

Estimating nests not present at the time of breeding surveys: an important consideration in assessing nesting populations

Peter C. Frederick,^{1,4} Julie A. Heath,^{1,5} Robert Bennetts,² and Heinz Hafner^{3,6}

¹ Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611–0430 USA

² U.S. National Park Service, Greater Yellowstone Network, 1648 South 7th Avenue, Bozeman, Montana 59715 USA

³ Station Biologique de la Tour du Valat, Arles, France

Received 23 February 2005; accepted 4 August 2005

ABSTRACT. Counts of nest starts are often used as indicators of the size of avian nesting populations, or of avian productivity. However, the accuracy of single or repeated counts of unmarked nests over time for estimating seasonal numbers of nests may be strongly affected by nest events that fall in between survey dates, or that occurred prior to or after the survey period. Accuracy may also be affected by uncertainty in the interpretation of counts due to overlap between starting and ending dates of asynchronous nests during the intervisit interval. To measure the combined magnitude of these effects on survey accuracy, we overlaid a monthly “survey” regime on known initiation and ending dates of 2055 nests of ciconiiform birds. Assuming all nests present on the date of simulated survey were counted, monthly surveys underestimated the true number of nest starts by 24–64%, depending on species and year. Using a simple model, we also demonstrate that accuracy does not increase much as survey frequency increases, and that significant estimation error can occur over a wide range of nest success values and degrees of asynchrony. We suggest that (1) these biases can be significant for surveys of many kinds of nesting birds including some territorial passerines, (2) this bias cannot be addressed by increasing survey frequency, and (3) the degree of re-nesting may be of critical interest for inferring breeding population size from nest count data. We suggest three possible approaches for modeling this error.

SINOPSIS. Estimando el número de nidos que no están presentes al momento de llevarse a cabo conteos reproductivos: consideraciones importantes para determinar la población que anida

El conteo de nidos que comienzan a ser construidos se utiliza comúnmente como un indicador del tamaño de la población que anida o de productividad aviar. Sin embargo, la exactitud de conteos simples o repetidos de nidos que no son marcados a través del tiempo (para estimar el número estacional de nidos, pudiera ser afectado por los eventos que ocurren en el nido entre conteos o que ocurren previo o posterior al periodo de examen. La exactitud también puede ser afectada por la incertidumbre en la interpretación de los conteos, debido al solapamiento entre las fechas de comienzo y terminación de construcción de nidos de forma asincrónica, durante el intervalo entre visitas. Para medir la magnitud combinada de estos efectos en la exactitud de los muestreos, sobrepusimos un conteo mensual en donde se desconocía la fecha de comienzo y terminación de 2055 nidos de ciconiformes. Asumiendo que todos los nidos, presentes en las fechas de los conteos simulados, eran incluidos, dichos conteos mensuales sub-estimaron entre el 24–64% de los nidos comenzados. La variación dependió de la especie y el año en que se llevo a cabo el conteo. Utilizando un modelo sencillo demostramos que la exactitud no incrementa con la frecuencia de los muestreos, y que puede ocurrir un estimado de error significativo sobre una amplia gama de valores para el éxito de anidamiento y grados de asincronía. Sugerimos que: (1) dichos sesgos pueden ser significativos para conteos de muchos tipos de aves incluyendo algunos paserinos territoriales, (2) el sesgo no puede ser subsanado incrementando el número de conteos, y (3) el grado de re-anidamiento puede ser crítico para inferir el tamaño de la población que anida. Sugerimos tres alternativas para evitar cometer los errores mencionados.

Key words: *Ardea alba*, *Eudocimus albus*, nest survey, population estimation, survey bias

⁴Corresponding author. Email: pfred@ufl.edu

⁵Current address: Biology Department, Hofstra University, Hempstead, NY 11549 USA.

⁶Heinz Hafner passed away after having participated fully in the writing of this manuscript as an author. This contribution is dedicated to his life of contributions to ornithology.

The numbers of breeding birds or their nests in an area are frequently of interest as indicators of ecological change, or as direct or indirect measures of fecundity or population size (Bibby 2000, Thompson 2002, Rosenstock et al. 2002, Bock and Jones 2004). The parameter measured varies widely according to the use of the data and the area under consideration (Table 1). For example, single counts of nests or birds at a single point in space and time may suffice to ascertain the presence or absence of breeding, or the species composition of an avian community. Although counts or estimates of numbers of nests might also be used as indices of breeding population size, the utility of such indices is highly dependent on the often unexamined relationship between numbers of breeding pairs and numbers of nests counted. Where nests are highly synchronous and easy to see and count, and renesting infrequent, a close match between nests counted and breeding pairs might be expected. However, where nesting is asynchronous and renesting and double-brooding more than trivial, numbers of nests will be a poor indicator of breeding.

