

THE POTENTIAL OF INTEGRATED POPULATION MODELLING[†]

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Summary

Recent work has shown how the Kalman filter can be used to provide a simple framework for the integrated analysis of wild animal census and mark–recapture–recovery data. The approach has been applied to data on a range of bird species, on Soay sheep and on grey seals. This paper reviews the basic ideas, and then indicates the potential of the method through a series of new applications to data on the northern lapwing, a species of conservation interest that has been in decline in Britain for the past 20 years. The paper analyses a national index, as well as data from individual sites; it looks for a change-point in productivity, corresponding to the start of the decline in numbers, considers how to select appropriate covariates, and compares productivity between different habitats. The new procedures can be applied singly or in combination.

Key words: census data; Common Birds Census; habitat differences; Kalman filter; lapwings; Leslie matrix models; maximum likelihood; multivariate normal approximation; productivity; ring-recovery data; state–space models; *Vanellus vanellus*; variable selection.

1. Introduction

The aim of recent research by Besbeas *et al.* (2002b) and Besbeas, Lebreton & Morgan (2003) has been to provide an integrated analysis of different types of census and demographic data on animals of the same species. We have observed that ecological data analysis is often piecemeal, involving separate studies of fecundity, survival and population size, and sometimes no attempt to check that the results from the different analyses are compatible. When such checks are made, they are typically ad hoc. Besbeas *et al.* (2002b) considered census and survival information for two British bird species. Some of the census information came from the Common Birds Census (CBC) of the British Trust for Ornithology (BTO); see Marchant *et al.* (1990 pp.3–11). In the CBC, annual territory counts are made at a number of survey sites, and an index is constructed from them to indicate changes in national populations. In this paper, we analyse CBC data from 1965–1998 on the northern lapwing (*Vanellus vanellus*). The CBC started in 1962, but the recording procedure only became standardized in 1965, and for this reason we exclude any observations made in the years 1962–1964.

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Besbeas *et al.* (2002b) devised a state–space model for the lapwing census data, and formed a likelihood by means of the Kalman filter, using appropriate normal variables to approximate binomial and Poisson random variables. A combined likelihood was then formed by multiplying together the census likelihood and a likelihood from a ring-recovery study of survival; this implies independence between the two component datasets, which is a requirement that is often satisfied. The parameter estimates that resulted from maximizing the combined likelihood then provided a simultaneous description of both datasets. State–space modelling of census data alone has been considered by various authors — see e.g. Freeman & Kirkwood (1995), Newman (1998) and Borchers, Buckland & Zucchini (2002 Chapter 13).

The elements involved in forming the census likelihood are illustrated here:

$$\begin{bmatrix} N_{1t} \\ N_{at} \end{bmatrix} = \begin{bmatrix} 0 & p\phi_1 \\ \phi_a & \phi_a \end{bmatrix} \begin{bmatrix} N_{1,t-1} \\ N_{a,t-1} \end{bmatrix} + \begin{bmatrix} \epsilon_{1t} \\ \epsilon_{at} \end{bmatrix}.$$

Here, N_{1t} and N_{at} denote the numbers of one-year-old female birds and female birds aged ≥ 2 years at time t respectively, and ϕ_1 and ϕ_a are respectively the annual survival probabilities of birds in their first year of life and of adults. We define $N_t = (N_{1t}, N_{at})$ and $N_t = N_{1t} + N_{at}$. The parameter p denotes the annual productivity of females per female, and the ϵ terms are errors, with variances which are given by suitable Poisson and binomial expressions, since we assume that $(N_{1t} | N_{t-1}) \stackrel{d}{=} \text{Pn}(p\phi_1 N_{a,t-1})$ and $(N_{at} | N_{t-1}) \stackrel{d}{=} \text{Bi}(N_{t-1}, \phi_a)$. Thus $\text{var}(N_{1t} | N_{t-1}) = p\phi_1 N_{a,t-1}$ and $\text{var}(N_{at} | N_{t-1}) = N_{t-1}\phi_a(1 - \phi_a)$. We assume no sex effect on survival and that breeding starts at age 2. The matrix above is a familiar Leslie matrix. We observe y_t , which in our initial analyses of the lapwing data was the CBC index, given by the measurement equation $y_t = (0, 1)^T(N_{1t}, N_{at}) + \eta_t$. We assume an observation error $\eta_t \stackrel{d}{=} N(0, \sigma^2)$. In some cases (see Section 3) it may be sensible for σ^2 to vary with $\{y_t\}$, but for an index we expect a constant variance to be appropriate.

