

Use of the superpopulation approach to estimate breeding population size: an example in asynchronously breeding birds

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Abstract. Many populations of animals are fluid in both space and time, making estimation of numbers difficult. Much attention has been devoted to estimation of bias in detection of animals that are present at the time of survey. However, an equally important problem is estimation of population size when all animals are not present on all survey occasions. Here, we showcase use of the superpopulation approach to capture–recapture modeling for estimating populations where group membership is asynchronous, and where considerable overlap in group membership among sampling occasions may occur. We estimate total population size of long-legged wading bird (Great Egret and White Ibis) breeding colonies from aerial observations of individually identifiable nests at various times in the nesting season. Initiation and termination of nests were analogous to entry and departure from a population. Estimates using the superpopulation approach were 47–382% larger than peak aerial counts of the same colonies. Our results indicate that the use of the superpopulation approach to model nesting asynchrony provides a considerably less biased and more efficient estimate of nesting activity than traditional methods. We suggest that this approach may also be used to derive population estimates in a variety of situations where group membership is fluid.

Key words: Ardea; asynchrony; bias; Eudocimus; Everglades; Jolly-Seber; mark–recapture; nest turnover; peak count; population size; superpopulation; waders.

INTRODUCTION

The need for reliable demographic information on animal populations has increased as scientists attempt to use attributes of populations to measure ecological change (Rosenstock et al. 2002, Thompson 2002) and to monitor endangered and game species (Gould et al. 2005). However, it is rare that entire breeding populations can be counted directly, and most attempts at estimating population size are approximations derived from incomplete surveys with various potential sources of bias (Williams et al. 2002, Frederick et al. 2006).

A huge amount of scientific inquiry has been directed toward understanding bias in animal population survey counts (as reviewed in Pollock and Kendall 1987, Bart et al. 2004), including visibility problems, interobserver variation in counting error, and misidentification of species (Rodgers et al. 1995, Frederick et al. 2003, Williams et al. 2008). Most studies of estimation error to date have focused on estimating animals that are present at the time of survey, and have only rarely recognized the problem of estimating animals that are present at

some point during the period of interest but that are not present at the time of survey (Frederick et al. 2006). This latter issue can arise when individuals are not individually identifiable, and they join and leave surveyed populations at an unknown frequency. This problem has been recognized in colonially breeding birds (Frederick et al. 2006), ungulates (Gould et al. 2005), and spawning fishes (Schwarz et al. 1993), among other taxa, as well as being a common circumstance at migration stopover sites (Williams et al. 2002).

Asynchronous group membership in the statistical population of interest, whether at large migratory stopover sites (Farmer and Durbian 2006) or within a defined breeding season, as for colonially nesting birds (Piazza and Wright 2004), can confound estimates of group size because individuals may be present before surveys begin during a season, after they end, or between consecutive survey occasions. Estimates of unmarked animals on any given date may not reflect true numbers, partly because some individuals may be present outside the dates of survey, and partly because novel (previously uncounted) individuals on any given survey may be confused with those present on a previous survey date. This is true even if the counts on each date are highly accurate. While the resulting bias may be negligible when aggregation or reproduction is highly synchronous, the degree of error in less synchronous species can be substantial (e.g., 47% in breeding wading birds

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[Frederick et al. 2006], 69–79% in shorebird populations at stopover sites during migration [Farmer and Durbian 2006]).

The magnitude of these underestimates illustrates the need for methods for estimating the size of populations where group membership or site fidelity is fluid. This problem may be approached by estimating the turnover of individuals within a population and incorporating this information into a population estimate using a mark–resight method. The superpopulation approach (Crosbie and Manly 1985, Schwarz and Arnason 1996), offers some potential for a solution. This method is a variation on the Jolly-Seber open-population capture–recapture model (Jolly 1965, Seber 1965). The approach includes inference about probabilities of entry into the sampled population, and the superpopulation is defined as the total number of animals that ever enter the sampled population between the first and last survey occasions. As such, estimating superpopulation size can be useful for populations in which group membership is dynamic and temporally unpredictable.

