J Raptor Res. 29(4):256–264

SURVIVAL AND POPULATION SIZE ESTIMATION IN RAPTOR STUDIES: A COMPARISON OF TWO METHODS

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ABSTRACT.—The Jolly-Seber model is a capture-recapture model that can provide less-biased survival and population size estimates than those produced from simple counting procedures. Parameter estimation by simple counts and Jolly-Seber methods are based on certain assumptions that directly determine the validity of estimates. Evaluation of assumptions for parameter estimation is a focus of this paper and used as a basis for determining which methods are more likely to produce better estimates. An example of population size and survival estimation for a peregrine falcon (*Falco peregrinus*) population in western Greenland is used to compare the two methods. Based on results from the Greenland peregrine population, and an assessment of the underlying assumptions of simple counts and the Jolly-Seber model, we suggest that Jolly-Seber estimation of survival and population size is less biased than simple counts in studies with marked birds. We recommend the use of a Jolly-Seber analysis of data when capture-recapture techniques are employed in raptor population studies.

KEY WORDS: *estimation*; Falco peregrinus; *Jolly-Seber*; *peregrine falcon*; *population size*; *simple counts*; *survival.*

Sobrevivencia y estimación del tamaño poblacional en estudios de rapaces: una comparación de dos métodos

RESUMEN.—El modelo Jolly-Seber es un modelo de captura-recaptura que puede proveer menor error en las estimaciones de sobrevivencia y tamaño poblacional que aquellos producidos por procedimientos de conteos simples. Parámetros de estimación por simples conteos y por métodos Jolly-Seber estan basados en ciertas presunciones que determinan directamente la validez de las estimaciones. La evaluación de presunciones para parámetros de estimación es el foco de este artículo y es usado como un base para determinar cual método probablemente produce las mejores estimaciones. Un ejemplo de estimación del tamaño poblacional y de sobrevivencia en una población de *Falco peregrinus* en West Greenland, se usó para comparar ambos métodos. Basados en los resultados de la población de *F. peregrinus* de Greenland y una medida de las presunciones fundamentales de conteos simples y del modelo Jolly-Seber, nosotros sugerimos que la estimación Jolly-Seber de sobrevivencia y tamaño poblacional tiene menos error que uno de un conteo simple en estudios con aves marcadas. Nosotros recomendamos el uso de un análisis Jolly-Seber de datos cuando se usan técnicas de captura-recaptura en estudio de poblaciones de rapaces.
[Traducción de Ivan Lazo]

Historically, biologists have relied on counts of unmarked birds or tallies of nests to create an index to raptor numbers or to estimate the number of breeding raptors in a study area (Hancock 1964, King et al. 1972, Whitfield et al. 1974). More recently, biologists have marked birds and resurveyed study areas to recapture or resight known individuals to estimate turnover, mortality, and population size (Mearns and Newton 1984, Newton 1986, Court et al. 1989, Lebreton et al. 1992). These estimates can be biased due to assumption violations and failure to use all available information, consequently leading to inaccurate results. In this paper, we discuss Jolly-Seber estimation (Jolly 1965, Seber 1965) as a useful method for obtaining survival estimates and population size estimates of raptors based on capture-recapture data of marked individuals. Recapture is a general term referring to either the actual capture of an individually marked bird, as in Mearns and Newton (1984), the resighting of individuals (Hestbeck et al. 1991), or both (Court et al. 1989)

The Jolly-Seber model has been described extensively in the literature (Cormack 1973, Seber 1982, Pollock et al. 1990) and has been the basis for several computer programs: POPAN-3 (Arnason and Schwarz 1987), RELEASE (Burnham et al. 1987), JOLLY (Pollock et al. 1990) and SURGE (Lebreton et al. 1992). Although the Jolly-Seber model has been applied in bird studies before (Stokes 1984, Spendelow and Nichols 1989, Pollock et al. 1990), it has seen limited use in raptor studies (Franklin et al. 1990, Noon et al. 1992). Noon et al. (1992) used a Jolly-Seber analysis to estimate survival of California spotted owls (*Strix occidentalis occidentalis*), but relied upon simple counts to estimate population size. Franklin et al. (1990) estimated the number of northern spotted owls (*Strix occidentalis caurina*) with empirical and Jolly-Seber methods. The Jolly-Seber estimates were used for density estimation, but no clear reason was given for the choice.