We can see that the productivity parameter p cannot be estimated from the census data alone; it appears only in the census likelihood, where it is confounded with the parameter ϕ_1 . However, the survival probability ϕ_1 is also present in the likelihood from analysis of the ring-recovery data, allowing us to estimate p from the combined analysis. This is very useful, as the productivity of a species in decline is a parameter that we particularly want to investigate. In some cases, as is true of the lapwing, we also have information on breeding success, from which we can produce a further separate likelihood on aspects of fecundity, that can be combined with the likelihoods for census and survival data to give a single likelihood for maximization. From unpublished studies, we have examples for the lapwing and for the linnet (*Carduelis cannabina*), another British species in decline. The data for these studies have been provided by the BTO, and the combined analysis can bring together in a single coherent study the data from three of the main surveys carried out by the BTO. We have found the combined analysis technique to be useful also for analysing data on teal (*Anas crecca*), grey seals (*Halichoerus grypus*) and Soay sheep (*Ovis aries*). See Besbeas, Kershaw & Morgan (2002a) and Besbeas *et al.* (2002c,d). An interesting feature of the grey seal analysis was that the census was the result of an aerial survey of pups, which can be identified by their white coats. Thus for seals, the young, not the breeding animals, were observed.

The combined likelihood approach described above has a potential deficiency in the way the separate component likelihoods are constructed and combined, for maximization. Combined analysis can be difficult when the component likelihoods are programmed in a range of different computer languages, by different authors. A solution to this problem is provided

by a further approximation, suggested and evaluated by Besbeas *et al.* (2003). Here, a multivariate normal approximation is adopted for the form of the likelihood of the survival data, making use of the parameter estimates and their corresponding estimates of error obtained from analysing the survival data alone. This means that particular programs or packages for survival and also for fecundity data need only be run once, to obtain the maximum-likelihood estimates of relevant parameters and their estimates of standard error and correlation. Besbeas *et al.* (2002d) give an example of an analysis using the multivariate normal approximation for a long-running study of Soay sheep on the island of Hirta in the St Kilda archipelago off the north-west coast of Scotland. The study provides a wealth of census, survival and fecundity information. The sheep are uniquely marked after birth by means of ear tags. In this case, the survival information results from a mark–recapture–recovery research program that takes place in the Village Bay study area of Hirta, whereas the population data are obtained from a census of the whole island. The disparity between the two areas justifies the assumption of independence needed when the census and survival likelihoods are multiplied together. Modelling sheep fecundity can be a complex procedure, as the sheep may twin, and the production of lambs can be a function of the age of the mother and of external factors such as the severity of the winter weather and the population pressure. In integrating the three different types of data for Soay sheep, multivariate normal approximations were made for both the fecundity and survival datasets. Additionally, as sheep census data are available for lambs, as well as male and female adults, it was possible to use a multivariate Kalman filter procedure.

We now explore further uses of the combined analysis, when considering different aspects of the lapwing data.

2. Accounting for different habitats

2.1. The data

Now that we can estimate productivity of lapwings, it is interesting to consider how productivity might vary with habitat. The CBC data arise from sites which may be classified as arable, grazing, mixed (i.e. grazing and arable) or ‘other’ (which are not farmland and could include estuaries, for example). We analyse indices that result from a generalized linear model analysis (ter Braak *et al.*, 1994) which estimates site effects (s_i for site i) and year effects (t_j for year j). We convert these indices into annual index values $\{y_j\}$ by means of the formula

$$y_j = \sum_i \exp(s_i + t_j).$$

This procedure is necessary because the CBC data are the result of surveys by volunteers, and over a period of some 35 years there are bound to be large numbers of missing values in the overall $year \times site$ database, a point to which we return in Section 3 of the paper. For example, the grazing index was based on 92 sites and 34 years, and there were 2417 missing values. The arable index was based on 46 sites and 34 years, and there were 1273 missing values. For illustration here we give detailed analysis of only the grazing and arable sites, and discuss the complete set of results later; the resulting indices are plotted in Figure 1. The study by Besbeas *et al.* (2002b) used CBC data from all 447 sites, and the arable and grazing sites account for just 138 of those. A further 183 sites are designated as mixed, 119 are designated as ‘other’, and the remaining seven are not specified and not analysed here.