A key to the superpopulation approach is the ability to track individuals over time and sampling occasions. Typically this involves marking a subset of individual animals or using a recognizable physical characteristic so that individuals that move around in space may be reliably identified or resighted. But in some cases, even unmarked individuals may be reliably identified and resighted based on location (Thompson and Gidden 1972, Albers 1976). Bird nests, for instance, are fixed in space, if not time, and individuals may be differentiated during the breeding period based on their association with a particular reproductive structure or location. As examples for this modeling approach, we use Great Egrets (*Ardea alba*) and White Ibises (*Eudocimus albus*) in breeding aggregations in the Everglades. These birds are conspicuous colonial nesters with different life histories and temporal nesting patterns.

For highly asynchronous or fluid populations such as wading bird colonies in the Everglades, we suggest that simple (raw) population counts may significantly underestimate true population size, depending upon how the raw counts are used. For example, we believe that underestimation will be common when investigators use either a single count/survey or the maximum count from multiple surveys over the period of interest to draw inference about abundance. We expect the difference between raw counts and model-based estimates to vary by species according to differences in reproductive phenology, timing of nesting, and nest failure rates (Frederick and Collopy 1989a, McCrimmon et al. 2001, Heath et al. 2009). And we expect that, though there may be interobserver variation in model-based estimates, this variation will be small compared to the difference between raw counts and superpopulation estimates.

METHODS

Survey methodology: peak counts and superpopulation estimates

We conducted monthly aerial surveys of breeding colonies of Great Egrets and White Ibises in the central and northern Everglades in 2005 and 2006 (Broward, Dade and Palm Beach counties, Florida, USA). Colonies were located using a systematic, 100% coverage search pattern on a monthly basis from January through June, and photographed each time with a high-resolution digital camera. Breeding individuals were easily distinguished as white targets on a green background, and the assumption that one nest means one bird is quite accurate during the incubation period (McCrimmon et al. 2001, Heath et al. 2009). We accepted the largest single-month count of the breeding season from these aerial photographs as the peak seasonal count for each species.

We also took aerial photographs on a semiweekly basis of areas of individually identifiable nests, in order to model population emigration and immigration (losses of nests and new entries to the colony). Nest locations were identified using natural or artificial landmarks, and nest locations were compared in printed photographs from week to week to document longevity of existing nests and occurrences of new nests. We conducted these surveys in three small Great Egret colonies and one large mixed-species colony in the central Everglades in one or both of the 2005 and 2006 breeding seasons. The mixed-species colony, Alley North (approximately 50 000 m²), was too large to conduct a complete survey, so we concentrated on subsections of the colony.

Presence–absence information for each uniquely numbered nest was coded as 0 (nest activity unknown, including cases in which the nest and parent/chicks were not visible, and cases where there was no photo of the nest area available on that date) or 1 (nest active, parent and/or chicks were visible). 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 activity in that location as a new nest start. Three independent observers analyzed the same set of semi-weekly photographs for one colony (Vacation Island) from the 2006 breeding season, to test the repeatability of the nest coding method.

Although we used the presence of a large white bird as an indication of nesting, these could have initially been roosting birds or birds temporarily standing away from their nests. We therefore eliminated first observations of all nests from the database, and so deleted “nests” that were seen only once. This may have caused some underestimation of total number of nest starts if the nest actually had been built and failed very early. Additionally, 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. Both these types of possible errors seem unlikely

to be very important given the relatively long courtship and egg-laying periods of these birds (McCrimmon et al. 2001, Heath et al. 2009) and the semiweekly frequency of aerial surveys. However, if either of these assumptions is incorrect, the effect in both cases is conservative, and results in an underestimation of the true numbers of nesting pairs.