In studies of breeding dynamics where bird populations are large (cf >1000 pairs), remote, or where nests are difficult to mark, counts of unmarked nests may be the only statistic that can be feasibly collected. Examples include breeding loons (Earnst et al. 2005), seabirds (Parrish and Zador 2003, Ronconi and Wong 2003, Rodway et al. 2003, Kokko et al. 2004, Gilchrist and Mallory 2005), shorebirds (Gratto-Trevor et al. 1998), and long-legged waders (Custer and Osborn 1977, Frederick and Collopy 1989, Runde et al. 1991, Ogden 1994, Barbraud et al. 2004). In many cases, such counts of nests or nesting pairs are interpreted either implicitly or explicitly to indicate flux in or size of breeding populations (Runde et al 1991, Ogden 1994, Gratto-Trevor et al. 1998, Ronconi and Wong

2003). In some cases, use of nest counts as an indicator of breeding population is justifiable based on reproductive biology and the nature of surveys (see Earnst et al. 2005). However, quantitative estimation of renesting or double-brooding is frequently lacking, but is needed to determine how closely numbers of nests match breeding population size. A second problem with using numbers of nests to estimate breeding population size lies in the estimation itself. In this article, we focus on several less well-recognized sources of error that pertain to quantifying numbers of nests.

Considerable effort has focused on the accurate detection, counting, or recording of birds or nests present during a survey or census (Nichols et al. 2000, Bart and Earnst 2002, Rosenstock et al. 2002, Frederick et al. 2003, Barbraud et al. 2004, Rodgers et al. 2005). Less attention has been paid to the problem of estimating nests not present at the time of survey. Unless nesting is highly synchronous, some proportion of nests may be missed if surveys do not occur throughout the season (Ralph and Scott 1981, Johnson and Krohn 2001, Simon et al. 2002, Barbraud et al. 2004). Although some high-latitude birds may initiate breeding over only a few weeks time, birds at temperate, tropical and subtropical locations may initiate nests over 6 mo or more (Simon et al. 2002, Piazza and Wright 2004). Even at a cool temperate location, Cherenkov (1998) found that one-time nest-mapping visits underestimated actual numbers of passerine nests by 1.5–10 times, depending on species, largely because of asynchrony. Similarly, Siegel et al. (2001) found that number of point-count visits to 48 North American sites strongly affected abundance estimates of songbirds because abundance fluctuated considerably during the breeding season.

Even when surveys span the entire nesting season, nests may be missed because they start and

Table 1. Conceptual arrangement of measurement parameters and desired population information about the nesting population.

Population or parameter of interest	Counts of nests or individuals	Total season nest starts	Renesting rate
Individuals or nests at one point in time	Yes	No	No
Numbers of nests during the entire nesting season	Yes	Yes	No
Individuals nesting over the entire season	Yes	Yes	Yes

end between successive survey dates (Mayfield 1961). Similarly, unless nests are individually identifiable, it is rarely possible to tell whether apparently new nests on successive surveys are the result of previously uncounted pairs nesting for the first time, or are previously-counted pairs that are renesting or continuing normal nesting. Depending on the assumptions made when interpreting these numbers, this might result in underestimation of the number of nests.

Consistently collected data that account for only part of the seasonal total might be reliably used as indices of annual reproduction. However, the use of such indices in annual comparisons relies heavily on the assumption that the degree of seasonal asynchrony or degree of nest turnover remains constant across comparison years. Nest turnover is here defined as the proportion of nests active at a given time that are also active at a later date, and is affected by nest failure, nest completion, new initiations, and renesting. The assumption of constant asynchrony or turnover across years may be invalid. For example, Piazza and Wright (2004) found that the degree of nest turnover and asynchrony in ciconiiform birds in Louisiana varied both within season and among years.

The problem of asynchrony and especially nest turnover as applied to estimating numbers of nests not present at the time of survey has rarely been quantified (Barbraud et al. 2004), and the general importance of this problem to studies of avian population change has not been systematically considered. In this article, we report direct measurement of this kind of survey error using a large sample of individual nest records of herons and ibises, and briefly model how this error might be affected by changes in frequency of surveys. We also explore several more general solutions to the problem.