The enumeration method has been compared to the Jolly-Seber model (Nichols and Pollock 1983, Pollock et al. 1990). Simple counting procedures differ from the enumeration method by considering only the captures or sightings at a given sampling occasion for population size estimation and only consecutive sightings for survival estimation. Believing that demographic parameter estimates are only as valid as the method used to obtain them, we have examined the assumptions behind simple counting procedures and the Jolly-Seber method. Data from peregrine falcon (*Falco peregrinus*) surveys in western Greenland (Mattox and Seegar 1988, W.S. Seegar, M.R. Fuller, W.G. Mattox, W.R. Gould unpubl. data) which, henceforth, we refer to as the Greenland study, are used to illustrate some differences among simple counts and estimates from the Jolly-Seber analysis. Based on an assessment of the underlying assumptions of simple counts and some uses of recapture-resighting data, we recommend capture-recapture techniques as a more appropriate means for evaluating raptor populations and suggest a Jolly-Seber analysis of such studies.

THE JOLLY-SEBER MODEL

In many situations, it is not feasible to assume a closed population; that is, that no births, deaths, emigration, or immigration occur. The Jolly-Seber model (Jolly 1965, Seber 1965) is a capture-recapture model allowing for an open population in which additions and/or deletions occur. The model produces estimates (and estimated standard errors) of survival (1 − mortality − emigration) and recruitment (births and immigrants) between sample periods, as well as population size estimates at the sampling occasions, given the following assumptions:

(1) All animals present at the *ith* sample of the population have equal probability of capture (p_i) $i = 1, \ldots, k$.
(2) All animals marked in the *ith* sample have the same conditional probability of surviving from time i to time $i + 1$ (ϕ_i) $i = 1,2, \ldots, k-1$.
(3) Marks are not lost and all are reported.
(4) All samples are instantaneous and each release is made immediately after the sample.

The survival estimator, ϕ_i, actually measures the return rate (1 − mortality − emigration), where the effects of mortality and emigration (assumed permanent) are not separable. The most general Jolly-Seber model allows for survival, recruitment, and capture probabilities to vary among sampling occasions. For a detailed description of the Jolly-Seber model, see Seber (1982) or Pollock et al. (1990).

Reduced-parameter versions of the Jolly-Seber model have also been proposed (Jolly 1982, Pollock et al. 1990) and have been incorporated along with the Jolly-Seber estimators in the computer package JOLLY (Pollock et al. 1990). The sequence of models, Model D assuming constant survival and capture rates, Model B assuming constant survival, and Model A, in which capture and survival rates vary over time, form a series of increasingly complex models. Goodness-of-fit tests (Brownie et al. 1986), which utilize individual capture history information and tests between models based on a conditional likelihood approach (e.g., Brownie and Robson 1983), can be particularly useful to raptor ecologists. Other special cases of the Jolly-Seber model, such as a death-only model, and generalizations, such as a temporary trap response model also are available in program JOLLY. The existence of such models allows for tests of assumptions to be made, which can serve to further validate the conclusions drawn from an analysis. Programs RELEASE and POPAN-3 contain simulation components that allow the user to evaluate the robustness of estimators to assumption violations using simulated survival data.

In many raptor studies, individual nest sites are checked every year (Falk and Møller 1988, Mattox and Seegar 1988, Geissler et al. 1990), rather than an entire area being surveyed completely and consistently (Mindell et al. 1987). The nest fidelity exhibited by peregrines (Mearns and Newton 1984, Court et al. 1989, Seegar et al. unpubl. data) and other raptors results in heterogeneous capture probabilities of the population. Previously marked birds are more likely to be resighted (recaptured) in the future than unmarked birds. We classify this result as heterogeneity rather than trap response because this fidelity is a natural characteristic of the birds, not a response to capture (i.e., "trap happy") at these sites. Fuller and Mosher (1987) discuss detectability in reference to external variables, such as the skill of the field personnel, weather, time of year, etc. In addition, characteristics of the birds themselves (age, sex, etc.) can cause differences in detectability. Fortunately, Jolly-Seber survival estimates are robust to heterogeneous capture probabilities (Carothers 1973, 1979), particularly in studies with relatively high capture probabilities (>0.50; Gilbert 1973).

