Integrating Mark–Recapture–Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters

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SUMMARY.   In studies of wild animals, one frequently encounters both census and mark–recapture–recovery data. We show how a state-space model for census data in combination with the usual multinomial-based models for ring-recovery data provide estimates of productivity not available from either type of data alone. The approach is illustrated on two British bird species. For the lapwing, we calibrate how its recent decline could be due to a decrease in productivity. For the heron, there is no evidence for a decline in productivity, and the combined analysis increases significantly the strength of logistic regressions of survival on winter severity.

KEY WORDS: *Ardea cinerea*; Birds; Census data; Herons; Kalman filter; Lapwings; Leslie matrix models; Maximum likelihood; Prediction; Productivity; Ring-recovery data; State-space; *Vanellus vanellus*; Winter weather.

1. Introduction

Monitoring programs for populations of wild animals employ various types of survey data, designed to quantify the different stages of the life cycle. A primary aim of mark–recapture–recovery studies is to estimate the annual survival probability, ϕ, of wild animals, which may vary with age and/or time. Examples are provided by Catchpole et al. (1998, 2000). Other studies estimate population size and indices of population size; we shall call the resulting data census data even though the data do not always estimate total numbers in a population. When census data are available, one might consider whether they are compatible with the estimated survival probabilities (cf., Kanyamibwa and Lebreton, 1992; Burnham, Anderson, and White, 1996). Integrated population models (Peach, Siriwardena, and Gregory, 1999; Siriwardena, Freeman, and Crick, 2001) incorporate survival rates into population models in an attempt to explain population declines. However, these approaches are piecemeal and ignore the sampling variability of the estimators of the demographic rates.

Census data contain information on survival, and this observation motivates our work. The advantages of our approach are that we model both data sets simultaneously, allowing accurate treatment of imprecision and correlation in the estimators, and we permit stochastic, rather than deterministic, population evolution. We form a combined likelihood that integrates both census and ringing information and obtain parameter estimates that maximize the combined likelihood. At the center of our strategy is a state-space model for population data. An appealing feature of the joint analyses that we shall present is that they do not require the census and ringing periods to coincide exactly. We illustrate the performance of the procedure with two extensive data sets.

2. Data

We analyze data on two important British bird species, the northern lapwing, *Vanellus vanellus,* and the grey heron, *Ardea cinerea.* We provide two examples because they support models of differing complexity, illustrate the flexibility of the modeling, and are representatives of two different kinds of census data. The lapwing in Britain has been declining for several years (Tucker, Davies, and Fuller, 1994) and has been placed on the Amber list of species of conservation concern in Britain (Gibbons et al., 1996). It can be regarded as an indicator species for farmland birds. Although not declining, the heron, as a top predator, is also an important bioindicator. For both of the species, we use national figures derived from data maintained by the British Trust for Ornithology (BTO). Naturally, therefore, if we try to relate survival to winter conditions, we can at best only expect an approximate relationship between estimates of survival and weather covariates. This is in contrast with more geographically restricted studies using local weather conditions, as in Catchpole et al. (2000).
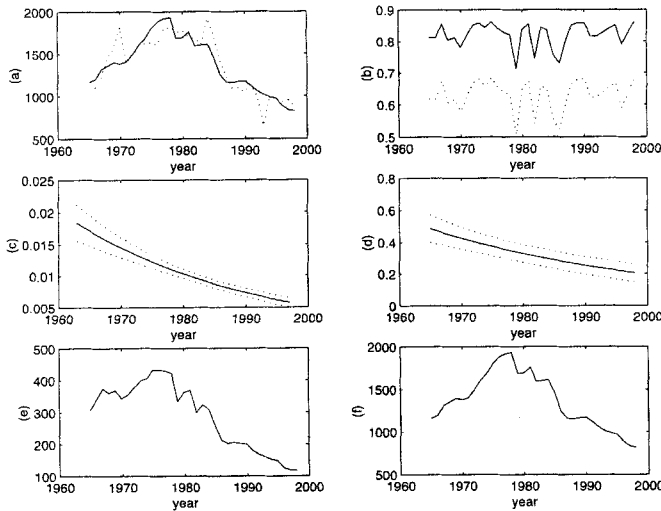
Figure 1. The result of fitting model $\phi_1(fdays)$, $\phi_a(fdays)/\lambda(year)/p(year)$ to the lapwing data. **a.** Observed census data (dotted line); fitted curve (solid line). **b.** $\hat{\phi}_a$ (solid line); $\hat{\phi}_1$ (dotted line). **c.** $\hat{\lambda}(year)$, with estimated 95% confidence bands. **d.** $\hat{p}(year)$, with estimated 95% confidence bands. **e.** Graph of $\hat{N}_{1,t}$. **f.** Graph of $\hat{N}_{a,t}$, equivalent to fitted curve in (a).

