two models were well supported by the data, and several others had some moderate level of support (Table 3-2; Appendix E for list of all tested models). Time had an important effect on all three population parameters in all supported models, but the interaction of time with group effect varied between models. All supported models indicated some effect of disturbance group on survival and encounter probabilities, and the majority of the models also indicated a disturbance group effect on entry probability (Table 3-2). The two well-supported models both had group effect as an additive effect on survival probability. According to the best-fit models, this difference did not vary appreciably with survey interval, regardless of how the survival probabilities themselves changed. Encounter probability varied with both group and time in an interactive fashion in the two best models. For the best fit model, entry probability was time-dependent but did not vary with group; for the next-best model (with a ΔAIC value of <2 , indicating some support for the model), entry probability varied with time and group in an additive manner, as for survival above.

Comparison of model-averaged encounter probabilities between disturbance groups for the Alley North White Ibis colony showed that encounter probability did not differ consistently according to disturbance regime. In some survey intervals encounter probability was higher for the disturbed group, and for others it was higher for the undisturbed group. Encounter probability seemed to vary widely among survey intervals and between geographic areas, regardless of level of researcher disturbance. Comparison of model-averaged survival estimates indicated that survival probability was higher in the disturbed area than the undisturbed area (Figure 3-3, Table 3-3). Entry probability in the disturbed area was lower than or equal to that in the undisturbed area (Figure 3-4, Table 3-3). Although the absolute differences in probabilities

between the two groups were considerably larger for survival estimates than for entry probability estimates, entry probabilities showed a proportionally larger effect of disturbance (Table 3-3).

Discussion

Nest success did not appear to be negatively impacted by researcher disturbance during incubation and nestling periods for either Great Egrets or White Ibises. However, model-averaged parameter estimates indicated that nest initiation was lower in the disturbed areas for both species when compared to control sites. This suggests that breeding birds may be sensitive to disturbance in the colony early in the nesting cycle.

Violations of Model Assumptions.

The \hat{c} value for the Vacation Island (Great Egret) model suite was larger than 3, indicating potential problems with model fit. There are biologically sound reasons why model assumptions regarding encounter and survival homogeneity may be false for nesting wading birds, and the lack of model fit we saw for this dataset may be partially due to one of these factors. Fortunately, however, both survival and encounter probability estimates in Jolly-Seber models tend to be robust to this type of heterogeneity, so long as average encounter probability is high (e.g., >0.5 ; Pollock et al. 1990); for Vacation Island, model-averaged encounter probability was 0.945, and for Alley North, it was 0.823.

Effects of Disturbance on Nest Survival

According to the two best-supported models for the Great Egret colony, researcher disturbance had no significant effect on nest survival or encounter probability. Researcher disturbance after the early egg-laying stage appears to cause no appreciable decrease in nest success for Great Egrets. This agrees with similar findings of lack of nest failure due to human disturbance later in the nesting cycle in Tricolored Herons, *Egretta tricolor* (Frederick and Collopy 1989b), Black-crowned Night Herons, *Nycticorax nycticorax* (Parsons and Burger

1982), and Snowy Egrets, *Egretta thula* (Davis and Parsons 1991). Although walk-in surveys do affect nest success for many taxa, perhaps resistance to disturbance in later nest stages is a common characteristic for wading birds.

Likewise, our single or multiple site visits to the White Ibis colony during incubation and early nestling stages did not appreciably decrease nest success. Moreover, nest survival was significantly higher in the disturbed area of the White Ibis colony than in the undisturbed area. This result is counter to generally accepted theory regarding the effects of walk-in ground disturbance on colonially nesting birds, but may be attributable to one of two several possible causes. First, the nests in the two sites may have belonged to different cohorts; based on the single walk-in survey of the undisturbed area, the average nesting stage appeared to be several days to a week behind the disturbed area. Nest initiation date has been found to be very important for nest success in White Ibises, presumably due to environmental variables associated with initiation date (Frederick and Collopy 1989a). A second potential cause of higher nest failure in the undisturbed area is that it was not as “undisturbed” as we thought; there was another team of researchers studying White Ibises at the same colony, and their frequency of visitation to different areas may have affected nest survival rates. Thirdly, it is possible that researcher presence may have discouraged the presence of predators in that area of the colony, although we consider this possibility to be unlikely, as researcher disturbance has been postulated to actually facilitate predation at a White Ibis colony in North Carolina (Shields and Parnell 1986).

Effects of Disturbance on Nest Initiation

It makes biological sense for entry probability to be time-dependent in all supported models, as for both species there tends to be a surge of initial nesting in a given area followed by lower levels of nest initiation thereafter (McCrimmon et al. 2001, Kushlan and Bildstein 1992).

However, for both Great Egrets and White Ibises, one of the two best models also included disturbance group as a factor in entry probability. For Great Egrets, the two models were so equally weighted that for all practical purposes they were indistinguishable using QAICc. This lends some support to the hypothesis that regular researcher disturbance causes depressed levels of nest initiation as compared to areas where nests remained undisturbed. Nest initiation rates are not often measured by researchers studying effects of disturbance (e.g., Carlson and McLean 1996, Burger et al. 1995), but decreased initiation has also been seen in Black Skimmers, *Rynchops niger* (Safina and Burger 1983) and Black-crowned Night Herons, *Nycticorax nycticorax* (Tremblay and Ellison 1979). Depressed nest initiation may not be universal; Frederick and Collopy (1989b) presented evidence that Tricolored Heron nest initiation may not be affected by researcher disturbance, although this question was not a primary focus of the research. However, the effect of disturbance on nest initiation likely varies by species and frequency of visitation (Götmark 1992), and the evidence for both Great Egrets and White Ibises indicates that further research is warranted on this topic.