METHODS

We used 2055 histories of marked nests of herons and ibises in southern Florida collected during repeated ground visits from 1986 to 1995. This data set exhibits considerable natural variation in nest success and degree of asynchrony over space (colonies spread over 3300 km²) and time (up to 5 yr). We wanted to know how many of those nests would have been detected using monthly counts where marked nests were not identified. To do this, we simply

counted the number of actual nests active on specific dates at monthly intervals. We assumed that all nests active on any survey date would have been detected and correctly counted, that nests were not individually identifiable to observers, and that survey dates encompassed the active dates of all nests in the sample.

We first visited marked nests once clutches were determined to be complete or nearly complete and every 5–8 d thereafter. A nest was considered active with the laying of the first egg, and inactive either after young left the nest or after the loss, destruction, or abandonment of the nest's contents. Following fledging or loss of the nest, new eggs or nests in the same location were treated as new nest starts. Because egg laying was often completed by the time of the first visit to any nest, laying dates were frequently inferred by back-counting from the hatching date of the first chick. We used 28 d as the incubation period for Great Egrets (*Ardea alba*), 22 d for Little Blue Herons (*Egretta caerulea*), Tricolored Herons (*Egretta tricolor*), and Snowy Egrets (*Egretta thula*), and 21 d for White Ibises (*Eudocimus albus*; Frederick and Collopy 1988). Successful nests were repeatedly visited until young were too mobile for us to accurately tally their status (14 d posthatching for White Ibises and herons in the genus *Egretta* and 21 d posthatching for Great Egrets).

We assumed a nest would be active, visible, and countable on any simulated survey date for a minimum of 5 d prior to the laying of the first egg. During this time, all species studied would have been in the process of nest building and courtship, when one or both members of the pair are nearly always present at the nest site. We also assumed that a nest with large young would be visible and countable for 2 weeks following the end of our artificially defined nestling period (Kushlan and Bildstein 1992, Frederick et al. 1993). After that time, young are considered fledged, and independent of the nest site. It should be noted that nest structures do not typically last long following the end of the nest cycle, either because they fall apart or are dismantled by neighboring birds. Thus, counting nest structures postreproduction was not possible.

We performed year and species-specific analyses for Great Egrets, White Ibises, and *Egretta* spp. herons. Within any year, the *Egretta* herons (Tricolored Herons, Snowy Egrets, and Little Blue Herons) were lumped together because

their nests and eggs are indistinguishable prior to hatching.

Individual nesting attempts were considered "counted" on the simulated survey if the nest initiation date occurred prior to or on the survey date, and the end date (failure or success) occurred after the survey date. Many of the longer-lived nests were therefore tallied on more than one survey.

We constructed a spreadsheet-based model to simulate the potential effects of degree of asynchronous nesting, nest failure rate, and survey frequency on probability of detecting a hypothetical group of nests. As with the field data, we assumed that all simulated active nests would be counted on any survey date. We used a total of 200 nests as the true number of attempts in any simulation run, and varied nest success by adjusting the numbers of failing nests. Date of failure was assigned according to a normal (or, in one case, a negative binomial) distribution within the nest cycle. Degree of nesting asynchrony was varied by adjusting the number of months over which the 200 nests were initiated, ranging from 30 to 274 d in monthly increments, and initiations were distributed normally within a given period. Each "run" consisted of 20 trials with the same conditions; in each trial the individual combinations of start and stop dates for nests were allowed to assort randomly. The resulting metric from any trial was the maximum

proportion of the 200 nests that were detected on any count date ("peak count"), and this measure was averaged over the 20 trials for any run. We varied the frequency of nest counts from one to four times per month.

RESULTS

Nest count efficiency: field data. Nests recorded in the field showed relatively asynchronous nesting, with new nests initiated throughout the study period of 3–4 mo (Fig. 1), and it is easy to see how any one survey or a peak count would be an inefficient way to estimate the total numbers of nests. The maximum or "peak" counts for any year were generally poor estimators of the actual numbers of nests initiated, ranging between 36% and 76% of the actual number of initiations for any species-year combination (Table 2). This suggests that the use of "peak" monthly counts underestimated the true number of nest starts by 24–64%. For each species and year, we had at least five simulated surveys during the breeding season. Depending on timing, underestimation could have been much higher if only a single survey were conducted.

The proportion of nests represented by the peak survey also varied considerably among years of study, in part, because the timing and degree of synchrony varied between years (Fig. 1).