*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 at some time during the entire study period and either survive until the next survey occasion or emigrate or die before they are available to be sampled (Schwarz et al. 1993, Schwarz and Arnason 1996). The model's calculated gross superpopulation size was originally defined as the total number of organisms that were part of the population of the study location, in the sense that they were present at some time during the period between the first and last sampling occasions (Cooch and White 2007). In our case, the superpopulation is 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 population 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 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 three parameters (survival ϕ , encounter probability p , and entry probability β) to vary with time, depending upon the model. For each colony, we tested a set of four candidate models: a fully time-dependent model (all parameters are time dependent, with a superpopulation estimate, N , for which there is a single estimate for the colony), a model with no time dependence for survival or encounter variables, 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 both bird species tend to exhibit a surge of initial nesting in an area followed by lower levels of nest initiation thereafter (McCrimmon et al. 2001, Heath et al. 2009). Thus, entry probabilities were allowed to be time-dependent in all models. For models with constrained p values, the initial p was not allowed to differ from p values in subsequent sampling occasions; detection probability varied primarily with presence/absence of an adult bird on the nest, and with the quality of aerial photographs. Neither of these sources of variation was

expected to cause differences in initial capture vs. recapture probabilities.

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 $p_k = p_{k-1}$ (where k is the final sample occasion) so that all survival and entry 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 . The gross superpopulation size N^* is a derived parameter of the POPAN model. It includes both the net superpopulation size N (all nests that enter the population and are available to be detected during at least one survey) and nests that enter and leave the population between consecutive surveys and thus are never available to be sampled. 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 can be estimated. This value can then be used to estimate gross entries, which includes new animals that are never available to be detected at a sampling occasion (Schwarz et al. 1993, Schwarz and Arnason 1996). The gross superpopulation size is estimated in MARK by 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 et al. 1993, Schwarz and Arnason 1996):

$$\hat{N}_i = n_i / \hat{p}_i$$

$$\hat{B}_i = \hat{N}_{i+1} - \hat{N}_i (\hat{\phi}_i)^{t_i}$$

$$\hat{B}_i^* = \frac{\hat{B}_i \ln([\hat{\phi}_i]^{t_i})}{[\hat{\phi}_i]^{t_i} - 1}$$

$$\hat{N}^* = \hat{N}_1 + \sum_{i=1}^{k-1} \hat{B}_i^*$$

where \hat{N}_i is the estimated total number of individuals (or active nests) in the population at sampling occasion i ; n_i is the number of individuals seen at occasion i ; p_i is the encounter probability at occasion i ; \hat{B}_i is the estimated number of individuals entering the population between sampling occasions i and $i+1$ and available for detection at occasion $i+1$; ϕ_i is the survival probability per sampling interval (expressed as a proportion of a week) between occasions i and $i+1$; t_i is the time between surveys i and $i+1$ (expressed as a proportion of a week);

\hat{B}_i^* is the estimated gross number of individuals entering the population between i and $i + 1$ (including nests that entered and departed between i and $i + 1$, estimated assuming a constant recruitment rate over time during the interval, after Schwarz et al. [1993] and Crosbie and Manly [1985]); \hat{N}^* is the estimated gross superpopulation size; and k is the total number of surveys.

We fit the four models to the data from the records of nest observations at each colony (Appendix A). We used an information-theoretic approach to model selection, and considered that a model with a ΔAIC_c value of less than 2 was relatively well supported by the data, while a model with a ΔAIC_c value of greater than 10 was not supported by the data (Burnham and Anderson 2002, Williams et al. 2002). We quantified the goodness of fit (GOF) of the most general model using chi-square tests to see if observed values varied from the expected number of surviving and encountered nests (Burnham et al. 1987). These tests evaluated the following assumptions inherent in Jolly-Seber models (Pollock et al. 1990, Cooch and White 2007): one, that 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); and two, that there is no heterogeneity in survival probability among individuals or cohorts.