We have found some effect of researcher disturbance on nest initiation in wading birds, but no discernible effect on nest success. This suggests that wading birds are vulnerable to disturbance early in the nesting period when they are considering nesting locations, but that they may be less sensitive once nesting has begun. It is important to note, however, that disturbance may affect choice of nesting area in the future, a possibility that has not been examined in wading bird species. Even when birds do not overtly react to disturbance during the current breeding season, they may avoid areas in ensuing seasons where they have been disturbed in the past, as has been found in several raptor species (Platt 1977, as cited in Götmark 1992; White and Thurow 1985) and for Adélie penguins (*Pygoscelis adeliae*) in Antarctica (Wilson et al.

1990, Young 1990; but see Fraser and Patterson 1997). Renesting rate may also be reduced in disturbed areas (Götmark 1992), but renesting rates in wading birds are unknown.

Perhaps more important than its evidence for disturbance effects, this study serves to reinforce earlier work in using remote means to infer effects of disturbance. We hope this new and widely applicable method of remotely measuring disturbance will prove useful for future research on this topic.

Table 3-1. Characteristics of the two best fit, lowest AIC models describing population parameters for Great Egret nests in the central Everglades, Florida. Model parameters are probability of survival (ϕ), encounter probability (p), probability of entry into the population (pent), and size of population (N). Each parameter was held constant over the entire survey period (\cdot), held constant for each group separately (group), allowed to vary with time (t), allowed to vary with both time and group (t^*g) or allowed to vary with both time and disturbance group in an additive fashion ($t+\text{group}$). Both models are about equally supported. Model 1 does not include disturbance group as an important factor in the probability of new nests entering the population over time; the second model does include the group parameter. Only models with greater than 1% support are included.

Model	Delta QAICc	QAICc weights	# parameters
{ $p(\cdot)\phi(\cdot)\text{pent}(t)N(\text{group})$ }	0	0.50147	22
{ $p(\cdot)\phi(\cdot)\text{pent}(t+\text{group})N(\text{group})$ }	0.0119	0.4985	23

Table 3-2. Characteristics of the best fit, lowest AIC models describing population parameters for White Ibis nests in the central Everglades, Florida. Model parameters are probability of survival (ϕ), encounter probability (p), probability of entry into the population (pent), and size of population (N). Each parameter was held constant over the entire survey period (\cdot), held constant for each group separately (group), allowed to vary with time (t), allowed to vary with both time and group (t^*g) or allowed to vary with both time and disturbance group in an additive fashion ($t+\text{group}$). Both highly supported models ($\Delta\text{AICc} < 2$) include disturbance group as an additive effect on nest survival and a multiplicative effect on encounter probability. There is some support for the importance of disturbance group on entry probability, but the most highly supported model (55% support) does not include disturbance group as an important factor in entry probability. Only models with greater than 1% support are included.

Model	ΔAICc	AICc weights	# parameters
{ $\phi(t+\text{group})p(t^*\text{group})\text{pent}(t)N(\text{group})$ }	0.000	0.545	19
{ $\phi(t+\text{group})p(t^*\text{group})\text{pent}(t+\text{group})N(\text{group})$ }	1.697	0.233	20
{ $\phi(t+\text{group})p(t+\text{group})\text{pent}(t)N(\text{group})$ }	3.939	0.076	16
{ $\phi(t^*\text{group})p(t^*\text{group})\text{pent}(t)N(\text{group})$ }	4.111	0.070	23
{ $\phi(t^*\text{group})p(t^*\text{group})\text{pent}(t+\text{group})N(\text{group})$ }	5.783	0.030	24
{ $\phi(t+\text{group})p(t^*\text{group})\text{pent}(t^*\text{group})N(\text{group})$ }	6.108	0.026	21
{ $\phi(t^*\text{group})p(t^*\text{group})\text{pent}(t^*\text{group})N(\text{group})$ }	7.420	0.013	26

Table 3-3. Comparison of model-averaged survival and entry probabilities between disturbance groups for the Alley North White Ibis colony. Phi=survival probability; pent=entry probability; interval number indicates survey interval (e.g., interval 1 denotes the time period between surveys 1 and 2). The percent different in daily probabilities between groups indicates the difference in the percentage of nests that survive or are initiated in the disturbed group in comparison to the undisturbed group; a negative difference indicates that the parameter estimate for the disturbed group was lower than that for the undisturbed group. Daily probabilities are calculated for phi as $((\text{disturbed weekly phi})^{1/7}/(\text{undisturbed weekly phi})^{1/7})-1 \times 100$. For pent, this value was calculated as $((\text{disturbed weekly pent})^7/(\text{undisturbed weekly pent})^7)-1 \times 100$.

Parameter	% Difference Between Disturbed and Undisturbed Groups (Daily Probabilities)
phi (interval 1)	2.72
phi (interval 2)	1.57
phi (interval 3)	2.73
phi (interval 4)	3.96
phi (interval 5)	11.00
pent (interval 1)	-29.75
pent (interval 2)	-48.99
pent (interval 3)	-48.01
pent (interval 4)	0.00
pent (interval 5)	0.00



A.



B.

Figure 3-1. Two types of artificial landmarks used in this study. A) Markers made of 10-cm diameter PVC pipe pounded into the ground and anchored with a steel fence post, topped with a 1.5-meter wide X. B) Markers made of 1x1 meter white cotton cloth, tied to vegetation.