Unlike survival estimates, population size estimates are not robust to heterogeneous capture probabilities. Marked birds with higher recapture (resighting) probabilities result in the underestimation of the population size. Carothers (1973) and Gilbert (1973) simulated the effects of heterogeneity on population size estimates, finding that the negative bias of the estimates can be severe. The magnitude of bias depends on the average capture probability and the degree of variation in capture probabilities among individuals (Pollock et al. 1990).

The second assumption of all marked animals having the same conditional probability of survival does not equate survival between marked and unmarked animals. However, in practice, biologists will want to make this equality in order that survival estimates will refer to the entire population. The experience of Mearns and Newton (1984) and that in the Greenland study (W.G. Mattox pers. comm.) suggests that marking (leg bands) has little or no effect on the survival of raptors. Age-specific differences in survival rates have been investigated by Manly (1970) who found survival and population size estimates were positively biased when young animals have lower survival probabilities than older animals. However, Manly (1970) concedes that age-specific differences are not of great importance unless mortality rates are strongly affected by age. Pollock et al. (1990) gives a thorough discussion of an age-dependent Jolly-Seber method. The studies discussed in this paper are of breeding-age birds, thus avoiding age-specific differences between adults and juveniles.

Any loss of marks by birds will result in the underestimation of survival rates, because birds that lose marks will be identified less often. In this scenario, population size estimates are not affected (Arnason and Mills 1981), although the precision of the estimators does change. Recent studies in which raptors have been double banded (Court et al. 1989, W.S. Seegar pers. comm.) provided little or no evidence of band loss.

THE SIMPLE COUNT OF MARKED BIRDS

Using simple counts, maximum mortality estimates (and thus minimum survival rates) are based on tallies of turnover and movement within the study area. To estimate turnover, birds must be marked for identification and then retrapped or resighted to determine whether or not a bird has returned to its previous nest site. Turnover estimates (and survival estimates) based on simple counts can be incorrect when they make an invalid assumption and do not use all of the information available for estimation. Turnover (p_t) is defined in Mearns and Newton (1984:349) as the proportion of territories where identified individuals were caught (seen) in successive years (n) that do not contain the same individual in the second year (n_d),

$$\hat{p}_t = n_d/n.$$

An estimate of maximum mortality (m_{max}) is then derived from turnover by accounting for known movements (n_k) within the study area,

$$\hat{m}_{max} = (n_d - n_k)/n.$$

By subtracting the known movements, the remaining proportion becomes the maximum mortality estimate. Minimum survival ($\hat{p}_s$) is simply,

$$\hat{p}_s = 1 - \hat{m}_{max}.$$

The estimate of turnover (as defined above) does not include vacancies by birds unless they are replaced by another identified bird, meaning that a site occupied one year and not occupied the next year is excluded from the turnover estimate. The implicit assumption made by simple counts is that all vacancies not replaced by another bird are a result of permanent emigration and none are due to the death of the birds. In many cases this is known to be untrue (marked birds are found dead elsewhere; Yates et al. 1988, Seegar et al. unpubl. data). Only when a bird is replaced by another identified bird is a vacancy considered to be caused by death of the individual. We argue that this formulation underestimates mortality, causes the maximum mortality estimate to be misleading, and uses only part of the available data that are useful for estimates.

The departure of a bird from a nest area in the Mearns and Newton (1984) study was always replaced by another individual (R. Mearns pers. comm.). The maximum mortality estimate derived when departures are always replaced by another individual is valid for the observed nest sites. However, in many studies, nest departures are not always replaced by other birds (James et al. 1989, Court et al. 1989). In these cases, the exclusion of nest-site vacancies from the turnover estimate can negatively bias the maximum mortality estimate. Court et al. (1989) recognized this imperfection in the commonly used definition of turnover and included known vacancies in their turnover and maximum mortality estimate. All prior occupancies can be used in this estimate, regardless of replacement by another bird. Nevertheless, this approach provides only a value for maximum mortality, because it cannot be used to account for emigration, or for undetected movement of birds within the study area.