We calculated GOF chi-square values using Program RELEASE (Burnham et al. 1987), available within MARK. The chi-square values generated for each test component were summed for the entire sampling period, and were divided by the degrees of freedom to obtain a variance inflation factor, \hat{c} (a measure of overdispersion in the data; Appendix A). Following Cooch and White (2007), we accepted that a \hat{c} value of 1 indicated good model fit, values of 1–3 indicated moderately good fit, and >3 indicated probable violation of model assumptions. For \hat{c} values of <1 (essentially meaning that the data are underdispersed), we followed the recommendation of Cooch and White (2007) in using a \hat{c} value of 1. The calculated \hat{c} values were used to adjust model-based precision estimates and modify AIC_c values to produce QAIC_c for use in model selection (Burnham and Anderson 2002).

Variance estimation

We used MARK's model averaging capability to compute the weighted average values and variances for parameters across all models. Unconditional standard errors (which incorporate uncertainty due to both variance within models and to uncertainty in model selection) were used to manually calculate 95% confidence intervals according to the following estimation procedure, which focuses on f_0 , the number of animals not captured (Rexstad and Burnham 1992, Williams et al. 2002):

Lower and upper confidence interval bounds for \hat{N}^* : $M_{k+1} + \hat{f}_0/C$, $M_{k+1} + \hat{f}_0C$, where M_{k+1} is the number of individual animals captured in k samples, $\hat{f}_0 = \hat{N}^* - M_{k+1}$,

and $C = \exp(1.96[\ln(1 + \text{var}[\hat{N}^*]/\hat{f}_0^2)]^{1/2})$. This estimation method assumes that f_0 is lognormally distributed (rather than requiring an assumption of normality for superpopulation estimates, which is often not the case for situations with small numbers of captures and recaptures; Williams et al. 2002).

Colony counts were treated as binomial random variables. Thus, the variance of a peak count value P was estimated as $\text{var}(P_i) = (1 - p)p\hat{N}_i^*$, where p is the probability that a member of the superpopulation (nest) was included in the peak count. The probability p was estimated using the inverse of the proportional difference between the peak count and gross superpopulation estimate, P_i/\hat{N}_i^* , and thus the variance of this proportional difference could be calculated using the delta method (Mood et al. 1974) as follows:

$$\begin{aligned} \text{var} \frac{\hat{N}_i^*}{P_i} &\approx \frac{(\hat{N}_i^*)^2}{P_i^2} \left[\frac{\text{var}(\hat{N}_i^*)}{(\hat{N}_i^*)^2} + \frac{\text{var}(P_i)}{P_i^2} \right] \approx \frac{(\hat{N}_i^*)^2}{P_i^2} \left[\frac{\text{var}(\hat{N}_i^*)}{(\hat{N}_i^*)^2} \right. \\ &\quad \left. + \left(1 - \frac{P_i}{\hat{N}_i^*} \right) \frac{P_i}{P_i^2} \right] \approx \left[\frac{\text{var}(\hat{N}_i^*)}{P_i^2} + \frac{\hat{N}_i^* (\hat{N}_i^* - P_i)}{P_i^3} \right]. \end{aligned}$$

Subsampling large breeding aggregations

For the smaller Great Egret colonies (120–200 m longest dimension), all or most of the colony could be covered in one or two photographic passes, and our counts and superpopulation estimates were for the entire colony. For the very large Alley North colony (approximately 2000 m longest dimension), we subsampled the colony during aerial surveys, resulting in a collection of geographically distinct year- and species-specific estimates of superpopulation size. We could not sample the colony randomly, as we had to rely on landmarks of some kind in order to have areas that could be relocated. However, despite this restriction, we were able to select sample areas in a variety of habitat types and nesting densities, and based on our knowledge of the colony and visual examination on nesting patterns from aerial photos, we believe our samples to be representative of the colony as a whole. We calculated a gross superpopulation size estimate for each combination of species, year and location (we refer to this as a sample) within the colony and compared it to the number of nests counted in that same sample on the survey date closest to the peak count date for the entire colony ("raw count"). We averaged the proportional differences between the gross superpopulation estimates and the raw counts across all samples. The ratio of averages (in our case, summed superpopulation estimates divided by summed raw counts) is less biased in some cases and has a smaller variance estimate than the average of ratios (Rao 2005), but it weights all nests in all samples equally, assuming that there is one underlying ratio between raw counts and superpopulation estimates that characterizes the entire colony. As nesting cohorts within the colony are likely to have varying levels of

TABLE 1. Peak counts and weighted superpopulation estimates for breeding colonies of White Ibises and Great Egrets in the Everglades.