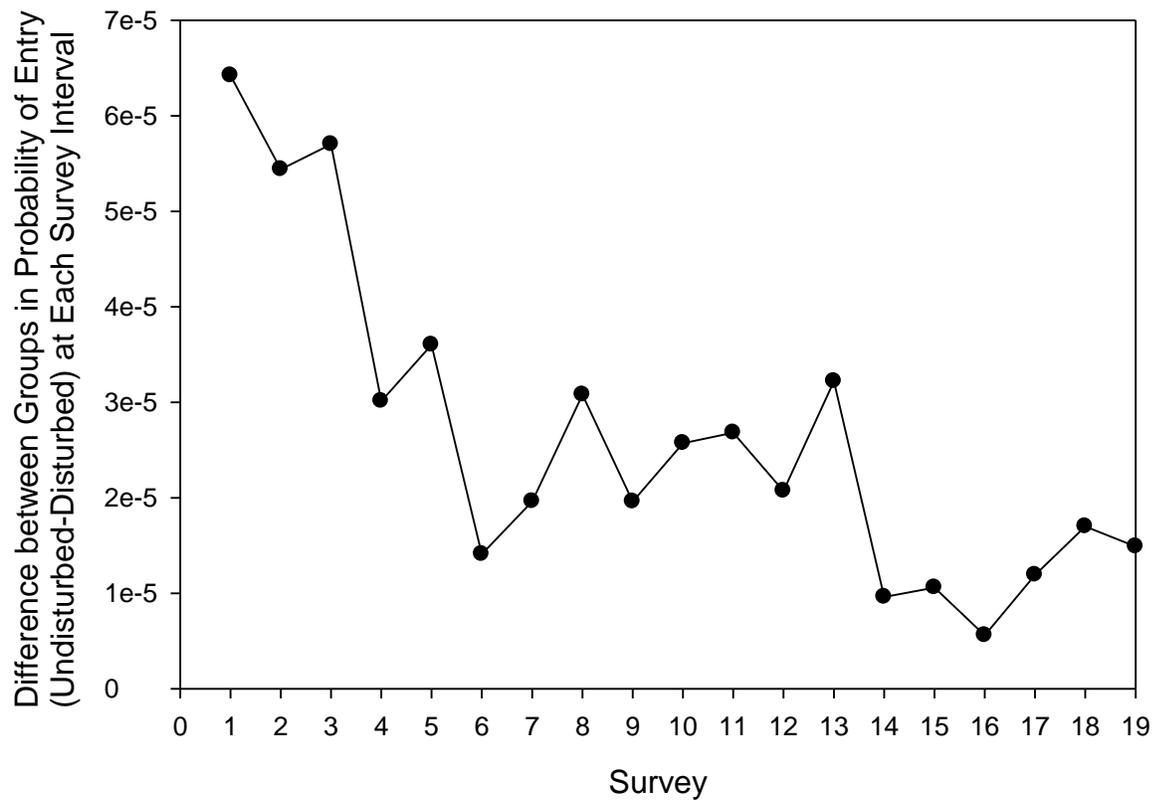


Figure 3-2. The difference in entry probabilities between disturbance groups at Vacation Island Great Egret colony as a function of time. Estimates are from second supported model, $\phi(\cdot)p(\cdot)pent(t+group)N(group)$. Y-axis is the probability of new nests being initiated in the undisturbed area, minus the probability of new nests entering the disturbed area, over each survey interval. Positive differences indicate the disturbed group had lower probability of new nest formation than the undisturbed group. Differences between groups are slight but remain positive over all survey intervals.

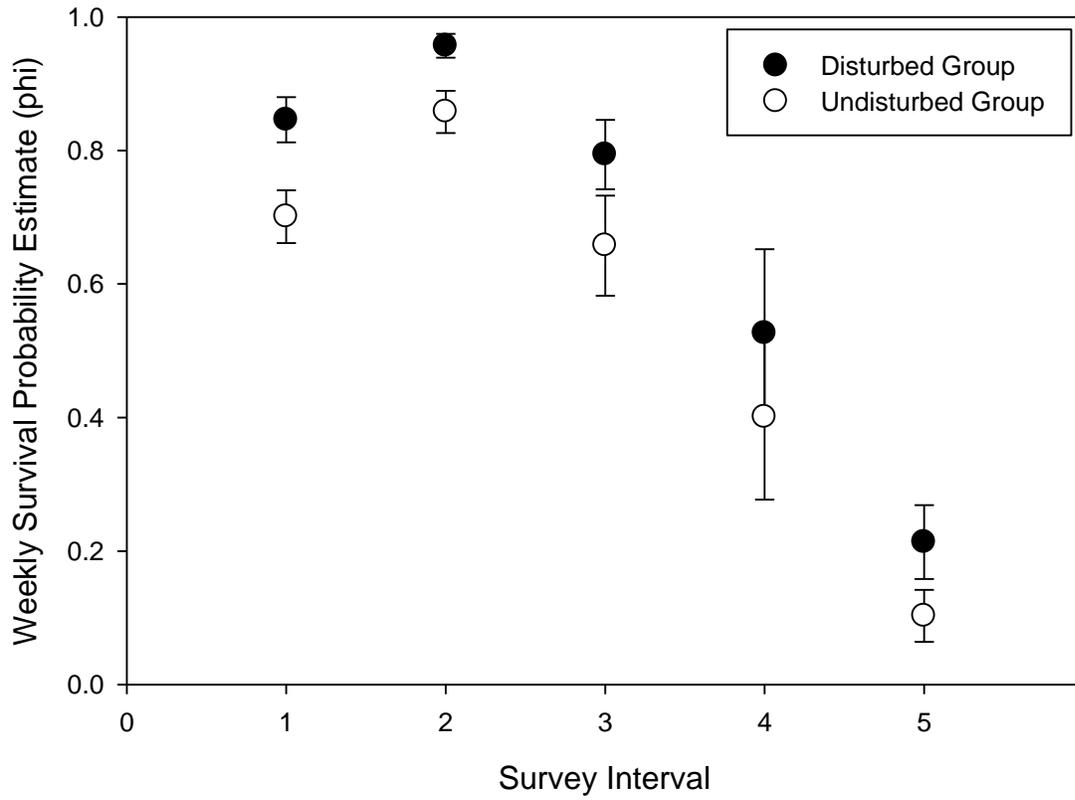


Figure 3-3. Model-averaged weekly survival probabilities for both disturbance groups at Alley North White Ibis colony as a function of survey interval (time). The disturbed group had higher nest survival across all survey intervals than the undisturbed group.