2.1 Bird Census Data

A key difference between the two species is that, for the more abundant lapwing, the census data we use are an index, derived from the Common Birds Census (CBC) (Marchant et al., 1990). Annual territory counts are made at a number of survey sites, and from these an index is estimated from a generalized linear model (Ter Braak et al., 1994); Fewster et al. (2000) have used a generalized additive model. Typically, most sites are not surveyed each year, resulting in many missing observations. The lapwing index is available from 1965 to 1998, and it is plotted in Figure 1a. By contrast, the heron census count estimates the total numbers of breeding pairs in England and Wales (Stafford, 1979). It was established in 1928 (Nicholson, 1929a,b) and is the longest running bird census in the world. We use the figures from 1928 to 1998, which are plotted in Figure 5a. Both sets of census data are printed in Besbeas et al. (2001a).

2.2 National Ring-Recovery Data

Each year, birds of both species are ringed as young throughout Britain, and records are kept of the total numbers ringed each year and of when birds are reported dead. For both species, we ignore the negligible amounts of data from the ringing of adult birds. We analyze the data on lapwings ringed as chicks during the years 1963–1997. A subset of these data corresponding to the ringing years, 1963–1992, have been analyzed by Catchpole et al. (1999), and we shall mention their findings later.

We also analyze the data on herons ringed as nestlings during the years 1955–1997. Previous modeling of British heron survival has been done by North and Morgan (1979) and Freeman and North (1990), and we shall make comparisons with their results later. The analyses presented here are the first estimates of British heron survival since 1990.

The recovery data are available from http://stat.tamu.edu/Biometrics/.

2.3 Weather Data

Because we are dealing with national ring-recovery data, we shall investigate relationships between model probabilities and measures of central England weather. There are several of these that might be used (cf., Catchpole et al., 1999). For instance, monthly temperatures are available from http://www.cru.uea.ac.uk/~mikeh/datasets/uk/cet.htm and daily temperatures can be obtained from http://www.badc.rl.ac.uk. We have undertaken detailed backward elimination of weather variables separately for each of the species of this article. The resulting picture is a complex one, which we shall report in a separate article. Our objective in this article is to demonstrate how well our combined analysis procedures work. For simplicity, therefore, we shall just use for each species the number of days in a year when the temperature was below freezing, *fdays*. This measure is calculated for central England and is mean centered for use in logistic regressions in the article. For year i, *fdays* measures the number of days below freezing between April of year i and March of year $(i + 1)$ inclusive. Thus, e.g., the largest value of *fdays* for the period is for the 1962/1963 winter. The weather regressions we present can be somewhat improved by the more detailed analysis mentioned above, especially regarding the timing of cold periods.

3. Models and Results

For both of the species, we shall not conduct an extensive model-selection exercise, which will be done in other articles.

3.1 Lapwing Data

We follow Catchpole et al. (1999), who analyzed the recovery data for the period 1963–1992. Their model incorporated separate first-year and adult annual survival probabilities, ϕ_1 and ϕ_a, respectively, and a reporting probability λ, which was a decreasing function of time; ϕ_1 and ϕ_a were logistic functions of measures of autumn and winter weather, respectively. For the recovery data, the likelihood, $L_r(\phi_1, \phi_a, \lambda)$, is a product of appropriate multinomial distributions.

In order to model the census data, we shall construct a separate likelihood using the Kalman filter. The CBC index is indicative of fluctuations in agricultural lowland England (Fuller, Marchant, and Morgan, 1985); however, we can treat it as an estimate of the total population of lapwing territories for the 447 sites of the survey. Let $N_{1,t}$ denote the number of 1-year old female birds at time t and $N_{a,t}$ denote the number of female birds aged ≥ 2 years at time t. We shall assume that breeding starts at age 2 (Cramp and Simmons, 1983), that all breeding birds and no others are censused, and that there is no emigration. If p denotes the annual productivity of females per female, then we can write the state-space transition equation as

$$\begin{pmatrix} N_1 \\ N_a \end{pmatrix}_t = \begin{pmatrix} 0 & p\phi_1 \\ \phi_a & \phi_a \end{pmatrix} \begin{pmatrix} N_1 \\ N_a \end{pmatrix}_{t-1} + \begin{pmatrix} \epsilon_1 \\ \epsilon_a \end{pmatrix}_t.$$

The matrix used here is the familiar Leslie matrix (Leslie, 1945) from population ecology. The annual indices, $\{y_t\}$, are related to the population level by the corresponding measurement equation, which is given as $y_t = (0, 1) \times (N_{1,t}, N_{a,t})' + \eta_t$. Thus, we denote the index at time t as

Table 1

Maximum-likelihood parameter estimates from fitting the model $\phi_1(fdays), \phi_a(fdays)/\lambda(year)/p(year)$ to the lapwing data (i) using ring-recovery data alone and (ii) using both the ring-recovery data and the census data. The estimated standard errors result from inverting a numerical approximation to the Hessian matrix at the maximum-likelihood estimate.