Database	Species	Year	Peak count for sample	\hat{N}^* (LCI-UCI)	Proportional difference between \hat{N}^* and peak count (LCI-UCI)
Vulture	Great Egret	2005	121	583 (539–674)	4.82 (4.46–5.57)
Vacation Island	Great Egret	2005	79	233 (223–252)	2.95 (2.83–3.19)
Vacation Island	Great Egret	2006	155	480 (476–491)	3.10 (3.07–3.17)
Cypress City	Great Egret	2005	107	268 (258–285)	2.50 (2.41–2.66)
Cypress City	Great Egret	2006	173	254 (251–260)	1.47 (1.45–1.50)
Alley North	Great Egret	2006	1193	2538 (2226–2943)	2.13 (1.87–2.47)
Alley North	White Ibis	2005	12 750	38 275 (25 443–64 080)	3.00 (2.00–5.03)
Alley North	White Ibis	2006	13 566	29 287 (26 448–32 706)	2.16 (1.95–2.41)

Notes: Peak counts are the maximum monthly one-time aerial survey counts of numbers of nests in colonies. \hat{N}^* is the model-averaged gross superpopulation estimate, with lower and upper confidence interval estimates (LCI and UCI). The Alley North \hat{N}^* estimates were derived from subsamples and extrapolated to the entire colony (Appendices A and B). The proportional difference between \hat{N}^* and peak counts, or raw counts, was calculated as $\hat{N}^*/(\text{raw count})$. The CI estimates for these colonies were developed using the variance in the average ratio between peak and raw counts, and under the assumptions that peak count values follow a binomial distribution and the difference in numbers of nests between peak counts and extrapolated superpopulation estimates will follow a lognormal distribution (Chao 1989, Rexstad and Burnham 1992, Williams et al. 2002).

nest turnover throughout the breeding season, we chose to take such variation into account when estimating an overall proportion for the colony, and used the average of ratios for the estimation procedure.

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

$$\frac{\sum_i (\hat{N}_i^*/R_i)}{n} = \frac{\hat{N}_{\text{colony}}^*}{P_{\text{colony}}}$$

where \hat{N}_i^* is the gross superpopulation estimate for sample i ; R_i is the raw count for sample i ; n is the number of samples in the colony for that year and species; and P_{colony} is the peak count for the colony. Cumulatively, $\sum_i (\hat{N}_i^*/R_i)/n$ is the average number of estimated nest starts per nest detected in the raw count. We solved the above equality for $\hat{N}_{\text{colony}}^*$ to obtain the entire colony's extrapolated superpopulation estimate:

$$\hat{N}_{\text{colony}}^* = \frac{(P_{\text{colony}}) \sum_i (\hat{N}_i^*/R_i)}{n}$$

Raw counts may be treated as binomial random variables, and we can thus estimate the approximate variance of the average ratio (e.g., Mood et al. 1974), and compute the variance of the colony-wide superpopulation estimates (Appendix B; e.g., Goodman 1960). Confidence intervals were estimated using this colony-wide variance estimate, with the peak count for the entire colony equating to M_{k+1} .

RESULTS

Interobserver error in tallying individual nest histories from photographs

For the Vacation Island colony in 2006, the superpopulation estimates derived from three different photo-interpreters were 509 nests (upper and lower confidence

intervals, or CIs, 500–518 nests); 409 nests (CIs 403–414); and 480 nests (CIs 476–491). Average interobserver error rate was 8% relative to the mean estimate of 466 nests. These estimates were 264–328% greater than the peak count of 155 nests (300% on average). The results presented below for all colonies are from the analysis of data by Observer 3.