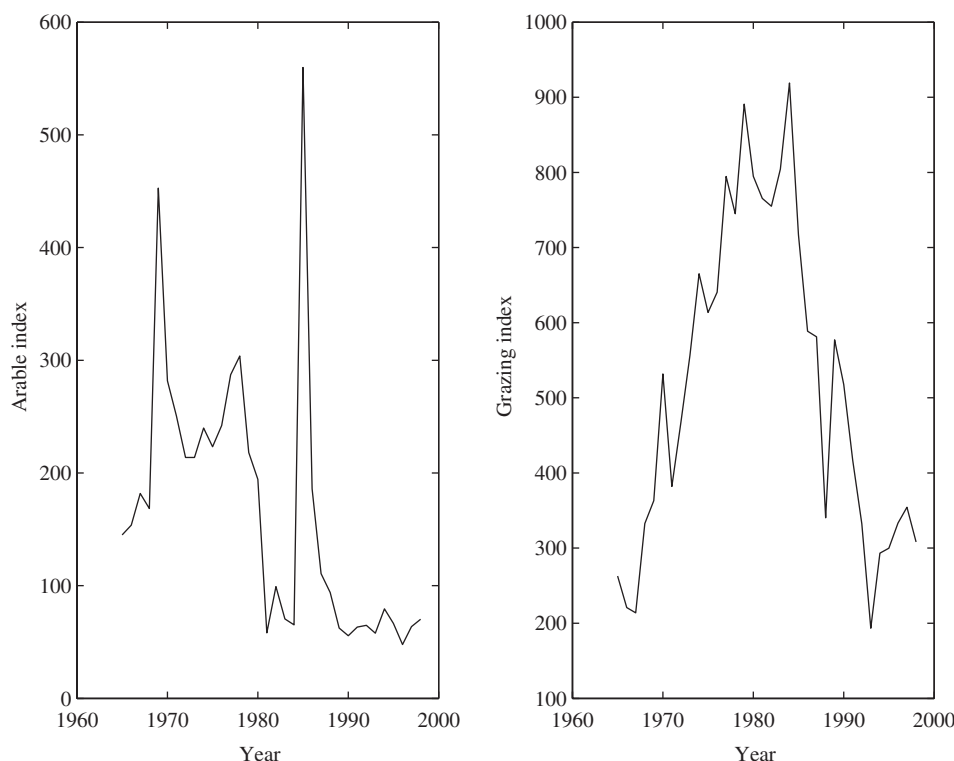


Figure 1. The CBC indices plotted separately for grazing and arable sites. The CBC index is sometimes given relative to a baseline year. As shown here, it is an estimate of the total population of lapwing territories for the corresponding sites of the survey (see text).

Both graphs in Figure 1 reveal some years in which there were large index values, relative to neighbouring years, and this is especially true of the arable index. There does not appear to be a biological explanation of these large changes; they may possibly be due to local movements of birds responding either to changes in cropping patterns or severe weather conditions in other parts of the country. It is possible that the indices may amplify small changes in the raw data. Here we take the CBC index values at face value.

2.2. The model

We form a combined likelihood for the case in which the ring-recovery component estimates overall survival, and does not produce a breakdown with regard to habitat. Accordingly, we use the state–space model given below, using superscripts A and G to indicate arable and grazing, respectively. Let $N_t = (N_{1t}^A, N_{at}^A, N_{1t}^G, N_{at}^G)$ and $y_t = (y_t^A, y_t^G)$, then

$$N_t = MN_{t-1} + \epsilon_t, \quad y_t = HN_t + \eta_t,$$

where $M = \begin{bmatrix} 0 & p^A\phi_1 & 0 & 0 \\ \phi_a & \phi_a & 0 & 0 \\ 0 & 0 & 0 & p^G\phi_a \\ 0 & 0 & \phi_a & \phi_a \end{bmatrix}$ and $H = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$.

Here, N_{1t}^A , for example, is the number of one-year-old female lapwings born, and assumed subsequently to breed, on arable land at time t , etc. Thus the model now assumes different productivities for arable sites, p^A , and grazing sites, p^G , and it also has different observation error standard deviations, σ^A and σ^G . Maximizing the likelihood from this model is equivalent to maximizing the product

$$L_c(\phi, p^A, \sigma^A; \mathbf{y}^A) L_c(\phi, p^G, \sigma^G; \mathbf{y}^G),$$

where $\phi = (\phi_1, \phi_a)$, \mathbf{y}^A (\mathbf{y}^G) denote all the observations on arable (grazing) sites over time. The subscript c indicates that the likelihood is being constructed for the relevant index alone, which is more computationally efficient. The likelihood can readily be extended to deal with more than two habitat types. This likelihood is then multiplied by the ring-recovery likelihood $L_r(\phi, \lambda)$, where λ represents the reporting probability of rings from dead birds; parameter estimates result from maximizing the combined likelihood. In the following we specify models by explicitly listing their parameters and indicating the variables those parameters are regressed on. For survival and reporting probabilities we use linear logistic regression, whereas for the productivity rates we use linear logarithmic regression. Previous modelling of lapwings (Catchpole *et al.*, 1999; Besbeas *et al.*, 2002b) suggests that it would be interesting to fit a model based on:

$$\phi_1(fdays), \phi_a(fdays), \lambda(year), p^A(year), p^G(year).$$

Here $fdays$ measures the number of days when a central England temperature was below freezing for each year running from April to the following March, and $year$ provides a regression on time.

2.3. Results

The results from fitting this model are given in Table 1. Besbeas *et al.* (2002b Section 4) show that for the lapwing data the survival information from the ring-recovery study, which spans 34 years, dominates the estimation of survival from the combined analysis; this is also true for (a) and (b) in Table 1. However, we can see that for the arable sites, although the productivity declines over the period, the decline is far less than for the grazing sites. We can formally test for equality of productivity between the two types of habitat, and when we do that we obtain a likelihood-ratio test-statistic of 14.7 on 2 degrees of freedom, which is highly significant. There is no evidence of a non-zero slope in the arable case, and refitting the model with zero slope only changes the likelihood by 1.18. The estimates of observation error variance for arable and grazing sites separately are substantially smaller than the corresponding estimate when all the sites are taken together, as would be expected. They may also be taken as equal (reduction in maximized log-likelihood of less than 1). The resulting estimates are illustrated in Figure 2. The fitted values of Figure 2 and corresponding later figures result from smoothing the state vector estimates (Harvey, 1989 p. 154).