		Parameter estimates		Estimated standard errors	
		(i)	(ii)	(i)	(ii)
ϕ_1	Intercept (β_0)	0.5158	0.5231	0.0675	0.0672
	Slope	−0.0241	−0.0228	0.0072	0.0070
ϕ_a	Intercept (δ_0)	1.5011	1.5210	0.0683	0.0690
	Slope	−0.0360	−0.0279	0.0051	0.0045
λ	Intercept	−4.5668	−4.5632	0.0350	0.0350
	Slope	−0.5729	−0.5841	0.0641	0.0636
p	Intercept (p_0)	—	−1.1513	—	0.0880
	Slope	—	−0.4323	—	0.0743
σ		—	159.4691	—	21.8712

y_t, assumed to be normally distributed with variance $\sigma^2_{\eta_t}$. We shall assume that we can approximate $N_{1,t}$ and $N_{a,t}$ as independent normal random variables and evaluate the variances of $\epsilon_{1,t}$ and $\epsilon_{a,t}$ by respective Poisson and binomial expressions. Thus, $\text{var}(\varepsilon_{1,t}) = p\phi_1 N_{a,t-1}$ and $\text{var}(\varepsilon_{a,t}) = \phi_a(1 - \phi_a)(N_{1,t-1} + N_{a,t-1})$. Sullivan (1992) and Newman (1998) have also used this kind of approach. (For the examples of this article, there is virtually no difference from using two binomial approximations.) This approximation prevents us from having to introduce unknown error variances, which may not be estimable. In order to simplify and obtain a set of estimable parameters, we also restrict $\sigma^2_{\eta_t} = \sigma^2$ for all t. Thus, the likelihood for the census data is written as $L_c(p, \phi_1, \phi_a, \sigma)$. In this likelihood, the parameters p and ϕ_1 only appear as a product. However, ϕ_1 also occurs in L_r, and so we may obtain a full-rank model, in which all parameters may in principle be estimated, from the joint likelihood, $L_j(\phi_1, \phi_a, \lambda, p, \sigma) = L_r(\phi_1, \phi_a, \lambda)L_c(p, \phi_1, \phi_a, \sigma)$. The assumption of independence made here is not likely to be violated. The general specification of a census data likelihood by a Kalman filter is given in the Appendix. We have fitted to the lapwing data the model $\phi_1(fdays)$, $\phi_a(fdays)/\lambda(year)/p(year)$, which indicates that both ϕ_1 and ϕ_a are logistic functions of the single covariate, $fdays$. Alternative link functions might also be used. Additionally, we let $\lambda(year)$, $p(year)$ denote, respectively, logistic and logarithmic regressions of λ and p on year. The maximum-likelihood point estimates from the joint data and also from the recovery data only are given in Table 1.

We can see that the joint analysis changes slightly the maximum likelihood estimates, as now the estimates describe both the data sets. There is little difference between the standard errors of the common parameters in the two analyses due to the dominance of the ring-recovery data. This will also be seen to be the case for the heron data. If we repeat the analysis with a subset of the recovery data, we find that the joint analysis produces substantially reduced estimates of standard error compared with the ring-recovery ones. An

example of this is provided in Besbeas et al. (2001b). For the ring-recovery data alone, due to the long run of the data, correlations between parameter estimators are typically quite small, ranging from −0.20 to 0.29. The addition of the census data has little effect on those correlations. However, there are now correlations of −0.49 between $\hat{p}_0$ and $\hat{\beta}_0$ and of −0.91 between $\hat{p}_0$ and $\hat{\delta}_0$, where p_0, β_0, and δ_0 are defined in Table 1. These are sensible findings because increasing p requires a decrease in survival to match the data. We would also expect a stronger result with the intercept estimate of the adult survival, $\hat{\delta}_0$, as found here.