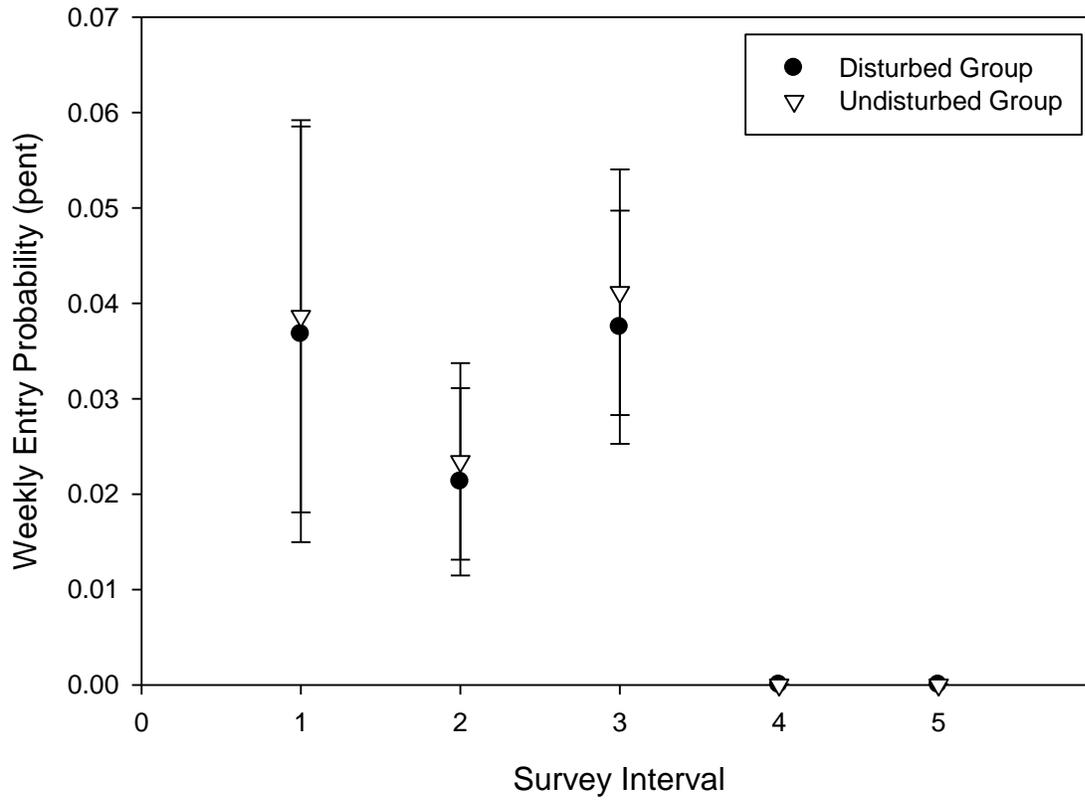


Figure 3-4. Model-averaged weekly entry probabilities for both disturbance groups at Alley North White Ibis colony as a function of survey interval (time). The undisturbed group had higher probability of nest initiation for the first three survey intervals. Both groups had near zero entry probability for the last two survey intervals.

APPENDIX A
SUPERPOPULATION MODEL OUTPUT (POPAN DATA TYPE) FOR ALL COLONIES

Table A-1. For each colony or sample, we tested a set of four candidate models: a general (fully time-dependent) model, a so-called “dot model,” in which survival and entry variables were held constant through time, and two models in which either encounter probability or survival probability was allowed to vary with time while the other was held constant (Cooch and White 2007). Probability of entry into the population (pent) would not be expected to hold constant throughout the season, since for both species there tends to be a surge of initial nesting in an area followed by lower levels of nest initiation thereafter. Thus, entry probabilities were allowed to be time-dependent in all models. For models in which survival probability ϕ (phi) and encounter probability p varied with time, not all parameters in the model were estimable. We set $p_1=p_2$ and $p_k=p_{k-1}$ so that all survival parameters were estimable in the model. In the model in which survival was held constant and encounter probability varied, the initial p value was still inestimable, so for this model we set $p_1=p_2$ and allowed all other encounter probabilities to vary. We used a sin link function to estimate survival and encounter parameters, a mlogit(1) function to estimate entry parameters, and a log link function to estimate superpopulation size N . A “t” notation indicates that the parameter is general (not restricted to be equal over time); a dot notation means that the parameter is restricted to be the same over all survey intervals. Models that were completely unsupported by the data (AICc weight of zero) are not included in the table. C-hat is a measure of the goodness of fit of the most general model; when c-hat was greater than 1 (indicating a lack of model fit), it was used to adjust the model-based variance and covariance estimates, and thus affected the relative model weights within the tested suite. C-hat values of less than 1 are not presented in the table.

Year Colony/ sample	Species	c-hat	Model	Δ AICc	AICc weights	Estimated N*	SE
2005 Vulture	GREG		{phi(t)p(t)pent(t)N}	0	0.82215	581.6979	34.8814
			{phi(t)p(.)pent(t)N}	3.062	0.17785	589.5230	17.2920
2005 Vacation Island	GREG	3.05	Model	Δ QAICc	QAICc weights	Estimated N*	SE
			{phi(.)p(.)pent(t)N}	0	0.87187	233.5631	6.6651
			{phi(t)p(.)pent(t)N}	4.3784	0.09765	228.1620	5.9515
			{phi(.)p(t)pent(t)N}	7.5307	0.02019	229.5506	4.9093
2006 Vacation Island	GREG	5.90	Model	Δ QAICc	QAICc weights	Estimated N*	SE
			{phi(.)p(.)pent(t)N}	0	1	479.9585	3.2767

Table A-1. Continued.