Population size estimates from simple counts are based solely on the number of birds seen or captured each year. Birds need not be marked for such calculations. The simple count method with unmarked birds effectively assumes detection probabilities of one, an invalid assumption in the Greenland study and many other cases (Grier 1977, Postovit 1979, Bird and Weaver 1988). Hodges et al. (1984) give reasons for true capture/resighting probabilities being less than one, ranging from unfavorable soaring conditions to obscured nesting and perching sites. Ground surveys are often subject to logistical constraints resulting from irregular terrain or impassable rivers (Mattox and Seegar 1988) that can cause some birds to have very low detection probabilities. Places in which nesting was once unknown (Mearns and Newton 1984), or was thought not possible can be overlooked (Pruett-Jones et al. 1981, MacLaren et al. 1984), only to find the presence of adults or offspring at a later date. In such cases, it is unknown how long a bird or nesting pair has been there. At the very best, population estimates of breeding birds based on simple counts should be seen as minimum population size estimates for each year.

COMPARISON OF METHODS

Over the period from 1983–91 in western Greenland, the same adult female peregrine falcons were identified on 125 occasions at 154 nest sites (n) in successive years. In this analysis, a nest site is included as many times as it was occupied in successive years, the unit of measure being one territory per year (Mearns and Newton 1984). Turnover was estimated (Seegar et al. unpubl. data) to be

$$\hat{p}_t = 18.8\% \ (29/154).$$

Adjusting the previous turnover estimate for five known movements, the estimated maximum mortality then was

$$\hat{m}_{max} = 15.6\% \ (24/154),$$

resulting in,

$$\hat{p}_s = 84.41\% \text{ minimum survival},$$

with the standard error (SE) of the proportion

$$\text{SE} = ((\hat{p}_s(1 - \hat{p}_s))/n)^{1/2} = 0.0292.$$

Jolly-Seber analysis uses the individual histories of all captured (marked) birds, including those that were not replaced when they vacated their nest site, thereby using all of the available information for survival estimation. Using program JOLLY (Pollock et al. 1990), the chi-square goodness-of-fit tests selected the model with constant survival and constant capture probability over the entire study as the best fitting model. Calculated in this way, the estimate of survival is

$$\phi_i = 78.80\% \ (\text{SE} = 0.0308),$$

indicating higher mortality than the "maximum" mortality estimate from simple counts. Capture probability was estimated to be 0.9361 (SE = 0.0246). In the same spirit as the simple count estimate, the survival estimate from the Jolly-Seber model should be viewed as a minimum survival rate, because the effects of emigration cannot be separated from the estimate. Jolly-Seber survival estimates are less biased than their simple count equivalents because the Jolly-Seber model does not assume vacancies without replacement by another bird are due only to emigration and it uses all of the available information. Although formal simulation studies in which parameter values are known have not been performed, statements concerning the bias of particular estimation methods in relation to other methods are appropriate when based on an assessment of the assumptions underlying the methods.

A common occurrence in field studies is that the sampling effort changes over time. Financial resources can vary, allowing for more or less area to

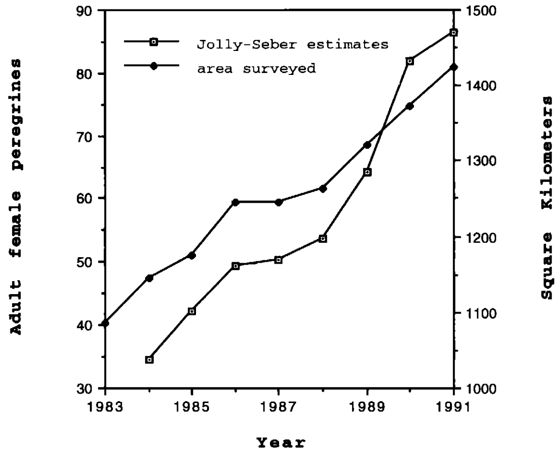

Figure 1. Population size estimates of adult female peregrine falcons and the respective amount of area surveyed in western Greenland from 1983–91.

be sampled, or the same area is sampled more or less intensively, personnel experience can vary, and weather can alter the survey effort (Grier 1977, Fuller and Mosher 1987). In the case of more effort, survival estimation using capture-recapture techniques is robust to changes because survival estimates are conditional upon time of first capture. The less desirable case is when survival must be based only on those animals found by a reduced level of effort.