We show in Figure 1 the results from maximizing the combined likelihood L_j. The confidence bands shown result from applying the δ-method. The decline of λ with time agrees with Catchpole et al. (1999) and more generally with Baillie and Green (1987). However, of greater interest to us is the time-varying behavior of ϕ_1, ϕ_a, and p. We can see that the decline in lapwing numbers since 1980 is compatible with a major drop in the productivity parameter p. An alternative explanation of the recent decline in lapwing numbers is that there is a decline in survival probability over time. There was no evidence for this in Catchpole et al. (1999) or for the more extensive ring recovery data set analyzed here (see Table 2, section (i)).

We can see from Table 2, section (ii) that, when we analyze the combined data, then alternative descriptions of the data result from constant p and declining probabilities of survival over time. Detailed studies of breeding lapwings have shown a decrease in chicks produced over the period. This is usually attributed to the switch from spring to autumn sowing of cereals and intensification of pasture management (see Wilson, Vickery, and Browne, 2001, and references therein). Thus, in order to demonstrate model performance, we shall here only consider the model $\phi_1(fdays), \phi_a(fdays)/\lambda(year)/p(year)$.

We show in Figure 2 the regression of $\hat{\phi}_1$ and $\hat{\phi}_a$ on $fdays$ combined with plots of $\hat{\phi}_{1,t}$ and $\hat{\phi}_{a,t}$ resulting from a model with separate ϕ_1 and ϕ_a parameters for each year, denoted by $\{\phi_{1,t}\}$ and $\{\phi_{a,t}\}$, respectively. These regressions are seen to provide a fair description of the relationship between annual survival and $fdays$. A model in which ϕ_1 and ϕ_a share a common slope parameter produces virtually no change to the likelihood.

Shown in Figure 1e is the smoothed estimate of $N_{1,t}$ (see Appendix). This demonstrates the large decline in $N_{1,t}$ in recent years, in line with the predicted fall in p in this model.

We do not provide a formal test of goodness-of-fit of the model, but in Figure 3, we plot the observed numbers of recoveries against the fitted numbers and also provide a Q-Q plot of the prediction errors from the Kalman filter, which are expected to have a normal distribution. In the latter case, the single large prediction error is due to the initial census value and is to be expected because of the way in which the Kalman filter analysis is initiated. Overall, there is no serious indication of lack of fit.

For any species, ecologists are interested in estimating $r_t = (N_{t+1}/N_t)$ (see Nichols and Hines, 2002), where N_t is the total population size at time t. Whichever of the two alternative models we select for the data, we obtain the same estimate of r_t. We plot $\log(\hat{r}_t)$ in Figure 4. Estimating the standard

Table 2

The results from fitting by maximum likelihood a range of models to the lapwing data. In (i), we fit only the ring-recovery data; in (ii), we fit both ring-recovery and census data. Here ℓ denotes the value of the log likelihood evaluated at the maximum likelihood estimate of the parameters. The AIC denotes the Akaike Information Criterion and $\triangle AIC$ indicates the difference between the model AIC value and the smallest AIC value. In (ii), we show in bold type the AIC values corresponding to alternative possible models for the combined data set, with $\triangle AIC \leq 2$.

Model	$-\ell$	No. of parameters	AIC	$\triangle$AIC
(i)				
$\phi_1(fdays), \phi_a(fdays)/\lambda(year)$	7156.33	6	14,325	
$\phi_1(fdays, year), \phi_a(fdays, year)/\lambda(year)$	7155.16	8	14,326	
(ii)				
$\phi_1(year), \phi_a(year)/\lambda(year)/p$	7409.54	8	14,835	52
$\phi_1(fdays), \phi_a(fdays)/\lambda(year)/p$	7398.40	8	14,813	30
$\phi_1(fdays), \phi_a(fdays, year)/\lambda(year)/p$	7382.37	9	**14,783**	—
$\phi_1(fdays, year), \phi_a(year)/\lambda(year)/p$	7401.14	9	14,820	37
$\phi_1(fdays, year), \phi_a(fdays, year)/\lambda(year)/p$	7381.45	10	**14,783**	—
$\phi_1(year), \phi_a(year)/\lambda(year)/p(year)$	7409.29	9	14,837	54
$\phi_1(fdays), \phi_a(fdays)/\lambda(year)/p(year)$	7383.38	9	**14,785**	2
$\phi_1(fdays), \phi_a(fdays, year)/\lambda(year)/p(year)$	7381.99	10	**14,784**	1
$\phi_1(fdays, year), \phi_a(fdays)/\lambda(year)/p(year)$	7383.36	10	14,787	3
$\phi_1(fdays, year), \phi_a(fdays, year)/\lambda(year)/p(year)$	7381.45	11	14,786	3

errors for the curves of Figure 4 is not straightforward, but these could be obtained from a bootstrap approach.