Year Colony/ sample	Species	c-hat						
2005 Cypress City	GREG	2.13	Model	Δ QAICc	QAICc weights	Estimated N*	SE	
			{phi(t)p(t)pent(t)N}	0	0.54436	267.7905	6.5382	
2006 Cypress City	GREG	3.03	Model	Δ QAICc	QAICc weights	Estimated N*	SE	
			{p(.)phi(.)pent(t)N}	0	0.9909	253.6486	2.1806	
			{phi(.)p(t)pent(t)N}	9.3855	0.00908	253.7785	2.1385	
			{phi(t)p(t)pent(t)N}	21.5337	0.00002	252.8228	2.1116	
2005 Alley North/IT 1	WHIB		Model	Δ AICc	AICc weights	Estimated N*	SE	
			{phi(.)p(t)pent(t)N}	0	0.83334	50.6863	1.9522	
			{phi(t)p(t)pent(t)N}	4.4872	0.0884	50.6636	1.8088	
			{phi(t)p(.)pent(t)N}	4.7363	0.07805	50.4216	1.5666	
			{phi(.)p(.)pent(t)N}	16.5396	0.00021	52.3654	2.1018	
2005 Alley North/IT 3	WHIB		Model	Δ AICc	AICc weights	Estimated N*	SE	
			{phi(.)p(t)pent(t)N}	0	0.96697	66.6686	1.9037	
			{phi(t)p(.)pent(t)N}	7.6176	0.02144	66.6758	1.9551	
			{phi(t)p(t)pent(t)N}	8.8484	0.01159	66.6722	1.9652	
2005 Alley North/ GST 1	WHIB		Model	Δ AICc	AICc weights	Estimated N*	SE	
			{phi(.)p(.)pent(t)N}	0	0.99953	19.0817	1.6889	
			{phi(t)p(.)pent(t)N}	15.8962	0.00035	19.5700	2.1732	
			{phi(.)p(t)pent(t)N}	18.1392	0.00012	19.3125	1.9709	
2005 Alley North/ GST 2	WHIB		Model	Δ AICc	AICc weights	Estimated N*	SE	
			{phi(t)p(.)pent(t)N}	0	0.41299	29.8978	2.6669	
			{phi(.)p(.)pent(t)N}	0.0292	0.407	29.3304	2.2952	
			{phi(t)p(t)pent(t)N}	2.0753	0.14632	29.2213	1.8967	
			{phi(.)p(t)pent(t)N}	5.0119	0.0337	28.2547	1.8534	
2005 Alley North/ GST 3	WHIB		Model	Δ AICc	AICc weights	Estimated N*	SE	
			{phi(.)p(.)pent(t)N}	0	1	11.5185	1.9025	

Table A-1. Continued.

Year	Colony/ sample	Species	c-hat					
2006	Alley North/Q1	GREG	1.83	Model	Δ QAICc	QAICc	Estimated weights N*	SE
				{phi(.)p(.)pent(t)N}	0	0.99628	55.9440	1.1204
				{phi(.)p(t)pent(t)N}	11.1937	0.0037	56.1124	1.2738
				{phi(t)p(t)pent(t)N}	21.4261	0.00002	56.0022	1.0206
2006	Alley North/Q2	GREG	1.18	Model	Δ AICc	AICc	Estimated weights N*	SE
				{phi(.)p(t)pent(t)N}	0	0.64806	59.0446	0.3013
				{phi(t)p(t)pent(t)N}	2.1356	0.22278	58.6230	0.2728
				{phi(t)p(.)pent(t)N}	3.256	0.12723	58.7090	0.9285
2006	Alley North/Q3	GREG	1.83	Model	Δ QAICc	QAICc	Estimated weights N*	SE
				{phi(.)p(.)pent(t)N}	0	0.9937	58.1478	1.4997
				{phi(.)p(t)pent(t)N}	10.2855	0.0058	58.0003	0.6814
				{phi(t)p(.)pent(t)N}	15.2309	0.00049	58.1257	1.5748
2006	Alley North/ GE SE 1	GREG	1.18	Model	Δ QAICc	QAICc	Estimated weights N*	SE
				{phi(.)p(.)pent(t)N}	0	0.99522	43.4679	0.1566
				{phi(.)p(t)pent(t)N}	10.678	0.00478	43.4806	0.1608
				{phi(t)p(t)pent(t)N}	19.8337	0.00005	73.5128	0.1368
2006	Alley North/ GE SE 2	GREG	1.53	Model	Δ AICc	AICc	Estimated weights N*	SE
				{phi(.)p(t)pent(t)N}	0	0.99995	73.4119	0.1206
				{phi(t)p(t)pent(t)N}	19.8337	0.00005	73.5128	0.1368
				{phi(t)p(.)pent(t)N}	7.9083	0.01846	54.2082	1.7665
2006	Alley North/ GE SE 3	GREG	1.46	Model	Δ QAICc	QAICc	Estimated weights N*	SE
				{phi(.)p(.)pent(t)N}	0	0.96247	54.2707	1.7800
				{phi(.)p(t)pent(t)N}	7.8966	0.01856	54.5926	2.0213
				{phi(t)p(t)pent(t)N}	15.0858	0.00051	54.8939	2.1892
2006	Alley North/ Q5-N	WHIB	1.46	Model	Δ QAICc	QAICc	Estimated weights N*	SE
				{phi(t)p(t)pent(t)N}	0	0.60102	94.3730	0.2798
				{phi(t)p(.)pent(t)N}	0.9321	0.37712	94.4772	1.2067
				{phi(.)p(t)pent(t)N}	6.6281	0.02186	94.2479	0.1886

Table A-1. Continued.