The difference between arable and grazing productivity identified here is in line with the findings of Chamberlain & Crick (2004) and it is of current biological interest. Since the mid-1970s there has been a drive for greater efficiency in British farming. This has resulted in the use of more insecticides, the removal of hedges to provide bigger fields, and more autumn sowing of crops (Chamberlain *et al.*, 2000). Following these changes there has been a decline in the numbers of many species of farmland birds, including lapwings. On the basis of our

TABLE 1

The results from fitting the model $\phi_1(fdays)$, $\phi_a(fdays)$, $\lambda(year)$, $p^A(year)$, $p^G(year)$ to ring-recovery data and census index data on lapwings, where for the census index data we only use sites which are designated as either arable or grazing for the length of the study. We show the maximum-likelihood parameter estimates for (a) $p^A(year) \neq p^G(year)$, (b) $p^A(year) = p^G(year) = p(year)$, and (c) the values from Besbeas et al. (2002b), when all the sites are used. With the exception of the observation error standard deviations, here and later, estimates are given on the appropriate transformed scale (either log or logistic). Estimated standard errors are obtained from inverting the observed Fisher information, and are shown in parentheses.

		(a)	(b)	(c)
ϕ_1	Intercept	0.519 (0.068)	0.518 (0.068)	0.523 (0.067)
	Slope	-0.024 (0.007)	-0.024 (0.007)	-0.023 (0.007)
ϕ_a	Intercept	1.510 (0.069)	1.507 (0.068)	1.521 (0.069)
	Slope	-0.031 (0.005)	-0.031 (0.005)	-0.028 (0.005)
λ	Intercept	-4.565 (0.035)	-4.566 (0.035)	-4.563 (0.035)
	Slope	-0.579 (0.064)	-0.579 (0.064)	-0.584 (0.064)
p^A	Intercept	-1.403 (0.201)		
	Slope	-0.535 (0.392)		
p^G	Intercept	-1.090 (0.095)		
	Slope	-0.981 (0.133)		
p	Intercept		-1.110 (0.094)	-1.151 (0.088)
	Slope		-0.910 (0.126)	-0.432 (0.074)
σ^A		96.969 (12.007)	111.466 (14.785)	
σ^G		84.581 (11.481)	86.034 (11.920)	
σ				159.469 (21.871)

results, we hypothesize that, although intensification has continued, any deleterious effects on lapwing productivity on arable land were greatest at the start of the time period covered in this paper. On grassland, however, there has been a relatively recent increase in the intensity of grazing (Chamberlain & Crick, 2004), which may have resulted in the loss of rough grass, and also produced more trampling and predation as a result. This ties in with the suggestion of McKeever (2003), that lapwings need heterogeneity in grassland, in the form of short grass for nesting and foraging but longer grass for protection.

When we also include data from mixed and 'other' sites, there is little change to the present results and we find that productivity on mixed sites parallels that on arable sites, whereas productivity on 'other' sites parallels that on grazing sites. These major differences in productivity have not been reliably demonstrated before. When dealing with national data, as here, one should realize that overall measures, such as of productivity, may be averaging out interesting differences at a finer scale, and it may be possible to obtain the finer scale in several different ways.

3. Analysing raw CBC data

3.1. The raw data

Few sites have many years when lapwings were recorded in appreciable numbers. We consider here just three such sites, with official CBC site numbers 146, 862 and 881. The data for those sites are presented in Table 2.

We use the integrated analysis approach to analyse raw CBC data for those three sites. The approach is similar to that of the last section, except that we are now using raw numbers,