3.2 *Heron Data*

For various reasons, such as their relative sizes, the reporting rates for herons are greater than those for lapwings. This

allows us to fit a more complex survival age structure. The transition equation is

$$\begin{pmatrix} N_1 \\ N_2 \\ N_a \end{pmatrix}_t = \begin{pmatrix} 0 & p\phi_1 & p\phi_1 \\ \phi_2 & 0 & 0 \\ 0 & \phi_a & \phi_a \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_a \end{pmatrix}_{t-1} + \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \\ \epsilon_a \end{pmatrix}_t,$$

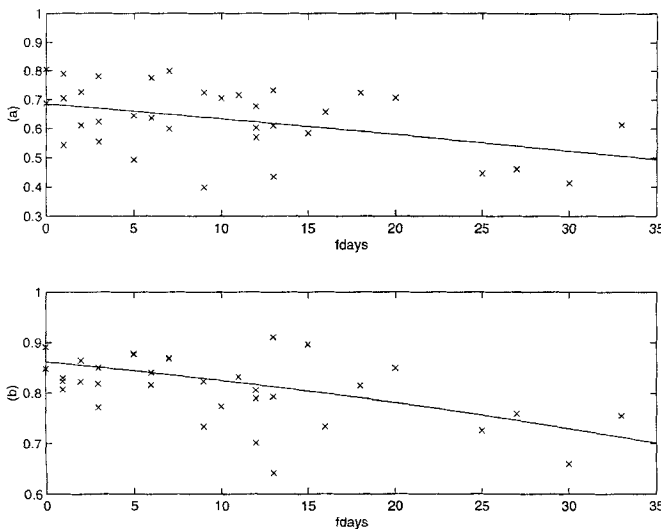where $N_{2,t}$ is the number of female herons of age 2 at time

Figure 2. A graphical demonstration of the logistic regressions of ϕ_1 and ϕ_a in the model, $\phi_1(fdays)$, $\phi_a(fdays)/$ $\lambda(year)/p(year)$, for the lapwing data. In (a), we graph $\hat{\phi}_1$, and in (b), we graph $\hat{\phi}_a$. Also plotted are the values $\{\hat{\phi}_{1,t}\}$ and $\{\hat{\phi}_{a,t}\}$, respectively, corresponding to having a separate value for ϕ_1 and ϕ_a for each year (see text).
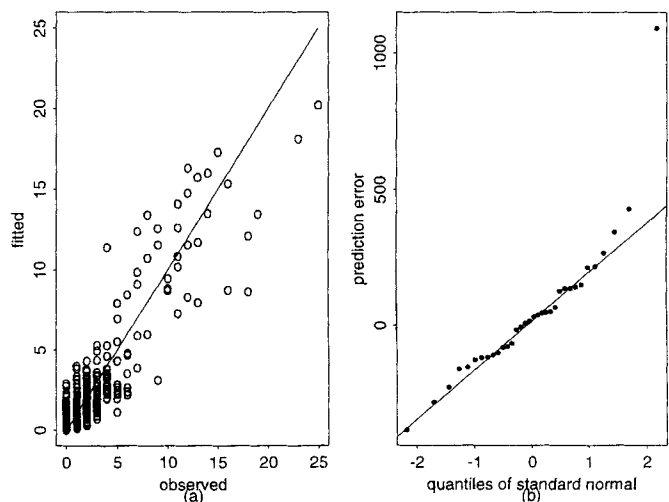
Figure 3. Graphical checks of goodness-of-fit of the model $\phi_1(fdays), \phi_a(fdays)/\lambda(year)/p(year)$ for the lapwing data: (a) observed numbers plotted versus expected numbers for the recovery data; (b) a Q-Q plot of the prediction errors from the Kalman filter.
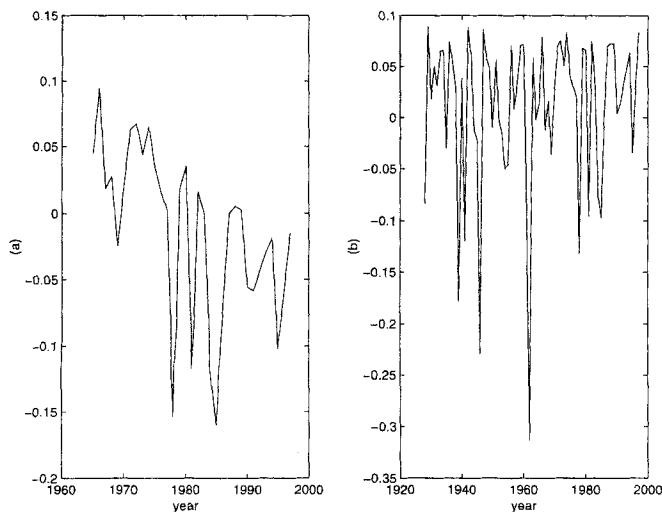
Figure 4. Plots of $\log(\hat{r}_t)$ for (a) lapwings and (b) herons.

t and $N_{a,t}$ is the number of female herons of age >2 at time t. The same normal approximations are made here as for the lapwing case.