Year Colony/ sample	Species	c-hat	Model	Δ AICc	AICc weights	Estimated SE	N*
2006 Alley North/ Q5-S	WHIB		Model				
			{phi(.)p(t)pent(t)N}	0	0.58865	69.2716	0.1492
			{phi(t)p(t)pent(t)N}	0.8875	0.37769	69.2778	0.1658
			{phi(t)p(.)pent(t)N}	5.7235	0.03365	69.1884	0.1357
2006 Alley North/Q6	WHIB	2.05	Model	Δ QAICc	QAICc weights	Estimated SE	N*
			{phi(t)p(.)pent(t)N}	0	0.95935	117.7637	1.9492
			{phi(t)p(t)pent(t)N}	6.9465	0.02976	117.8758	1.9548
			{phi(.)p(t)pent(t)N}	8.9562	0.01089	136.0672	47.3142
2006 Alley North/Q6-S	WHIB	2.12	Model	Δ QAICc	QAICc weights	Estimated SE	N*
			{phi(t)p(t)pent(t)N}	0	0.91789	123.7821	2.0607
			{phi(.)p(t)pent(t)N}	5.5923	0.05603	123.6286	2.2899
			{phi(t)p(.)pent(t)N}	7.1216	0.02608	123.3685	1.9028
2006 Alley North/Q7	WHIB		Model	Δ AICc	AICc weights	Estimated SE	N*
			{p(.)phi(.)pent(t)}	0	0.44667	34.1004	0.5192
			{p(.)phi(t)pent(t)}	0.2508	0.39403	34.3604	0.7027
			{phi(t)p(t)pent(t)N}	2.694	0.11614	34.3604	0.7027
			{phi(.)p(t)pent(t)N}	4.674	0.04316	34.1004	0.5192
2006 Alley North/Q8	WHIB	1.00	Model	Δ AICc	AICc weights	Estimated SE	N*
			{phi(t)p(t)pent(t)N}	0	0.75027	34.9722	1.1473
			{phi(.)p(t)pent(t)N}	3.0504	0.16324	35.9532	2.7331
			{phi(t)p(.)pent(t)N}	4.3348	0.08589	35.1331	1.9966
			{phi(.)p(.)pent(t)N}	14.2487	0.0006	36.2411	2.0097
2006 Alley North/Q9	WHIB		Model	Δ AICc	AICc weights	Estimated SE	N*
			{phi(.)p(t)pent(t)N}	0	0.99985	30.9664	1.5501
			{phi(t)p(.)pent(t)N}	17.7047	0.00014	31.1015	1.2478
			{phi(t)p(t)pent(t)N}	24.3684	0.00001	31.0495	1.1575
2006 Alley North/Q10	WHIB	1.15	Model	Δ AICc	AICc weights	Estimated SE	N*
			{phi(t)p(t)pent(t)N}	0	1	98.3859	1.2228

APPENDIX B
CALCULATION OF STANDARD ERRORS FOR EXTRAPOLATED SUPERPOPULATION
ESTIMATES FROM ALLEY NORTH SAMPLES

We conducted aerial surveys and photo analysis of sample areas from the large Alley North wading bird colony (WCA-3A) in 2005 (White Ibises) and 2006 (White Ibises and Great Egrets). Samples were surveyed for different amounts of time, based upon where nesting was occurring and the availability of good-quality photographs for each area. We calculated a gross superpopulation estimate (N^*) for each sample for however long it was surveyed, using MARK's POPAN data function. We took the number of nests present in each sample on the survey date closest to the colony peak count date as the raw count (the equivalent of the peak count for the individual sample). The superpopulation estimates with standard errors were then compared to the raw counts for all samples in order to obtain a ratio expression of the difference between the two estimates. We divided the superpopulation estimate by the raw count for each sample, to obtain each sample ratio, then averaged these ratios across all samples. We averaged individual ratios rather than finding a summed ratio across all samples, as it is unlikely that there is one underlying level of nest turnover within the colony; different nesting cohorts within the colony are likely to have different levels of nest turnover at different times within the breeding season.

The average ratio of this proportional error across all samples was our estimated colony-wide proportional difference between the peak count and extrapolated superpopulation count, as follows:

$$(\sum(N^*_i/RC_i))/n = (N^*_{colony}/PC_{colony})$$

N^*_i is the superpopulation estimate for sample i ; RC_i is the raw count for sample i ; n is the number of samples in the colony for that year and species. Cumulatively, $(\sum(N^*_i/RC_i))/n$ is the average ratio of the total number of nest starts to the number of nests seen in the raw count.

PCcolony is the peak count for the colony. We solved for “N*colony,” the entire colony’s extrapolated superpopulation estimate.

We also calculated the variance of the ratio estimate, in order to calculate 95% confidence intervals for the colony-wide superpopulation estimate. Both the sample size and the raw counts of the samples are fixed values, and thus the only variance that remains to be calculated in the ratio estimate is the superpopulation variance for each estimate. The variance of the average ratio, $\text{var}(\mu)$, is equal to 1 divided by the square of the sample size n , multiplied by the sum (across all samples) of 1 divided by the square of the sample raw count, multiplied by the variance of the sample superpopulation estimate. This variance of the superpopulation estimate for a sample, $\text{var}(N^*)$, is equal to the square of the standard error of the estimate (which is calculated by Program MARK). Therefore it is a simple task to calculate $\text{var}(\mu)$, the variance of the ratio of superpopulation estimates to raw counts for all samples:

$$(\sum(N^*_i/RC_i))/n = \mu$$

$$\text{var}(\mu) = \text{var}(\sum(N^*_i/RC_i)/n) = (1/n^2) \cdot \text{var}(\sum(N^*_i/RC_i)) = (1/n^2) \cdot \sum((1/RC_i^2) \cdot \text{var}(N^*_i))$$

$$\text{var}(N^*_i) = SE_i^2$$

where RC =peak count, N^* =superpopulation estimate, n =sample size, μ =ratio of raw counts to superpopulation estimates for all samples, and SE =standard error of the superpopulation estimate. This calculation ignores any covariance between the raw count and superpopulation estimate. However, judging by the comparison of peak counts to superpopulation estimates for the small Great Egret colonies examined in this study (Figure 2-6), we would suggest that this covariance is probably fairly small, and may be safely excluded from our calculations.