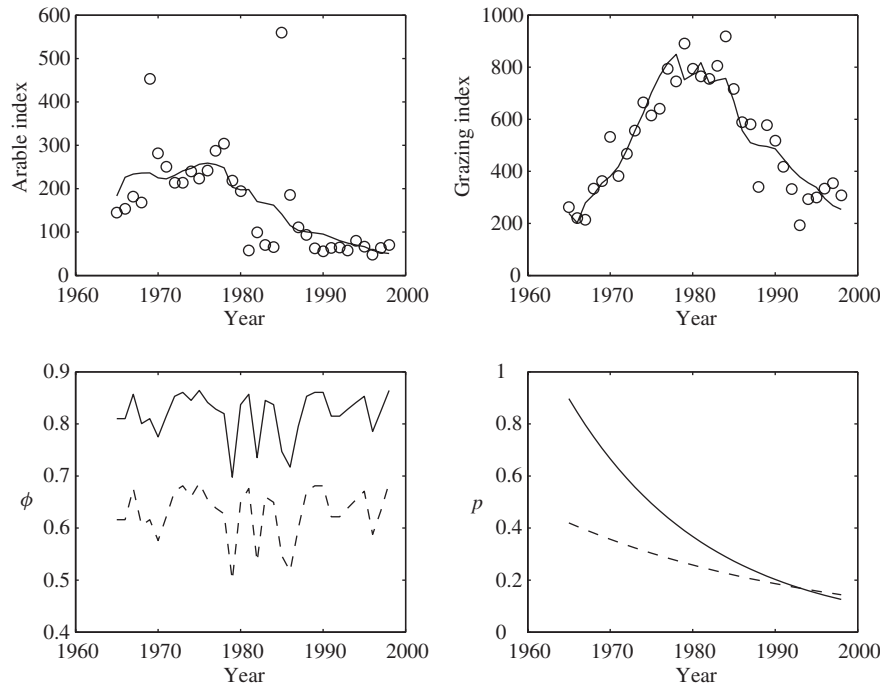


Figure 2. Graphs summarizing the fits to the ring-recovery data and the separate arable and grazing indices of Figure 1. For the indices, the observed values are given as circles and the fitted values are given as solid lines. In both cases these are the number of birds aged > 1. Also shown are the estimates of the productivity for the two types of site (p^A is given by the dashed line and p^G is given by the solid line), and also the estimates of ϕ_1 and ϕ_a (where $\phi_1 < \phi_a$).

TABLE 2
Counts of lapwing territories on individual CBC sites 146, 862 and 881.
A ‘–’ indicates that no count took place during that year.

Year	CBC site			Year	CBC site		
	146	862	881		146	862	881
1965	–	–	–	1982	12	29	6
1966	–	–	–	1983	14	39	5
1967	–	–	–	1984	16	33	2
1968	–	10	–	1985	15	33	9
1969	–	12	–	1986	3	41	4
1970	–	17	–	1987	3	34	6
1971	–	18	–	1988	4	3	4
1972	–	8	–	1989	1	28	4
1973	1	19	–	1990	4	30	13
1974	2	19	7	1991	2	14	19
1975	2	16	8	1992	2	6	13
1976	2	25	8	1993	1	11	7
1977	4	37	5	1994	1	12	8
1978	6	39	4	1995	1	10	11
1979	11	47	5	1996	5	–	6
1980	10	41	10	1997	8	–	6
1981	8	48	5	1998	2	–	3

TABLE 3

Maximum-likelihood estimates for parameters when we perform a combined analysis of raw count data for sites 146 (productivity p^{146}), 862 (productivity p^{862}) and 881 (productivity p^{881}). In (a) we assume a common observation error variance, whereas in (b) the observation error variance is site-specific. Estimates of standard error are shown in parentheses.

		(a)	(b)
ϕ_1	Intercept	0.516 (0.067)	0.516 (0.068)
	Slope	-0.024 (0.007)	-0.024 (0.007)
ϕ_a	Intercept	1.498 (0.067)	1.502 (0.067)
	Slope	-0.033 (0.005)	-0.035 (0.005)
λ	Intercept	-4.567 (0.035)	-4.567 (0.035)
	Slope	-0.576 (0.064)	-0.574 (0.064)
p^{146}	Intercept	-0.924 (0.318)	-0.662 (0.245)
	Slope	-2.228 (1.253)	-2.246 (0.828)
p^{862}	Intercept	-1.018 (0.167)	-1.060 (0.177)
	Slope	-1.394 (0.427)	-1.443 (0.497)
p^{881}	Intercept	-1.184 (0.385)	-1.089 (0.326)
	Slope	0.238 (0.808)	0.123 (0.662)
σ^{146}			2.244 (0.306)
σ^{862}			7.698 (1.240)
σ^{881}			3.195 (0.608)
σ		4.821 (0.509)	

rather than indices. In view of the overall sparsity of the CBC data, it is attractive to be able to perform a combined analysis of individual site data. In this instance, for lapwings, we only analyse three sites, but for other species one could envisage analysing many more. In this case, the census part of the combined likelihood takes the form given by

$$L_c(\phi, p^{146}, \sigma^{146}; y^{146}) L_c(\phi, p^{862}, \sigma^{862}; y^{862}) L_c(\phi, p^{881}, \sigma^{881}; y^{881}),$$

where p^i , σ^i and y^i denote the productivity, observation error standard deviation and counts, respectively for the i th site, $i = \{146, 862, 881\}$.

3.2. Results

A likelihood-ratio test of equality of error variances for the three sites produces a test-statistic of 26.54 on 2 degrees of freedom, which is highly significant. In contrast, from Table 1 we can see that there was no evidence that the arable and grazing sites had different error variances. It is interesting to observe the effect of assumptions of equality of error variances on the parameter estimates and the estimated standard errors, provided in Table 3. When we incorrectly assume equal error variances, then only site 862 appears to have a productivity parameter with a slope that is significantly different from zero. However, when we have distinct error variances, then only site 881 appears to have constant productivity. We can see, from Table 2, that the counts on the three sites have different ranges, and the estimates of the different error variances directly reflect these differences of range. Forcing the error variances to be the same gives sites 146 and 881 (especially site 146) larger variances than the counts themselves suggest is appropriate, which biases the estimation of the slopes of p^{146} and p^{881} , as well as inflating their estimates of standard error.