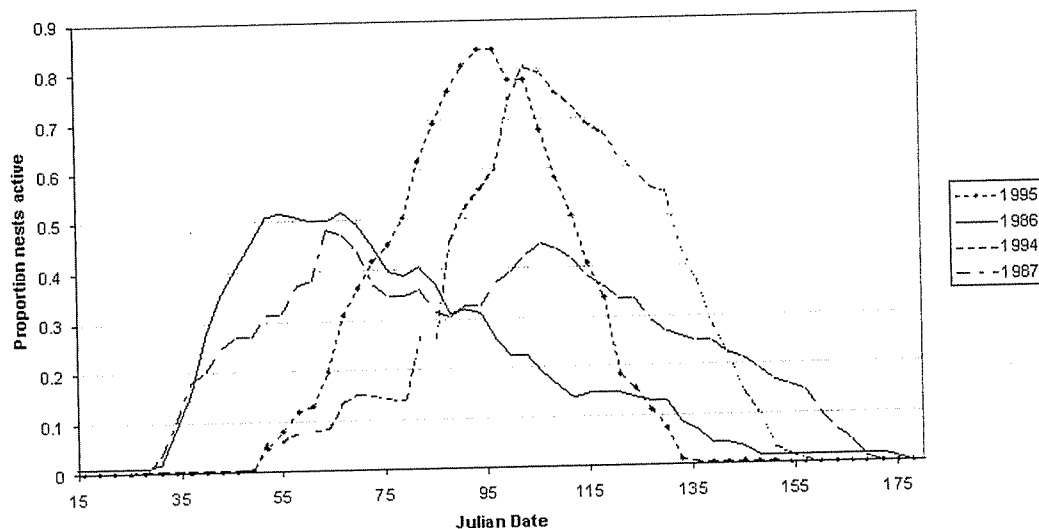


Fig. 1. Pattern of Great Egret nest initiations over four nesting seasons in the Everglades (Florida) expressed as the proportion of all nests initiated during the season that were active on any day.

Table 2. Summary of numbers of wading bird nests with known start and end dates "detected" by simulated monthly counts.

Species	Year	<i>N</i> (nests)	Peak "count"	Proportion of true nests in peak count
Great Egrets	1986	248	103	0.414
Great Egrets	1987	89	38	0.427
Great Egrets	1994	371	284	0.765
Great Egrets	1995	186	126	0.677
White Ibises	1986	245	102	0.416
White Ibises	1987	227	85	0.374
Egretta Herons ^a	1986	248	92	0.369
Egretta Herons	1987	344	193	0.561
Egretta Herons	1995	97	70	0.722
Mean probability of detection				0.525

^aTricolored Herons, Little Blue Herons, and Snowy Egrets combined.

Standard deviations of the annual errors were 16%, 14%, and 2% of the interannual mean for Great Egrets, *Egretta* herons, and White Ibises, respectively. The apparently small variation associated with bias in estimating White Ibis nests may be an artifact of the small sample size (2 yr) over which the interannual variation in nest count efficiency was estimated.

Simulation model results. To exemplify some basic response patterns, we used a nest cycle length of 69 d and normal distributions for both nest initiation and nest failure date. The proportion of nests detected during monthly surveys generally increased with both nest success and degree of synchrony (Table 3). For any given degree of nesting synchrony, the relationship between nest success and proportion of nests detected with monthly surveys was linear and positive, with slopes of the relationship increas-

ing with degree of synchrony (range of slopes 0.22–0.36).

Generally, nest detection probability increased with degree of nest synchrony. For example, probability of detection increased by an average of 43% when comparing nests initiating over 1 mo with those initiating over 9 mo.

The effect of increasing survey frequency on nest detection rate was slight (Fig. 2). Over all of the nest success and synchrony combinations, increasing nest survey frequency from one to four surveys per month produced an average increase in nest detection rate of only 3.9% (1.9% SD).

Importantly, these simulation results were generated from "counts" that occurred on predetermined dates spaced evenly throughout any period of observation. Because we performed many iterations of randomized combinations of

Table 3. Proportion of true nest starts detected using monthly surveys of a simulated population of 200 nests with a 69 d nest cycle by nest success and degree of synchrony in nest starts (see Methods for description of model conditions).

