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QUANTIFYING CHANGES IN ABUNDANCE WITHOUT COUNTING ANIMALS: EXTENSIONS TO A METHOD OF FITTING INTEGRATED POPULATION MODELS.

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Abstract

Integrated population modelling techniques combine information from population surveys and independent demographic studies to estimate population size, survival and productivity rates simultaneously. We review the development of the approach, and investigate further the potential to incorporate sources of population survey data other than those currently employed. Generally, the simpler the field protocol, the more data can be gathered; in the simplest case only a list of species encountered when a site is surveyed might be recorded. We extend the integrated approach to the case of presence/absence survey data from species lists. We consider specifically the extent to which high-quality demographic data, used in conjunction with an ecologically sound model, may result in credible estimates of change and the drivers of it in the context of either counts or presence/absence survey data. We propose an approach to practical model fitting, applicable in either context, using standard software and we illustrate its performance in practice. Examples are based on simulated data and records of species with very different trend and ecology, and they are used to compare approaches.

Introduction

A number of criteria are used to identify species or populations of conservation concern, and to motivate appropriate responses (see e.g. Eaton et al. 2008). Among these criteria, substantial long-term population decline is perhaps the most dependent upon statistical sampling, especially for species that remain widespread, and too common for the entire population to remain under close annual assessment over a long period. Most of the UK's declining farmland bird species, for instance, come into this category (Fewster et al. 2000), and analyses of survey data for these have acquired considerable strategic importance. In such cases, estimation of population size is rarely attempted, rather an index proportional to it is usually derived.

Once a declining species is identified, effective remedies require more detailed ecological study, specifically the identification of the stage(s) of the life-cycle causing the decline. This in turn requires a sampling study, and models describing the data arising in terms of demographic parameters such as survival and reproduction. Such models require appropriate complexity, in terms of age-specific and temporal variability, to yield appropriate conclusions about the cause of decline. This, however, makes great demands on the gathering of sufficient data to support such models, and in practice it can be difficult to obtain enough information to provide precise estimates of all the parameters.

Over the last decade, a number of integrated approaches to sampling and modelling have been developed. These combine information from population size and demographic data, and tie the estimation of a trend, and the complex underlying

demography, into a single process. Specifically, Integrated Population Modelling (IPM) combines data gathered from two or more profoundly differing field protocols, uniting methodology from the areas of population and capture-recapture modelling. The end result is a model for population change being constructed from demographic parameters. Both the distribution of the annual counts, and that of the demographic data, are thus parameterised in terms of common parameters, and these are estimated by modelling all sources of data simultaneously. The greater effective sample size of the combined data results in a potential for more precise estimates. Furthermore, an integrated approach provides estimates that are consistent between the different data sources, and has the advantage of being able to estimate parameters otherwise not estimable when analysing the separate sources alone.

We begin this paper with a brief review of IPM to date. We then consider further the contribution of the population survey data, with a view specifically to investigating the extent to which IPM can be adopted in analyses of survey data more limited in form than have been considered in previous publications. In a geographically closed population, all structural change can be attributed to mortality and reproduction. Thus, if all demographic rates in a biologically credible model for such a system were known to an unrealistic level of precision, population changes could be quantified directly from these, even in the absence of any additional data from a survey directly quantifying such change. One might consider then just how limited the survey data can become while the integrated approach, with demographic data on a substantial but realistic scale, remains viable. This is explored through both simulated data and data gathered on different species from established surveys in the UK; as the latter are made in count form, a comparison of methods for data of differing degrees of

complexity naturally arises. We conclude with a summary and discussion of the likely future developments in the area.

Integrated Population Modelling

A brief history

Developments in the estimation of both abundance and demography, and inference about the relationship between them, have developed over the past decade in both classical (Besbeas et al. 2002, 2003, 2005; Borysiewicz et al 2009; Tavecchia et al. 2009) and Bayesian (Brooks et al. 2004, 2008; Schaub et al. 2007; King et al. 2008) frameworks. See Schaub and Abadi (this volume) for a comprehensive bibliography regarding the prevalent models.

Originally, the approach adopted census information or a previously estimated index of abundance as subject to the subsequent fitting of a population model (Besbeas et al. 2002). For survey data arising from multiple sites, Besbeas et al (2005) introduced a single-stage approach for analysing the survey data directly that is feasible when the number of sites is small. Besbeas and Freeman (2006) and Cave et al (2010) provide methodology for fitting models to data from a much larger number of individual sites, also fitting the models directly to data at this finer resolution. A common feature of integrated methods to date is the use of count-based survey information. Here we examine the approach in Besbeas and Freeman (2006) further, and consider expansion to include data of a kind much less refined in nature – simple lists of sites at which a species was, or was not recorded. This type of data are much easier to obtain in large

quantities and may be the only data available for some species and locations, and this observation motivates our work.

Models for site-specific counts

Suppose annual counts C_{it} of a species of interest at site i, $i=1, \ldots, S$, are taken in the breeding season of year t, $t=1, \ldots, T$. These counts are typically modelled as independent Poisson observations with expected values μ_{it} dependent upon two factors, the site and the year, expressed as parameters s_i and y_t respectively, and additive on a log scale (Besbeas and Freeman, 2006; Freeman et al., 2007b; Cave et al., 2010):

(1)　　$C_{it} \sim Po(\mu_{it}), \quad i = 1,...,S, \ t = 1,...,T$

(2)　　$\log(\mu_{it}) = s_i + y_t.$

This model allows for geographical variation, but constrains the temporal trend to be the same at each site. For parameter identifiability, an arbitrary parameter such as y_1 or s_1 is constrained to zero.