The results of the modelling are displayed in Figure 3. The estimates of ϕ_1 and ϕ_A are indistinguishable from those of the last section, and so are suppressed here.

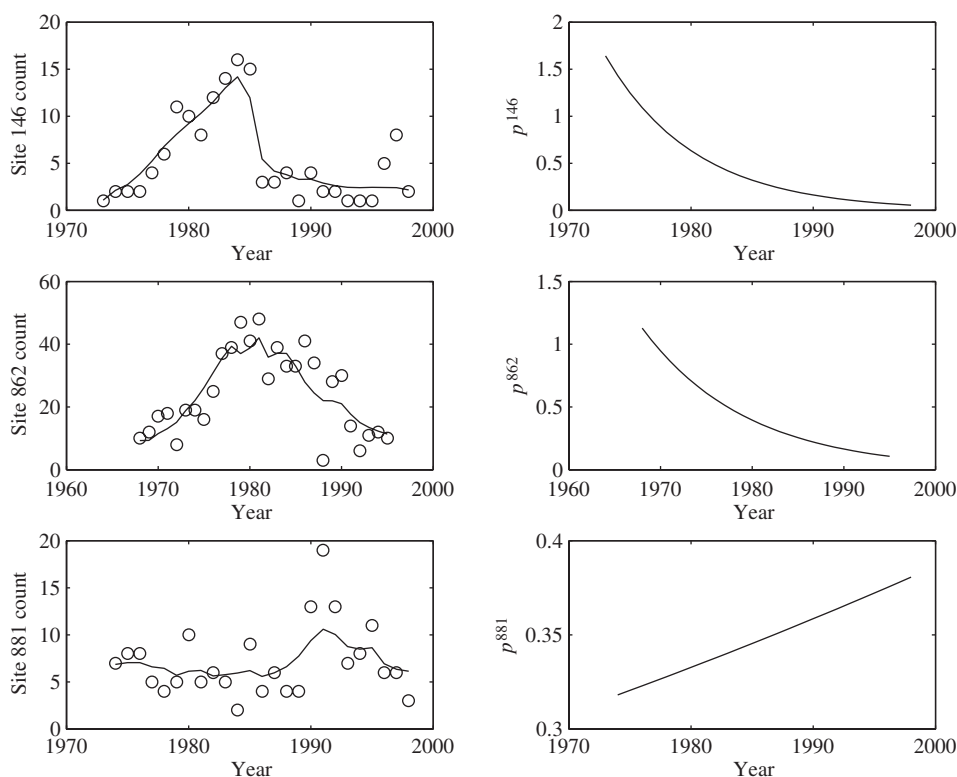


Figure 3. Graphs summarizing the fits to the raw counts on the three sites, nos 146, 862 and 881. As in Figure 2, the observed counts on the three plots are shown as circles and the fitted values are shown as solid lines. In both cases these are the number of birds aged > 1 . Also shown are the estimates of productivity for each site.

Once again, we observe that there are significant differences in productivity, in this case between sites. Site 146 is an estuarine site, site 862 is a grazing site, and site 881 is a mixed site. Hence the site-level analysis is consistent with the analysis of the last section, in that the grazing and estuarine sites have strongly declining productivity, and the mixed site does not.

When dealing with raw counts, rather than indices, it might be sensible for the observation error variance to vary over time, and to be taken as proportional to the count each year, or perhaps the square of the count. With either of these approaches there is a downward shift in the fitted census curves of Figure 3, as the Kalman filter procedure places greater emphasis on small counts, with relatively small variances, and there are consequent changes in the estimates of productivity. We have found for this application that taking the variance proportional to the count squared is not as good as taking the variance proportional to the count, which we recommend for problems of this kind. However for the data of Table 2, the conclusions regarding productivity do not change when the variance is proportional to the count.

4. Switching productivity

One aspect of the results of Table 1 is that the reporting probability of dead animals exhibits a steady decline over time. This is a regularly reported fact (see e.g. Catchpole *et*

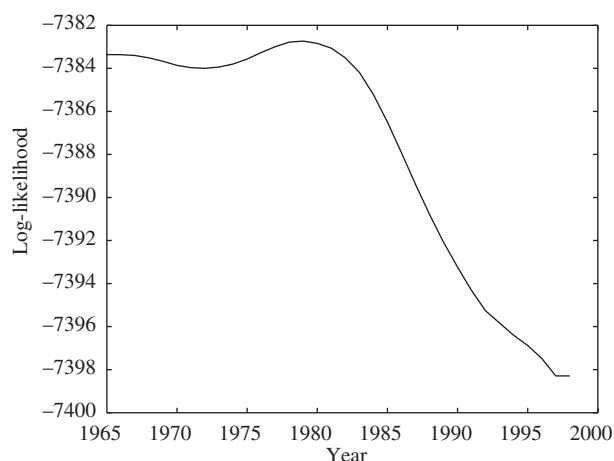


Figure 4. The log-likelihood for the model with a switching year for productivity. Here the log-likelihood is plotted against the year when the switch is assumed to be taking place. Note that the models with the switch year at 1995 or 1996 are possibly singular, whereas the model with the switch in 1997 is singular (the productivity for 1997 cannot be estimated uniquely).

al., 1999; Baillie & Green, 1987). However, the decline in productivity of birds might be attributable to changes in farmland practice, and it is interesting to see whether there is any evidence in the data that might allow us to pinpoint when such changes had an effect on lapwing productivity. We can, therefore, assume constant productivity up to a certain time-point, and then a logarithmic decline over time since then. In Figure 4, we show the log-likelihood resulting from assuming such a switching model, and how it changes as one changes the year of switching.