Nest Synchrony (months)	Proportion of successful nests (normally distributed dates of failure)							
	0.95	0.85	0.75	0.65	0.55	0.45	0.35	0.25
1	0.994	0.956	0.918	0.887	0.853	0.814	0.780	0.741
2	0.955	0.907	0.896	0.887	0.871	0.866	0.847	0.832
3	0.951	0.906	0.868	0.837	0.795	0.752	0.720	0.671
4	0.854	0.790	0.739	0.712	0.657	0.629	0.614	0.591
5	0.775	0.739	0.705	0.672	0.634	0.592	0.579	0.532
6	0.683	0.639	0.609	0.582	0.550	0.510	0.484	0.472
7	0.658	0.626	0.589	0.566	0.532	0.497	0.484	0.449
8	0.597	0.556	0.526	0.509	0.479	0.456	0.437	0.419
9	0.550	0.524	0.502	0.490	0.459	0.437	0.421	0.394

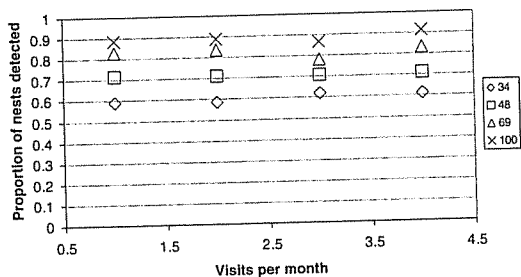


Fig. 2. Effect of nest survey frequency on nest detection efficiency, over a range of nest cycle lengths (symbols).

start and end dates for individual nests within any trial, this effectively produced an average detection probability for each trial. To researchers and managers, it may be more useful to know the range of possible detection probabilities that might be encountered on a randomly selected count date within the peak nesting period. To simulate this, we averaged the maximum and minimum probabilities of detection across all possible days of counting during the peak month of nesting for any simulation run (Table 4). Differences between maximum and minimum probabilities of detection ranged from 0.024 to 0.536 over the range of nest success (0.25–0.95) and the range of nest synchrony (1–9 mo).

DISCUSSION

Using field data and modeling, we have demonstrated that variation in nest success and in degree of nesting synchrony can have a large

effect on interpreting nest counts as true estimates of nesting attempts. In all cases, estimates derived from simulated counts were smaller than the actual numbers of nests.

The magnitude of this kind of error was often not trivial. Even with monthly surveys that assumed 100% detection of active nests, the sample of nest starts in our field data would have been undercounted by over 47%. Our modeled results suggest that large errors are possible over a wide range of asynchrony and nesting success values. The effects of visibility bias and counting error of nests present at the time of survey were assumed to be zero in the model runs, but in a real-world situation these detection errors would be nonzero (Frederick et al. 2003), and additive to the error we estimated.

Our results are clearly a worst-case scenario because of the metric chosen—numbers of nest starts. When reproductive output or population productivity is the main focus of a study, numbers of nest starts may be of interest, and the errors we have illustrated are likely to be appropriate. Although numbers of nest starts could be a good indicator of breeding population size in some instances, the two metrics may not be closely related when renesting or double-brooding are frequent. Our example treated all nest starts as independent. If many of the “new” nests were actually re-nests, the degree of estimation error indicated for numbers of nests could be a large overestimate of error in population size. For this reason, degree of renesting may be a critical parameter to measure if breeding population is the real parameter of interest in surveys.

Table 4. Differences in maximum and minimum nest detection probabilities associated with “counts” on randomly selected days within the peak third of nesting activity. Nest cycle length was 69 d, initiation and failure dates were normally distributed, and count frequency was monthly.

Nest Synchrony (months)	Probability of nest success							
	0.95	0.85	0.75	0.65	0.55	0.45	0.35	0.25
1	0.025	0.113	0.178	0.237	0.319	0.410	0.455	0.536
2	0.253	0.302	0.345	0.361	0.333	0.321	0.304	0.292
3	0.171	0.141	0.122	0.109	0.129	0.174	0.185	0.221
4	0.213	0.228	0.237	0.251	0.263	0.248	0.232	0.207
5	0.089	0.074	0.071	0.068	0.075	0.091	0.096	0.122
6	0.121	0.125	0.129	0.133	0.140	0.141	0.140	0.128
7	0.070	0.058	0.063	0.060	0.058	0.076	0.081	0.095
8	0.065	0.087	0.092	0.101	0.115	0.124	0.121	0.118
9	0.051	0.054	0.048	0.052	0.055	0.059	0.068	0.077