The corresponding measurement equation is then $y_t = (0, 1, 1)(N_{1,t}, N_{2,t}, N_{a,t})' + \eta_t$. Thus, in this model, we assume that, in the annual census, what are counted are nests constructed by birds aged ≥ 2. We also give the 2-year-old and adult age classes equal productivity, p, which is again the number of females produced by a female. The analysis then follows the same lines as above. We fit a similar model viz $\phi_1(fdays), \phi_2(fdays), \phi_a(fdays)/\lambda(year)/p(year)$, but we now find that regression of p on year is not significant. When this model is fitted with constant productivity, we get $\hat{p} = 0.9551(0.0671)$, in contrast with the much lower values for the lapwings, shown in Figure 1. As a result, although the heron population is particularly susceptible to winters with long periods of freezing, it always rebounds quickly when winters are less severe. The survival estimates, shown in Figure 5, are, by contrast, substantially lower for herons than for lapwings. Although the fit to the census data is unable to match the full extent of the two major population crashes of the period, the general agreement is very good. We can see from Figure 5d that, for all t, $\hat{N}_{a,t} > \hat{N}_{1,t} > \hat{N}_{2,t}$. It is interesting to note from Figure 5d how $\hat{N}_{1,t}$, $\hat{N}_{2,t}$, and $\hat{N}_{a,t}$ vary over time. We note especially how the particularly cold winter of 1962/1963 affects the different fractions of the population differentially, both in magnitude and in timing. Regressions of $\hat{\phi}_1$, $\hat{\phi}_2$ and $\hat{\phi}_a$ on $fdays$, together with $\{\hat{\phi}_{1,t}\}$, $\{\hat{\phi}_{2,t}\}$, and $\{\hat{\phi}_{a,t}\}$, are in Besbeas et al. (2001a) and are similar in appearance to those in Figure 2.

These new analyses reveal significant regressions of both ϕ_2 and ϕ_a on $fdays$. The parameter estimates and their estimates of standard error are given in Table 3. We note from Table 3 that $|\hat{\beta}| > |\hat{\gamma}| > |\hat{\delta}|$, indicative of a greater sensitivity to $fdays$ in younger birds. However, as with lapwings, the change in log likelihood with the parallel regression model of $\beta = \gamma = \delta$ is minimal (0.67). It is noticeable that the combined analysis reduces the standard errors of $\hat{\beta}, \hat{\gamma}$, and $\hat{\delta}$ (cf., Table 1). For $\hat{\gamma}$ and $\hat{\delta}$, this combines with an increase in absolute terms in
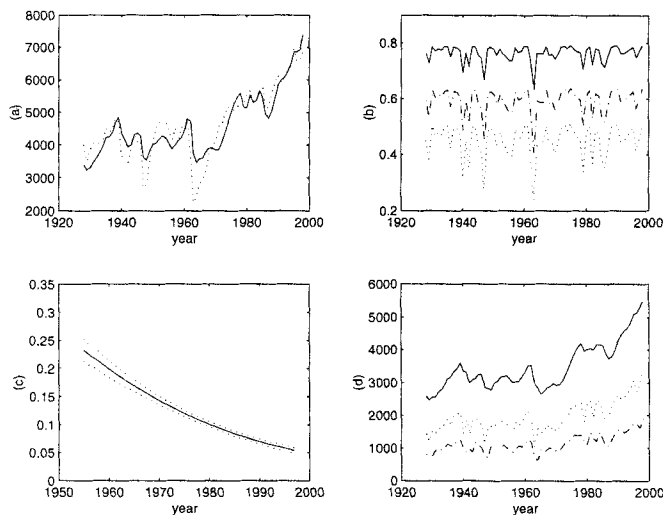