Here we are analysing the CBC indices, for all the plots in the dataset. While this identifies 1979 as the switch year with the largest likelihood, we can see from Figure 4 that there is very little difference in log-likelihood between having a switch year in 1979 and not having one at all. There is increasing evidence, from 1983 onwards, that there is an earlier decline in productivity which would not be captured by a switch later than 1983. We show in Figure 5 the results from assuming a switch year in 1979; parameter estimates are given in Table 4.

5. Selection of covariates

Above, and in earlier papers on using the Kalman filter, we have used the number of annual frost days, *fdays*, as a measure of winter severity. However, this has been for convenience, especially as we wanted to make a comparison between lapwing and grey heron (*Ardea cinerea*) analyses, so that using the same single covariate was helpful. However, for lapwings, Catchpole *et al.* (1999) considered a range of possible weather covariates, and selected between them using score tests. This was feasible because they divided each year into three main periods, namely the breeding season, April–June, the autumn period, July–October, and the winter period, November–February. We have looked more closely at the single measure of frost days, on a monthly basis, for the months of November, December, January, February and March, and we have used backward elimination to reduce the number of months needed for each of the logistic regressions of ϕ_1 and ϕ_A . In addition, we have considered whether

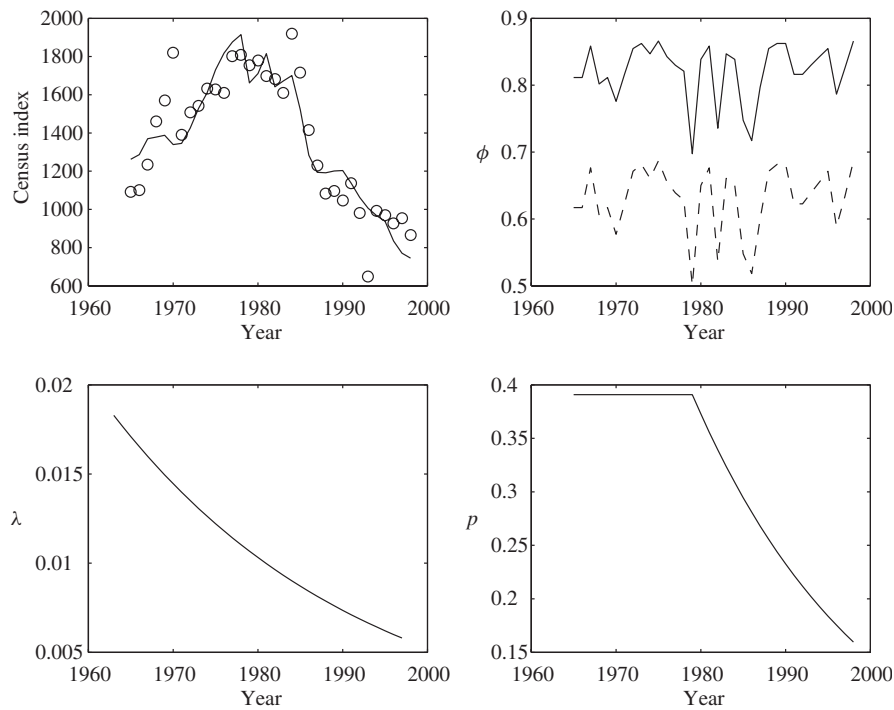


Figure 5. Graphs summarizing the fit to the entire census index, with a switching year at 1979. As in Figure 2, for the index, the observed values are given as circles and the fitted values are given as the solid line. Also shown are the reporting rate, λ , the productivity, p , and the two survival probabilities, ϕ_1 and ϕ_a , where $\phi_1 < \phi_a$.

TABLE 4

Maximum-likelihood estimates when (a) the switching year is 1979, compared to (b) the values from Besbeas *et al.* (2002b) in which there is a steady decline in productivity from the start of the study. Estimates of standard error are shown in parentheses.

		(a)		(b)	
ϕ_1	Intercept	0.522	(0.068)	0.523	(0.067)
	Slope	-0.024	(0.007)	-0.023	(0.007)
ϕ_a	Intercept	1.520	(0.069)	1.521	(0.069)
	Slope	-0.031	(0.004)	-0.028	(0.005)
λ	Intercept	-4.564	(0.035)	-4.563	(0.035)
	Slope	-0.581	(0.064)	-0.584	(0.064)
p	Intercept	-1.387	(0.118)	-1.151	(0.088)
	Slope	-0.448	(0.083)	-0.432	(0.074)
σ		160.837	(21.222)	159.469	(21.871)

it would be helpful to have a quadratic time-dependence of both λ and p , as Catchpole *et al.* (1999) used a quadratic dependence of λ on time. In our work we have analysed ring-recovery data from 1963–1997, in contrast to Catchpole *et al.* (1999) who analysed only the ring-recovery data from 1963–1992.