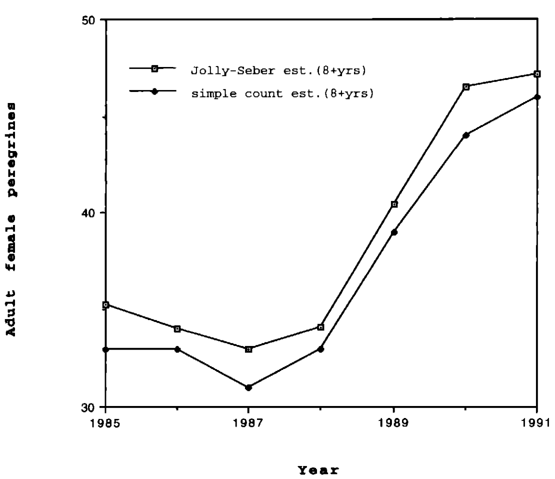

Figure 2. Population size estimates of adult female peregrine falcons from simple counts and the Jolly-Seber model for an area surveyed with constant effort over at least 8 yr.

Use of the Jolly-Seber model provides comparatively good survival estimates and less biased population size estimates than the simple count method. However, more difficulties arise when considering population size estimation. Changing the sampling effort over time causes population size estimates to be misleading. If the intensity with which sampling occurs or the amount of area sampled increases over time, then increases in counts do not necessarily reflect population size increases (Franklin et al. 1990). Female peregrine falcon population size estimates from the Greenland study (Seegar et al. unpubl. data) are given in Fig. 1. Population size estimates were computed using the capture histories of all female peregrines marked over the study period (1983–91). Some females were seen but never captured and thus did not have a recorded capture history. The number of females seen each year, but which remained unmarked, was added to the population size estimates from the Jolly-Seber analysis (after adjusting for the estimated capture probability) to more accurately reflect population levels for a given year. Trend analysis using Lehmann's test (Lehmann 1975) resulted in a significant positive trend ($P < 0.0002$). However, the amount of area sampled (Fig. 1) also had a similar positive trend ($P < 0.0002$). Based only on this information, one cannot conclude the number of female peregrines increased.

Areas must be defined that are sampled equally every year; i.e., a constant-size area sampled with equal intensity, before a proper trend analysis of population size can be executed (Bromley 1988). In the Greenland study, an area in which nests were surveyed consistently for at least 8 yr was determined. Population estimates (Fig. 2) for this area again showed a significant upward trend ($P = 0.0331$). Although in this case the results agree with those calculated with unequal effort, in some instances the resulting tests based on constant sampling area might lead to different conclusions than those based on unequal area samples. It is important to keep the sampled area sizes constant, or at the very least, to carefully document the amount of area sampled and the intensity with which it is sampled to allow for density estimation and subsequent trend analysis.

Unlike the Jolly-Seber survival estimates, unequal capture probabilities for marked and unmarked birds (resulting from nest site surveys of birds with high nest-site fidelity) can lead to serious

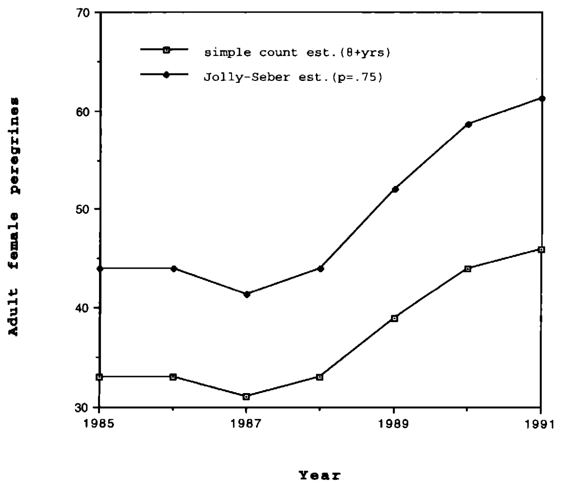

Figure 3. Population size estimates of adult female peregrine falcons from simple counts and the Jolly-Seber model assuming an estimated capture probability, $\hat{p}$ = 0.75, for an area surveyed with constant effort over at least 8 yr.