Figure 5. The result of fitting model $\phi_1(fdays)$, $\phi_2(fdays)$, $\phi_a(fdays)/\lambda(year)/p$ to the heron data. **a.** Observed census data (dotted line); fitted curve (solid line). **b.** $\hat{\phi}_a$ (solid line); $\hat{\phi}_2$ (dash-dotted line); $\hat{\phi}_1$ (dotted line). **c.** $\hat{\lambda}(year)$, with estimated 95% confidence bands. **d.** Graphs of $\hat{N}_{a,t}$ (solid line); $\hat{N}_{2,t}$ (dash-dotted line); $\hat{N}_{1,t}$ (dotted line).

the point estimates, leading to increased significance of the regressions. Likelihood-ratio test statistics of the hypothesis that $\gamma = \delta = 0$ are 9.74 and 34.34 for just the recovery data and for the combined data, respectively. Previous modeling of British heron survival (North and Morgan, 1979; Freeman and North, 1990) had $\gamma = \delta = 0$. With the greater power resulting from the larger data sets of this article, we can conclude that severe winters affect heron survival at all ages, and the significance of this result is greatly increased when the combined data are used.

Similar comments can be made regarding goodness-of-fit

Table 3

Maximum-likelihood parameter estimates from fitting the model $\phi_1(fdays), \phi_2(fdays), \phi_a(fdays)/\lambda(year)/p$ to the heron data (i) using ring-recovery data alone and (ii) using both the ring-recovery data and the census data. The standard errors are estimated as described in the caption to Table 1.

		Parameter estimates		Estimated standard errors	
		(i)	(ii)	(i)	(ii)
ϕ_1	Intercept	-0.2024	-0.1908	0.0480	0.0476
	Slope (β)	-0.0309	-0.0217	0.0054	0.0048
ϕ_2	Intercept	0.3745	0.3842	0.0725	0.0725
	Slope (γ)	-0.0155	-0.0166	0.0068	0.0060
ϕ_a	Intercept	1.1655	1.1871	0.0701	0.0701
	Slope (δ)	-0.0110	-0.0140	0.0052	0.0038
λ	Intercept	-2.0309	-2.0294	0.0254	0.0254
	Slope	-0.8302	-0.8337	0.0461	0.0460
p		—	0.9551	—	0.0671
σ		—	464.7502	—	43.4774

and parameter estimators as was done for lapwings (Besbeas et al., 2001a). The graph of $\log(\hat{r}_t)$ is given in Figure 4b. The contrast between the two populations is striking.

4. Information

If one fits the $\phi_1, \phi_a/p$ model to the census data sets alone, then it is possible to obtain maximum-likelihood estimates of the parameters, ϕ_a, σ, and the product $\theta = (p\phi_1)$. However, this three-parameter model is near-singular (Catchpole, Kgosi, and Morgan, 2001). At the maximum, the Hessian matrix has eigenvalues (0.196, 12.398, 5100.159) and (0.688, 30.015, 1709.015) for the lapwing and heron data, respectively. The presence of the small eigenvalues suggests that the corresponding likelihood surfaces are somewhat flat. The profile likelihood contours for θ and ϕ_a indicate a close relationship between the estimators of θ and ϕ_a. As the census data likelihood does not provide strong information on θ and ϕ_a, it is therefore not surprising that we cannot discriminate between alternative models for p for the lapwing case. However, it is therefore particularly interesting that we can estimate p from the joint analysis. Furthermore, if one considers just the parameters in the survival parts of the models illustrated in this article, then the ratio of the determinants of the generalized variance using only ring-recovery data to the same from the joint analysis is 1.37 for lapwings and 5.53 for herons. As there are 4 (6) survival parameters for lapwings (herons), to obtain values on a per-parameter basis, we may take 1/4 and 1/6 roots of these values, respectively, to get 1.0826 and 1.3298. For the longer heron data set, therefore, there is an appreciable benefit in analyzing the combined data. The information in the census data can be expected to depend on σ as well as on the length of the data and how many fractions of the population are observed. We see from Tables 1 and 3 that $\hat{\sigma} = 159.47$ and $\hat{\sigma} = 464.75$ for lapwings and herons, respectively. These values appear to be the right order of magnitude because, after fitting a smoothing spline to the census data, the standard deviation of the residuals is 132 and 288 for lapwings and herons, respectively.