If we drop the February measure of frost days as a covariate for ϕ_1 , with an approximate Wald-test statistic of -1.74, then the final model, with no Wald-test statistics of less than

2.77 in absolute terms, just has linear time-dependence for both λ and p , a regression on December frost days for ϕ_1 , and regression on frost days for January, February and March for ϕ_a . This model has 11 parameters, and the maximized log-likelihood for the model is -7379.63 , producing an Akaike Information Criterion (AIC) value of 14 781. This contrasts with the corresponding model used earlier, which regresses ϕ_1 and ϕ_a on the annual number of frost days, $fdays$, producing a maximized log-likelihood value of -7383.36 , and, with nine parameters, an AIC of 14 785. Thus, from a purely numerical perspective, the model derived in this section appears to be slightly better than the simpler one used earlier. Additionally, it may have a biological interpretation: we are assuming in our models that lapwings breed from the age of 2 years. The birds can be expected to first encounter bad weather in the December of their first year of life, which may result in the weakest birds dying then. Also, first-year birds are not concerned with reproduction. Perhaps the influence of the January–March months on the survival of older birds might be related to preparations for breeding, or to the hypothesis that breeders and non-breeders winter in different geographical areas. Most British lapwings return to their natal area to breed. Similar conclusions have been drawn from repeating this exercise for grey herons.

6. Discussion

The approach described in this paper, combining likelihoods from different models to produce a single integrated analysis, provides an attractive synthesis of otherwise disparate aspects of modelling. However, the approach is based on normal approximations, and these could be inappropriate for numbers as small as some of those of Table 2. Nevertheless, we have seen in Section 3 that the results obtained are sensible and interpretable. Thus there is scope for studies of the robustness of these approximations. An alternative to using the Kalman filter to produce a likelihood for census data, if site counts are small, is to model directly the changes in site-occupancies using an appropriate mechanistic model. An example of this approach is provided by Upton & Lampitt (1981). Our multivariate normal approximation technique for the combination of likelihoods appears reasonably robust, but here too it should not be forgotten that approximation is involved.

We have used a classical approach to integrated modelling in this paper, based on the Kalman filter. The approach is relatively straightforward and computer programs written in MATLAB can be obtained from one of us (PB). We have made assumptions of linearity and normality. Durbin & Koopman (2001 Part II) is devoted to issues of nonlinearity and non-normality, and suggests approaches which can be used in those cases. Non-linearity can arise in studies of density dependence (see e.g. Thomas *et al.*, 2005). A simple way to relax the assumptions of both normality and linearity is to adopt a Bayesian approach to modelling, and this has been done for census data alone by Millar & Meyer (2000), Rivot (2003) and Thomas *et al.* (2005), typically making use of informative priors. The work of Section 3 of this paper has been replicated by Brooks, King & Morgan (2004). They have shown that even for counts as small as those of Table 2, modelling via the Kalman filter is remarkably robust with respect to the assumption of normality. We speculate that if nonlinear modelling is needed, then it may be possible to accommodate it within the standard Kalman filter framework by means of appropriate iterative methods.

A further interesting feature of the modelling of Section 3 has been the importance of checking model assumptions, for instance with regard to equality of error variances, when that is appropriate. Incorrect assumptions can produce biased results, and must be avoided. It

is common to assume homogeneity in models, and Section 2 has shown how the assumption of a common productivity for sites of different types can produce a useful working model, which may conceal interesting variation at a finer level of analysis.

A further aspect of the Kalman filter procedure which requires investigation is how important it is for the different datasets considered to be independent. For example, the census, survival and fecundity information that are available on the red deer (*Cervus elaphus*) studied on the Island of Rum, also off the west coast of Scotland, all relate to the same animals. One might anticipate that dependence would not appreciably affect parameter estimates, but would have some effect on estimates of standard error and correlation. For the models that have been considered in combination we have not undertaken model-selection in the integrated analysis. However, combining datasets improves power, and different models might be selected from within an integrated analysis, through the use of score tests for example (Catchpole & Morgan, 1996; Catchpole, Morgan & Boucher, 1997; Catchpole *et al.*, 1999). Our analyses of the data illustrated in Figure 1 assume that there is no movement of animals, but patterns in Figure 1 suggest that local movement may be taking place. The fitted curves from the Kalman filter procedure appear to describe the overall trends quite well. It would be interesting to extend the state–space models to try to incorporate both dispersal and movement between several different sites. It is a simple matter to include migration probabilities in the state–space formulation, and this would parallel the recent developments in multi-site capture–recapture modelling — see e.g. Schwartz, Schweigert & Arnason (1993) and Thomas *et al.* (2005).

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