- , B. A. HYLTON, J. A. HEATH, AND M. RUANE. 2003. Accuracy and variation in estimates of large numbers of birds by individual observers using an aerial survey simulator. *Journal of Field Ornithology* 74: 281–287.
- GILCHRIST, H. G., AND M. L. MALLORY. 2005. Declines in abundance and distribution of the Ivory Gull (*Pagophila eburnea*) in arctic Canada. *Biological Conservation* 121: 303–309.
- GRATTO-TREVOR, C. L. V. H. JOHNSTON, AND S. T. PEPPER. 1998. Changes in shorebird and eider abundance in the Rasmussen Lowlands, NWT. *Wilson Bulletin* 110: 316–325.
- JODICE, P. G. R., S. L. GARMAN, AND M. W. COLLOPY. 2001. Using resampling to assess reliability of audiovisual survey strategies for Marbled Murrelets at inland forest sites. *Waterbirds* 24: 331–344.
- JOHNSON, C. M., AND W. B. KROHN. 2001. The importance of survey timing in monitoring breeding seabird numbers. *Waterbirds* 24: 22–33.
- KOKKO, H., M. P. HARRIS, AND S. WANLESS. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the Common Guillemot *Uria aalge*. *Journal of Animal Ecology* 73: 367–376.
- KUSHLAN, J. A., AND K. L. BILDSTEIN. 1992. White Ibis (*Eudocimus albus*). In: *The Birds of North America*, No. 9 (A. Poole, P. Stettenheim, and F. Gill, eds.). Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D. C.
- LINK, W. A., AND J. R. SAUER. 1997. Estimation of population trajectories from count data. *Biometrics* 53: 63–72.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73: 255–261.
- NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117: 393–408.
- OGDEN, J. C. 1994. A comparison of wading bird nesting dynamics, 1931–1946 and 1974–1989 as an indication of changes in ecosystem conditions in the southern Everglades. In: *Everglades: the ecosystem and its restoration* (S. and J. C. Ogden Davis, eds.), pp. 533–570. St. Lucie Press, Del Ray Beach, FL.
- PARRISH, J. K., AND S. G. ZADOR. 2003. Seabirds as indicators: an exploratory analysis of physical forcing in the Pacific Northwest coastal environment. *Estuaries* 26: 1044–1057.
- PIAZZA, B. P., AND V. L. WRIGHT. 2004. Within-season nest persistence in large wading bird rookeries. *Waterbirds* 27: 362–367.
- RALPH, C. J., AND J. M. SCOTT. 1981. Estimating numbers of terrestrial birds. *Studies in Avian Biology* 6.
- RODGERS, J. A., P. S. KUBILIS, AND S. A. NESBITT. 2005. Accuracy of aerial surveys of waterbird colonies. *Waterbirds* 28: 230–237.
- RODWAY, M. S., H. M. RGEHR, AND J. W. CHARDINE. 2003. Status of the largest breeding concentration of Atlantic Puffins, *Fratercula arctica*, in North America. *Canadian Field-Naturalist* 117: 70–75.
- RONCONI, R. A., AND S. N. P. WONG. 2003. Estimates of changes in seabird numbers in the Grand Manan Archipelago, New Brunswick, Canada. *Waterbirds* 26: 462–472.
- ROSENBERG, D. K., D. F. DESANTE, K. S. MCKELVEY, AND J. E. HINES. 1999. Monitoring survival rates of Swainson's Thrush (*Catharus ustulatus*) at multiple spatial scales. *Bird Study* 46: 198–208.
- ROSENSTOCK, S. S., D. R. ANDERSON, K. M. GIESEN, T. LEUKERING, AND M. F. CARTER. 2002. Landbird counting techniques: current practices and an alternative. *Auk* 119: 36–45.
- RUNDE, D. E., J. A. GORE, J. A. HOVIS, M. S. ROBSON, AND P. D. SOUTHALL. 1991. Florida atlas of breeding sites of herons and their allies: update 1986–1989. Nongame Wildlife Program Technical Report No. 10, Florida Game and Freshwater Fish Commission, Tallahassee, FL.
- SCHWARZ, C. J., AND A. N. ARNASON. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52: 860–873.
- SIEGEL, R. B., D. F. DESANTE, AND M. P. NOTT. 2001. Using point counts to establish conservation priorities: how many visits are optimal? *Journal of Field Ornithology* 72: 228–235.
- SIMON, J. C., T. K. PRATT, K. E. BERLIN, J. R. KOWALSKY, S. G. FANCY, AND J. S. HATFIELD. 2002. Temporal variation in bird counts within a Hawaiian rainforest. *Condor* 104: 469–481.
- THOMPSON, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. *Auk* 119: 18–25.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2001. *Analysis and management of animal populations*. Academic Press, San Diego, CA.