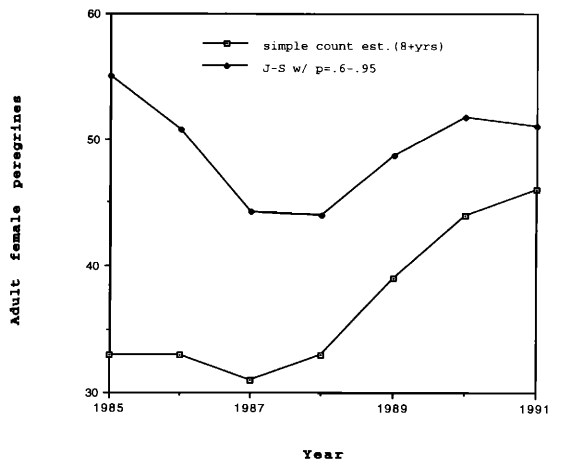

Figure 4. Population size estimates of adult female peregrine falcons from simple counts and the Jolly-Seber model assuming estimated capture probabilities increase steadily from $\hat{p}$ = 0.60 to $\hat{p}$ = 0.95 for an area surveyed with constant effort for at least 8 yr.

positive bias in the estimated capture probabilities, resulting in a negative bias in the estimated population sizes from the Jolly-Seber model. Under this sampling regime, birds nesting at unknown or unsurveyed sites within the sampling area can have capture probabilities as small as zero. For the Greenland study area in which nests were consistently surveyed for at least 8 yr, the reduced-parameter model estimated a constant capture probability of 0.9541 (SE = 0.0254). Although heterogeneity has inflated the capture probability estimate, the bias from simple counts will always be greater than or equal to that associated with the Jolly-Seber estimate because simple counts assume capture probabilities to be one. In addition, the full parameter Jolly-Seber model (if selected) allows for variable capture probabilities, which may result from variable weather conditions, personnel experience, etc.

Population size estimates of female peregrines in the Greenland study from the Jolly-Seber model and simple counts (Seegar et al. unpubl. data) are given in Fig. 2. The relatively small differences in this case will become more pronounced in other situations with simple counts exhibiting even greater bias where capture probabilities are lower. Figure 3 compares the expected Jolly-Seber population size estimates for the area sampled at least 8 yr to simple count estimates when the probability of capture is estimated to be 0.75.

In the above case a constant capture probability was assumed. By allowing for variable capture probabilities over time, use of the Jolly-Seber model to estimate population size can lead to differences in the interpretation of trends as compared to the simple count method that assumes a constant capture probability of one. Suppose, for example, capture probabilities were estimated to have constantly increased in the Greenland study from 0.60–0.95; i.e., the research group became more skilled in locating peregrines as the study progressed. The differences in population size estimates under this scenario are illustrated in Fig. 4. As before, the Jolly-Seber model estimates a greater number of peregrines, but the allowance of variable capture probabilities by the Jolly-Seber model can also change the interpretation of population trends.

Jolly-Seber population size estimates can be more biased than simple counts in the event individuals temporarily emigrate from the population. Under such circumstances, the Jolly-Seber model assumes the individuals remained in the population undetected, thus lowering the capture probability estimate and inflating the population size estimate. Grier (1977) noted that lack of detection of an individual found in later surveys is more likely attributed to missing an individual that was present in the population rather than the individual having temporarily emigrated. Even studies in which the same entire area was thoroughly surveyed, checking all potential nest sites (Mearns and Newton 1984), the researchers acknowledged the possibility of having capture probabilities less than one (R. Mearns pers. comm.). For this reason, we suggest that Jolly-Seber population size estimates are more likely to be less biased than simple counts and should be used and regarded as minimums for their respective areas.

DISCUSSION

Simple count estimates of population size and survival rates require different study designs. When population estimation is the sole purpose of a study, the simple count method does not require birds to be marked; however, it is necessary for the size of the area sampled, the effort, and bird detectabilities to remain constant to enable the determination of trends over time. Once an area has been defined by a particular set of nests, it is essential that those nests be surveyed thoroughly every year, and, if possible, the entire area should be surveyed. Because simple counts assume capture probabilities of one, population size estimates will be negatively biased unless this assumption is valid. Because detectability usually is not one and may vary over the study period, we suggest that capture-recapture techniques be used when possible, and a Jolly-Seber type of analysis be applied.

Certainly, studies in which birds are marked require considerably more effort than studies that do not. However, it is necessary to mark birds when survival estimates are desired. Where survival estimates require the marking of birds in the population, the size of the sampling area need not be constant. Effort should be directed toward marking and releasing as many birds as possible, and toward resighting the birds in the future. When individuals are present, they must be identified by band or not, and if unbanded, should be captured when possible and banded.