5. Discussion

We have shown how one can combine in a single analysis census and ring-recovery data. The work extends naturally to encompass recapture and integrated recovery and recapture data (cf., Catchpole et al., 1998; Lebreton et al., 1995). The work has been illustrated on data from two major studies and has produced new and sensible results. We tried fitting a model containing a parameter to link directly y_t to $N_{a,t}$ instead of assuming that $E(y_t) = N_{a,t}$. However, the linking parameter was estimated at a boundary of the parameter space. It appears that it is not possible within the current framework to estimate parameters of this kind. We shall investigate how to use the fitted models to predict population developments in the future. However, the work presented here will also be extended in a large number of alternative ways. For instance, we can undertake detailed variable selection rather than just using *fdays*; we can let p and λ vary with age; for lapwings, we can use a change-point approach to detect the time point at which the decline in productivity began, provide separate analyses for sites of different habitat, and use raw site data rather than the results of a generalized linear model fitted to the site data; for herons, we have experimented with

adding time trends to the model presented here. This suggests that, after the population crash of 1963, there may have been an increase in ϕ_2, but this possibility requires further study; we can also give the work a full Bayesian context. There needs to be a study of when the normality approximation might breakdown and the possible bias that may then result. We are aware also that treatment of nonlinear and nonnormal state-space models is an area of on-going research. However, by far the most exciting development is to incorporate nest-record data, supplied by the BTO. This produces a third likelihood component, making use of models such as those of Pollock and Cornelius (1988) and Aebischer (1999), and provides independent information on some components of the productivity, p. Such an analysis will provide an integrated population model, which unites three of the major national surveys carried out at the BTO. All of the possibilities mentioned here are topics of current research. The computer programs used in the work of the article are all written in MATLAB and are available on request from the first author. The computational challenge of analyzing together data sets that singly would be analyzed by different programs and packages is solved by making appropriate multivariate normal approximations, described in Besbeas et al. (2001b).

RÉSUMÉ

Dans les études sur les animaux sauvages, on rencontre fréquemment des données de marquage-recapture et de recensement. Nous montrons comment un modèle à espace d'état pour les données de recensement, combiné à des modèles classiques de type multinomial pour des données de marquage-récupération, fournit des estimations de productivité qui ne pourraient être obtenus à partir d'un seul type de données. Cette approche est illustrée à partir de deux espèces d'oiseaux d'Angleterre. Pour le vanneau, nous mesurons comment son récent déclin peut être du à une baisse de productivité. Pour le héron, il n'y a pas d'argument pour une baisse de productivité, et l'analyse combinée accroî t significativement la puissance des régressions logistiques de la survie sur la rigueur hivernale.

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APPENDIX

Kalman Filter Theory

Suppose we observe the univariate time series, $\{y_t, 1 \leq t \leq T\}$, to which we want to fit a model, with parameter vector $\boldsymbol{\theta}$.

If we let $Y_T = (y_1, y_2, \ldots, y_T)$, the likelihood $L(\boldsymbol{\theta}; Y_T)$ for the parameter vector $\boldsymbol{\theta}$ may be shown to be

$$L(\boldsymbol{\theta} \mid Y_T) = p(Y_T \mid \mathbf{N}_0, \boldsymbol{\theta})$$

$$= \left\{ \prod_{t=2}^{T} p(y_t \mid Y_{t-1}, \mathbf{N}_0, \boldsymbol{\theta}) \right\} p(y_1 \mid \mathbf{N}_0, \boldsymbol{\theta}), \quad (A.1)$$

where $\mathbf{N}_0$ is the initial state vector and $p(y_t \mid Y_{t-1}, \mathbf{N}_0, \boldsymbol{\theta})$ is the conditional distribution of y_t given all the observations at time $t - 1$, i.e., Y_{t-1}. We make the customary vague prior assumptions with regard to $\mathbf{N}_0$ (Harvey, 1989, p. 121).

In the general case, the conditional distributions in (A.1) can be calculated recursively via the Kalman filter (see Harvey, 1989, p. 162–165), although they may have to be evaluated numerically using, e.g., the method of Kitagawa (1987). See also Durbin and Koopman (2000). However, if the transition and measurement errors in the model are normally distributed, the conditional distribution of y_t given Y_{t-1} is also normally distributed. It is therefore characterized by its first two moments, which are given directly by the usual form of the Kalman filter (Harvey, 1989, p. 105–106). Furthermore, the likelihood function of (A.1) may be recast as follows:

$$\log L(\boldsymbol{\theta} \mid Y_T)$$

$$= -\frac{T}{2} \log 2\pi - \frac{1}{2} \sum_{t=1}^{T} \log f_t - \frac{1}{2} \sum_{t=1}^{T} \frac{(y_t - y_{t|t-1})^2}{f_t},$$

where $y_{t|t-1}$ and f_t can also be obtained from the Kalman filter. This expression is sometimes known as the prediction error decomposition form of the likelihood.

The fitted values of Figures 1 and 4 result from smoothing the Kalman filter estimates (Harvey, 1989, p. 154).