Superpopulation estimates

Depending upon the individual colony, the best-supported model was fully time-dependent; allowed only the entry probability β to vary with time; or, in the case of some Alley North subsamples, allowed ϕ or p to vary with time (Appendix A). There was no single model that appeared to best fit all colonies for either species. Likewise, the QAIC_c weight for the best-supported model varied considerably by colony. However, the difference among estimated \hat{N}^* values derived from different models, even those with quite dissimilar QAIC_c weights, was small (less than 5% in all cases; Appendix A). So the differences among high-ranking models in details about the processes generating the data did not translate into substantive differences in estimates of colony size.

Superpopulation estimates for Great Egret colonies were 147–482% of the peak counts, while White Ibis superpopulation estimates were 216–300% of peak counts (Table 1). In all eight year-colony situations, the peak counts for colonies were well outside the 95% confidence intervals for the superpopulation estimates. These results collectively suggest that the bias introduced by asynchrony and associated counting problems is quite large. However, although peak counts consistently underestimated numbers of nest starts, the degree of underestimation varied widely among colonies and years (Table 1). This was true even for colonies as little as 25 km apart (Cypress City and Vacation Island colonies).

There were some possible violations of model assumptions related to homogeneity in survival and capture probability. Survival and capture probability are

both unlikely to be the same for all nests, due to differences in nesting stage and nest microhabitat (Mayfield 1975, Frederick and Collopy 1989b). However, 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 locations and years.

DISCUSSION

The estimates of numbers of nest starts that incorporated asynchrony and detectability bias were significantly different from, and very much larger than, the peak counts in all eight colonies and years. Asynchrony in nest initiation and failure, rather than problems with nest detectability, was the major source of bias in our peak count estimates. Independent estimates of visual bias for Great Egrets and White Ibises (Kushlan 1979, Williams et al. 2008) are at least an order of magnitude smaller than the combined effects of asynchrony and detectability reported here (47–382%). Due to the large sample sizes in our study, we had very good power for our goodness-of-fit tests to detect tested deviations from model assumptions. Problems with model fit, while in some cases detectable, were probably not biologically significant in terms of estimated numbers of surviving or encountered nests.

While superpopulation estimates from different observers were relatively similar (and hugely different from peak counts), inter-observer comparisons indicate a potential problem with initial detectability—that is, recognizing a nest as such, and beginning to follow it in photographs. Once a nest has been identified in a previous photograph, it may be more likely to be looked for and found again on later dates. This would lead to an underestimate of nest starts, an underestimate of population size, and an overestimate of precision of the population estimate. Depending upon the population of interest and available survey techniques, in some cases superpopulation estimates could be selectively “ground-truthed,” to determine initial detectability for observers. A more versatile alternative would be to estimate detection probabilities for new nests using data from multiple observers; extending the superpopulation approach to the robust design would incorporate such data and provide a reasonable approach to dealing with this potential problem. However, visibility bias in our particular study system is a problem for a variety of reasons (Williams et al. 2008), and problems with initial detectability are likely to be inherent to this system, rather than common to most uses of the technique.

Error rates for peak counts, relative to nest start estimates, were similar between Great Egrets and White Ibises. Variation in error rates was much larger between years and between colonies during the same year than between species (Table 1; see also Frederick et al. 2006). This suggests that factors affecting nest success and asynchrony are quite variable over time and/or space. Because of this high temporal and spatial variation,

population estimation cannot be easily generalized, and populations may need to be estimated for individual colonies and seasons, as we have done here. The removal of all first nest sightings prior to analysis allowed for a conservative handling of first detection, and we have focused in this example on providing estimates of total numbers of nest starts occurring throughout a nesting season. However, in species with high nest failure and re-nesting frequencies, the nesting population (numbers of pairs) would be expected to be smaller than the numbers of nest starts (Piazza and Wright 2004). Since this difference could in some cases be substantial, this technique should be used in conjunction with studies of re-nesting frequency as necessary.