Studies in which survival estimates and population size are of interest require both marking of birds and constant sampling effort. The presence of marked birds in the population allows for stronger, more sophisticated analyses than simple counts. Capture-recapture techniques lend themselves to the Jolly-Seber model as an appropriate tool for better estimating the important parameters of survival and population size. The Jolly-Seber model allows for less biased estimates of minimum survival and minimum population size than the respective estimates from simple counts whether the purpose is survival estimation, population estimation, or both. The availability of such Jolly-Seber-based computer programs as JOLLY and POPAN-3 facilitate the use of capture-recapture analysis to provide the best estimates based on all the data gathered.

ACKNOWLEDGMENTS

The Division of Biotechnology (U.S. Department of Army) and the Migratory Bird Research Branch of the Patuxent Wildlife Research Center (National Biological Service) provided financial support. K.H. Pollock and D.M. Bird lent verbal support and critical reviews of my paper. D.A. Boag, B.R. Noon, and G.C. White also provided many useful comments on the manuscript. W.S. Seegar conceived the project and led the field work to gather the data we use to illustrate methodology. We thank W.S. Seegar, W.G. Mattox, T. Maechtle, M.A. Yates, and other members of the Greenland Peregrine Falcon Survey for their efforts.

LITERATURE CITED

ARNASON, A.N. AND K.H. MILLS. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Can. J. Fish. Aquat. Sci.* 38:1077–1095.

——— AND C.J. SCHWARZ. 1987. POPAN-3: Extended analysis and testing features for POPAN-2. Charles Babbage Research Centre, St. Norbert, MB, Canada.

BIRD, D.M. AND J.D. WEAVER. 1988. Peregrine falcon populations in Ungava Bay, Quebec, 1980–1985. Pages 45–49 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID U.S.A.

BROMLEY, R.G. 1988. Status of peregrine falcons in the Kitikmeot, Buffin, and Keewatin Regions, Northwest Territories, 1982–1985. Pages 51–57 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID U.S.A.

BROWNIE, C., AND D.S. ROBSON. 1983. Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly-Seber model. *Biometrics* 39:437–453.

———, J.E. HINES AND J.D. NICHOLS. 1986. Constant-parameter capture-recapture models. *Biometrics* 42:561–574.

BURNHAM, K.P., D.R. ANDERSON, G.C. WHITE, C. BROWNIE AND K.H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *Am. Fish. Soc. Monogr.* 5.

CAROTHERS, A.D. 1973. The effects of unequal catchability on Jolly-Seber estimates. *Biometrics* 29:79–100.

———. 1979. Models for capture-recapture. Pages 217–255 *in* R.M. Cormack, G.P. Patil and D.S. Robson [EDS.], Sampling biological populations. Statistical ecology series, International Cooperative Publ. House, Fairland, MD U.S.A.

CORMACK, R.M. 1973. Commonsense estimates from capture-recapture studies. Pages 225-234 *in* M.S. Bartlett and R.W. Hiorns [EDS.], The mathematical theory of the dynamics of biological populations. Academic Press, New York, NY U.S.A.

COURT, G.S., D.M. BRADLEY, C.C. GATES, AND D.A. BOAG. 1989. Turnover and recruitment in a tundra population of peregrine falcons *Falco peregrinus*. *Ibis* 131:487–496.

FALK, K. AND S. MØLLER. 1988. Status of the peregrine falcon in south Greenland: population density and reproduction. Pages 37–43 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID U.S.A.

FRANKLIN, A.B., J.P. WARD, R.J. GUTIÉRREZ AND G.I. GOULD, JR. 1990. Density of northern spotted owls in northwest California. *J. Wildl. Manage.* 54:1–10.

FULLER, M.R. AND J.A. MOSHER. 1987. Raptor survey techniques. Pages 37–65 *in* B.A.G. Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

GEISSLER, P.H., M.R. FULLER AND L. MCALLISTER. 1990. A trend analysis for raptor nest surveys: an example with peregrine falcon data. Pages 139–143 *in* J.R. Sauer and S. Droege [EDS.], Survey designs and statistical methods for the estimation of avian population trends. USDI Fish and Wildl. Serv., Biol. Rep. 90, Washington, DC U.S.A.

GILBERT, R.O. 1973. Approximations of the bias in the Jolly-Seber capture-recapture model. *Biometrics* 29: 501–526.

GRIER, J.W. 1977. Quadrat sampling of a nesting population of bald eagles. *J. Wildl. Manage.* 41:438–443.