Thus the average ratio of raw counts to superpopulation estimates for all samples (μ), with its associated variance, may be used with the peak count for the entire colony in order to estimate the superpopulation estimate for the entire colony. We assumed that the average ratio between the superpopulation estimates of samples and the raw counts of samples is equivalent to the ratio between the superpopulation estimate for the entire colony and the peak count for the colony.

The 95% confidence intervals for μ were calculated as $\mu \pm 2\sqrt{\text{var}(\mu)}$. As the peak count for the colony is considered to be a fixed variable (it does not have an associated variance estimate), these 95% CIs may be used to directly estimate the 95% CIs for the colony superpopulation estimate.

Example: The 2005 White Ibis samples. The sample raw counts, superpopulation estimates, and standard errors for the superpopulation estimates are shown below.

Sample	Raw count	N*	SE of N*
IT 1	28	51	1.91
IT 3	36	67	1.91
GST 1	3	19	1.69
GST 2	14	30	2.38
GST 3	4	12	1.90

Substituting these values into the equations listed above, we find an average proportional difference between superpopulation estimate and raw count of 3.00198, and a variance for this value of 0.02318:

$$\begin{aligned} \mu &= (\sum(N^*_i/RC_i))/n = ((51/28)+(67/36)+(19/3)+(30/14)+(12/4))/5 = 3.00198 \\ \text{var}(\mu) &= (1/n^2) \cdot \sum((1/RC_i^2) \cdot \text{var}(N^*_i)) = (1/n^2) \cdot \sum((1/RC_i^2) \cdot SE_i^2) \\ &= (1/5^2) \cdot (((1/(28^2)) \cdot 1.91^2) + ((1/(36^2)) \cdot 1.91^2) + ((1/(3^2)) \cdot 1.69^2) + ((1/(14^2)) \cdot 2.38^2) + \\ &((1/(4^2)) \cdot 1.90^2)) = 0.02318 \end{aligned}$$

Confidence intervals for the average sample ratio μ may then be calculated as follows:

$$95\% \text{ CIs for } \mu = \mu \pm 2\sqrt{(\text{var}(\mu))} = 3.00198 \pm 2\sqrt{(0.02318)} = 2.69743, 3.30643$$

The peak count for this colony in 2005 was 12,750 nests. As this colony peak count is a fixed value, we simply multiply this peak count by μ and its associated CIs to find the extrapolated superpopulation estimate (38,275 nests) and confidence intervals for the entire colony (34,392; 42,157):

$$\text{Colony } N^* = 12750 \cdot 3.00198 = 38,275$$

$$\text{Colony LCI} = 12750 \cdot 2.69743 = 34,392$$

$$\text{Colony UCI} = 12750 \cdot 3.30643 = 42,157$$

APPENDIX C
SAMPLE BUDGET FOR DEVELOPING PEAK COUNT AND SUPERPOPULATION
ESTIMATES

The superpopulation method for estimating asynchrony bias is much more labor- and flight-intensive than many current monitoring techniques, as frequent surveys are required to follow individual nests through time from the air. For the purposes of this budgetary analysis we assumed that weekly surveys provided sufficient accuracy in superpopulation estimation (Table 2-4), but the necessary frequency of surveys will depend upon the synchrony in nesting of the species of interest and upon the desired precision of the result. For this exercise, we calculated labor and flight costs for a 3-month breeding season, surveying a Great Egret colony with a peak count of 458 nests and a superpopulation estimate of 666 nests. The hypothetical colony was 45 km from the airport, and in this exercise it was the only colony being surveyed. Estimated labor time, flight time, and associated costs are listed in Table C-1. According to these sample calculations, superpopulation estimation can be roughly four times as costly as peak count estimation in terms of flying and 20 times as costly in terms of labor for photographic analysis; overall, the superpopulation estimate is roughly five times more costly to produce. Costs of transportation to and from the airport, overhead costs, etc. are not included in this analysis.

Clearly these relative values will vary depending upon length of breeding season, number of flights conducted per month for the superpopulation estimation, labor costs per hour, cost of plane rental per hour, and other factors. However, we hope that this example provides some guidance for managers trying to determine the proper tradeoff between monetary cost and estimation accuracy for monitoring breeding colonies. As a concluding comment, we would like to note that a cheaper survey method that gives unreliable (or uninterpretable) estimates is no bargain; cash-strapped managers may want to consider surveying intensively every 2–3 years

(and obtaining useful estimates), rather than surveying annually using a peak count or related method and failing to obtain useful information.

Table C-1. Sample budgets for superpopulation estimation and peak count estimation of breeding population size for a hypothetical Great Egret colony.