Peak counts and other incomplete survey methods have long been recognized as likely to provide poor estimates of true population size, but in the absence of alternatives, they have been used as indicators of relative change in population size (James et al. 1996, Link and Sauer 1998, Farmer and Durbian 2006). In the examples we have presented, it seems clear that peak counts or uncorrected survey information will reflect different proportions of the true breeding population size from year to year, and therefore cannot be used reliably even as an indicator of population dynamics. Peak counts and other incomplete survey methods may be relatively cheap and logistically easy to conduct, but our examples suggest that with the potentially large and variable bias associated with these methods, they are no bargain.

General use of the superpopulation approach

This type of analysis is applicable to many other animal populations with large aggregations and fluid group membership, including both breeding and migratory groupings. We caution that random or stratified random sampling designs may be advisable in some cases to capture the full heterogeneity in population membership and detectability among cohorts within the population. For example, detectability may vary due to individual habitat selection, or due to sex- or age-specific differences in behavior. This problem may also be approached through the use of visibility (e.g., as assessed by the investigator) as a grouping variable or individual covariate in the model. It is essential that all uses of the superpopulation approach include an examination of model fit for potential violation of model assumptions.

In our case, individuals were tracked over a five- to six-month breeding season, but it might be equally useful to estimate emigration and immigration over a shorter period (hours, days, or weeks) at aggregation points, such as migratory stopover sites. In cases where individual animals are not physically marked, there may be alternative options to identify and track individuals, such as continuous video surveillance or the technique illustrated in this paper.

Number of nests (breeding pairs) was a quantity of primary interest in our study, as an estimate of system state needed to make state-dependent management

decisions. However, in some situations the rate of population change ($\hat{\lambda}_t^*$) may be of equal or more interest than \hat{N}_t^* , and, when it is, there are some advantages to estimating $\hat{\lambda}_t^*$. Estimates of abundance based on models for open populations have long been known to exhibit substantial bias in the face of certain common violations of model assumptions (e.g., Carothers 1973, Pollock et al. 1990, Williams et al. 2002). For some violations (e.g., heterogeneous detection probabilities) estimators for ratios of abundance such as $\lambda_t = N_{t+1}/N_t$ exhibit less bias than those for abundance itself (Hines and Nichols 2002, Williams et al. 2002). Indeed, λ_t is the quantity of primary interest in some studies and is closely related to the concept of “trend,” which is a focal quantity for many monitoring programs. Rate of change in superpopulation size from year to year can be estimated as a derived parameter using the approach presented here, $\hat{\lambda}_t^* = \hat{N}_{t+1}^*/\hat{N}_t^*$, where t denotes year or breeding season. It might also be possible to develop methods to estimate it more directly, as has been done for standard open models (e.g., Pradel 1996).

CONCLUSIONS

We believe that asynchronous population membership is a more common problem in population counts than has been recognized in the literature. We suggest that peak or “snapshot” counts of mobile or asynchronously occurring animals will often result in significant undercounts of true population size, and that especially where group membership is staggered and/or temporally unpredictable, simple counts may be misleading even when used as qualitative indicators of change in population size. Although we examined an extreme case (long nesting period and substantial potential for asynchrony, highly variable annual nest failure rates, and potential for poor nest visibility), many animal populations may show similar characteristics, such as seabird colonies, ungulate herds (Gould et al. 2005), fish aggregations (Schwarz et al. 1993) birds at migration stopover locations, and many kinds of animal social and mating aggregations. Given the strong biases that have now been demonstrated for peak counts as population estimates (this study, Frederick et al. 2006) it seems wise to use alternative approaches wherever possible. We believe that the superpopulation approach developed here deserves serious consideration in other studies of abundance for asynchronous systems.

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APPENDIX A

Superpopulation model output (POPAN data type) for all colonies (*Ecological Archives* E092-070-A1).

APPENDIX B

Calculation of standard errors, superpopulation estimates, and confidence intervals for Alley North samples (*Ecological Archives* E092-070-A2).