HANCOCK, D. 1964. Bald eagles wintering in the southern Gulf Islands, British Columbia. *Wilson Bull.* 76: 111–120.

HESTBECK, J.B., J.D. NICHOLS AND R.A. MALECKI. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72: 523–533.

HODGES, J.I., JR., J.G. KING AND R. DAVIES. 1984. Bald eagle breeding population survey of coastal British Columbia. *J. Wildl. Manage.* 48:993–998.

JAMES, P.C., I.G. WARKENTIN AND L.W. OLIPHANT. 1989. Turnover and dispersal in urban Merlins *Falco columbarius*. *Ibis* 131:426–429.

JOLLY, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.

———. 1982. Mark-recapture models with parameters constant in time. *Biometrics* 38:301–321.

KING, J.G., F.C. ROBARDS AND C.J. LENSINK. 1972. Census of the bald eagle breeding population in southeast Alaska. *J. Wildl. Manage.* 36:1292–1295.

LEBRETON, J.D., K.P. BURNHAM, J. CLOBERT AND D.R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62.

LEHMANN, E.L. 1975. Nonparametrics. Holden-Day, Inc., San Francisco, CA U.S.A.

MACLAREN, P.A., D.E. RUNDE AND S.H. ANDERSON 1984. A record of tree nesting praire falcons in Wyoming. *Condor* 86:487–488.

MANLY, B.F.J. 1970. A simulation study of animal population estimation using the capture-recapture method. *J. Appl. Ecol.* 7:13–39.

MATTOX, W.G. AND W.S. SEEGAR. 1988. The Greenland peregrine falcon survey, 1972–1985, with emphasis on recent population status. Pages 27–35 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID U.S.A.

MEARNS, R. AND I. NEWTON. 1984. Turnover and dispersal in a peregrine (*Falco peregrinus*) population. *Ibis* 126:347–355.

MINDELL, D.P., J.L.B. ALBUQUERQUE AND C.M. WHITE. 1987. Breeding population fluctuations in some raptors. *Oecologia* 72:382–388.

NEWTON, I. 1986. Individual performance in sparrowhawks: the ecology of two sexes. Pages 22–29 *in* H. Ouellet [ED.], Acta XIX Congressus Internationalis Ornithologicci. Univ. Ottawa Press, Ottawa, Canada.

NICHOLS, J.D. AND K.H. POLLOCK. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. *J. Mammal.* 64:253–260.

NOON, B.R., K.S. MCKELVEY, D.W. LUTZ, W.S. LAHAYE, R.J. GUTIÉRREZ AND C.A. MOEN. 1992. Estimates of demographic parameters and rates of population change. Pages 175–186 *in* J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutiérrez, G.I. Gould, Jr. and T.W. Beck [EDS.], The California spotted owl: a technical assessment of its current status. USDA For. Serv. Gen. Tech. Rep. PSW-GTR 133.

POLLOCK, K.H., J.D. NICHOLS, C. BROWNIE AND J.E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107.

POSTOVIT, H.R. 1979. Population estimates of breeding raptors in the North Dakota Badlands. M.S. thesis, North Dakota State Univ., Fargo, ND U.S.A.

PRUETT-JONES, S.G., C.M. WHITE AND W.R. DEVINE. 1981. Breeding of peregrine falcons in Victoria, Australia. *Emu* 80:253–269.

SEBER, G.A.F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.

———. 1982. The estimation of animal abundance and related parameters. Macmillan, New York, NY U.S.A.

SPENDELOW, J.A. AND J.D. NICHOLS. 1989. Annual survival rates of breeding adult roseate terns (*Sterna dougallii*). *Auk* 106:367–374.

STOKES, S.L. 1984. The Jolly-Seber method applied to age-stratified populations. *J. Wildl. Manage.* 48:1053–1059.

WHITFIELD, D.W.A., J.M. GERRARD, W.J. MAHER AND D.W. DAVIS. 1974. Bald eagle nesting habitat, density, and reproduction in central Saskatchewan and Manitoba. *Can. Field-Nat.* 88:399–407.

YATES, M.A., K.E. RIDDLE AND F.P. WARD. 1988. Recoveries of peregrine falcons migrating through the eastern and central United States, 1955–1985. Pages 471–483 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc., Boise, ID U.S.A.

Received 17 February 1995; accepted 5 July 1995