	Superpopulation estimate	Peak count estimate
Hours of editing and printing photos:	10	0
Hours of photo analysis:	50	3
Cost of labor/hr:	\$10	\$10
Total analysis costs:	\$600	\$30
km to colony:	45	45
km/min flight time:	1.75	1.75
Flight time per survey (min):	51.48	51.48
Flights per season:	12	3
Season length (weeks):	12	12
Hours flight time for season:	10.30	2.57
Cost per hour flying:	\$160	\$160
Cost of flights for season:	\$1,647	\$412
Cost of labor flying time:	\$103	\$26
Total flying costs:	\$1,750	\$438
Total cost:	\$2,350	\$468

APPENDIX D
MODEL SUITE FOR STUDY OF EFFECTS OF GROUND DISTURBANCE ON GREAT EGRETS

Table D-1. All models for Vacation Island Great Egret colony's analysis from Chapter 3. A "t" notation indicates that the parameter is general (not restricted to be equal over time); "group" means that the parameters is allowed to vary by group but not by time; "group*t" indicates that the variable is allowed to vary with time and to change over time in a different way in each group; "group+t" means that the parameter is allowed to vary with time, but that the variations change in a similar way between groups over each survey interval (essentially, that the difference is additive rather than multiplicative), and a dot notation means that the parameter is restricted to be the same over all survey intervals. N, population size, is allowed to vary by group in all models, as the number of nests in each group is different. The entire model suite for these parameters included 125 potential models. Most of these models were not run and are not included in the table, either because it became clear during modeling that they were not going to be a good fit for the data or because the models failed to converge.

Model	Δ QAICc	QAICc weights	# parameters
{p(.)phi(.)pent(t)N(group)}	0	0.50147	22
{p(.)phi(.)pent(t+group)N(group)}	0.0119	0.4985	22
{p(t)phi(.)pent(t)N(group)}	21.4128	0.00001	40
{p(t)phi(group)pent(group+t)N(group)}	22.4091	0.00001	42
{p(t)phi(group)pent(t)N(group)}	22.4092	0.00001	42
{p(.)phi(group)pent(group*t)N(group)}	31.94	0	42
{p(t)phi(group+t)pent(group+t)N(group)}	49.3695	0	59
{p(t)phi(t)pent(t)N(group)}	53.0026	0	58
{p(group)phi(group)pent(group*t)N(group)}	53.5716	0	42
{p(t)phi(group)pent(group*t)N(group)}	54.2869	0	60
{p(group*t)phi(.)pent(.)N(group)}	54.29	0	44
{p(t)phi(.)pent(group*t)N(group)}	55.3114	0	59
{p(t)phi(group*t)pent(group)N(group)}	74.404	0	60
{p(group*t)phi(.)pent(group*t)N(group)}	88.5037	0	79
{p(.)phi(group)pent(.)N(group)}	14636.2824	0	5
{p(.)phi(group)pent(group)N(group)}	14640.2926	0	7
{p(group)phi(.)pent(.)N(group)}	14641.7839	0	6
{p(.)phi(group*t)pent(.)N(group)}	14688.8833	0	41
{p(t)phi(group)pent(group)N(group)}	14801.6243	0	25
{p(.)phi(.)pent(group)N(group)}	14820.9384	0	4
{p(group*t)phi(.)pent(group)N(group)}	14837.2927	0	44
{p(.)phi(.)pent(.)N(group)}	26347.0759	0	4

APPENDIX E
MODEL SUITE FOR STUDY OF EFFECTS OF GROUND DISTURBANCE ON WHITE
IBISES

Table E-1. All models for Alley North White Ibis colony’s analysis from Chapter 3. A “t” notation indicates that the parameter is general (not restricted to be equal over time); “group” means that the parameters is allowed to vary by group but not by time; “group*t” indicates that the variable is allowed to vary with time and to change over time in a different way in each group; “group+t” means that the parameter is allowed to vary with time, but that the variations change in a similar way between groups over each survey interval (essentially, that the difference is additive rather than multiplicative); and a dot notation means that the parameter is restricted to be the same over all survey intervals. N, population size, is allowed to vary by group in all models, as the number of nests in each group is different. The entire model suite for these parameters included 125 potential models. Most of these models were not run and are not included in the table, because it became clear during modeling that they were not going to be a good fit for the data.

Model	$\Delta AICc$	AICc weights	# parameters
{phi(t+g)p(t*g)pent(t)N(g)}	0	0.54463	19
{phi(t+g)p(t*g)pent(t+g)N(g)}	1.69680	0.23316	20
{phi(t+g)p(t+g)pent(t)N(g)}	3.93850	0.07601	16
{phi(t*g)p(t*g)pent(t)N(g)}	4.11060	0.06974	23
{phi(t*g)p(t*g)pent(t+g)N(g)}	5.78330	0.03022	24
{phi(t+g)p(t*g)pent(t*g)N(g)}	6.10840	0.02569	21
{phi(t*g)p(t*g)pent(t*g)N(g)}	7.41990	0.01333	26
{phi(t+g)p(t+g)pent(t*g)N(g)}	9.4766	0.00477	18
{phi(t*g)p(t)pent(t)N(g)}	12.8334	0.00089	19
{phi(t+g)p(t+g)pent(t+g)N(g)}	13.0595	0.00079	17
{phi(t)p(t*g)pent(t)N(g)}	14.3942	0.00041	18
{phi(g)p(t*g)pent(t)N(g)}	16.5615	0.00014	17
{phi(t*g)p(t)pent(t*g)N(g)}	16.6314	0.00013	22
{phi(g)p(t*g)pent(t*g)N(g)}	17.5562	0.00008	19
{phi(t+g)p(t*g)pent(.)N(g)}	21.8437	0.00001	17
{phi(t)p(t)pent(t)N(g)}	32.8912	0	14
{phi(g)p(t*g)pent(g)N(g)}	43.9314	0	14
{phi(.)p(t)pent(t)N(g)}	45.552	0	11
{phi(t)p(.)pent(t)N(g)}	46.3739	0	10
{phi(t)p(t)pent(.)N(g)}	52.6684	0	14
{phi(t)p(t)pent(.)N(g)}	109.867	0	11
{phi(.)p(.)pent(t)N(g)}	325.708	0	6
{phi(.)p(.)pent(.)N(g)}	361.315	0	4

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BIOGRAPHICAL SKETCH

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