Fitted counts under such a model can be added to produce an estimate of abundance across all sites, assuming perfect detectability. Alternatively, an index of relative abundance is derived as $Y_t \propto e^{y_t}$. In fitting an integrated model to these indices, successive values of Y_t are related by an appropriate population model containing demographic parameters, for at least some of which information from external sources of data is available. Many studies to date have concentrated upon passerine birds (Peach et al. 1999; Siriwardena et al. 2001; Freeman and Crick 2003; Freeman et al. 2007b; Cave et al. 2010) assumed to begin breeding at age one. Under an assumption

of no net movement between sites, and following the precedent in these papers a deterministic model of the general form:

$$(3) \qquad Y_{t+1} = Y_t \ (\phi_{at} + \phi_{1t} P_t), \quad t = 1,\ldots,T-1$$

is adopted. Here ϕ_1 and ϕ_a denote respectively the annual survival probabilities of newly-fledged and older (hereafter 'adult') birds, and P is the annual productivity of young (females per female). It is straightforward to show that:

$$(4) \qquad \log(\mu_{it}) = \ s_i + y_1 + k'_t, \quad i = 1,\ldots,S, \quad t = 1,\ldots,T,$$

where k'_t is the log-transformed cumulative growth since the start of the survey, expressed in terms of demographic parameters (see Freeman et al. 2007b):

$$(5) \qquad k'_1 = 0; \qquad k'_t = \sum_{j=1}^{t-1} \log \left(\phi_{aj} + P_j \phi_{1j} \right), \quad t = 1,\ldots,T.$$

The expected count at a site in year t is thus given by that in year 1 multiplied by a succession of annual proportional changes, cumulative values of which are given (log-transformed) by (5). This formulation allows us to fit the population model directly to the data from the sites, as we shall see below. The model in Eq. 4 can be regarded as a special case of the model in (2) where the y_t are unconstrained. In general, however, the resulting model is overparameterized and the demographic parameters in (3) are unidentifiable. Thus if these are brought into the model, substituting for the year effects y_t, then they are not estimable from the count data alone. However, an integrated approach in which the resulting likelihood from (1) combined with (4) is multiplied by likelihoods for independent sets of data, dependent upon the same demographic parameters, might be used to allow estimation of the full set of parameters. The principle extends to species requiring models of a more complex age-structure (Besbeas et al. 2002; Besbeas and Freeman 2006; Reynolds et al. 2009). We shall only consider the simple model (4) here; an account of further age-dependence,

and extension to stochastic versions of the deterministic model (3), is currently in preparation.

To date, dead recoveries of ringed birds have been the source of information on survival in several studies, and data of this kind will be assumed here for later simulations. Both data and model are assumed to follow a familiar form (e.g. White and Burnham 1999) in which recoveries of dead birds are classified by year of ringing and year of recovery and those of each cohort are assumed independently, multinomially distributed. In the present context, the model is parameterised in terms of the survival probabilities ϕ_1 and ϕ_a, shared with the population model, and an additional parameter λ, which is the probability of a marked bird being recovered and reported after death. The likelihood for the data is product multinomial in form - see Freeman and Morgan (1992) for details.

An extension to models for presence/absence data

IPM of the kind adopted for counts as above is in principle readily adapted in appropriate circumstances to the simpler case of annual records of presence/absence (P/A) at each site. Assuming the duration and field protocol at each site were kept constant, then even if the *numbers* of birds encountered in such a survey were not recorded, the assumption that they follow a Poisson distribution allows a model in which the probability that the species was absent from the record is given by:

(6)   *Pr*(Species not recorded at site *i* in year *t*) = *Pr*(C_{it} =0) = exp(-exp($s_i + y_t$))

The probability that a species is recorded is treated as equivalent to the probability that the count is not zero. A binomial likelihood with complementary log-log link function for binary data Z_{it}, recording whether a species was recorded (Z_{it}=1) or not (Z_{it}=0) at site *i* in year *t,* therefore follows (see also Wright 1991). The observations Z_{it} can either be fitted in terms of s_i and y_t, or the y_t , *t*>1, can be replaced via Y_t by a recursive population model such as (3) and the resulting likelihood multiplied by likelihoods for independent ringing data, or such demographic data as might be available, forming an integrated model.

A note on fitting integrated models

In the context of either count or P/A survey data, once annual changes are modelled via demographic parameters rather than as freely-estimated year effects, the model for the survey data becomes non-linear. While the number of demographic parameters in some models may be extensive, these can often be reduced by the use of covariates. However, large-scale surveys can cover hundreds of different sites, and the corresponding site effects make the likelihood for an integrated model a function of several hundred variables, complicating the iterative non-linear maximisation. We provide below an approach for facilitating model-fitting when the number of survey sites is large. For illustration, we consider hereafter data from the ringing and subsequent recovery of birds after death as the sole auxiliary data source, adopting models and notation accordingly. However, the approach is general and not restricted to incorporating ring-recovery data alone.

The motivation for this approach is based on the observation that while the model for the survey data is non-linear, it remains linear conditional upon any chosen set of values for survival and productivity. This provides a means of greatly accelerating the process of parameter estimation via a profile likelihood approach. Given a fixed set of values for the demographic parameters, the corresponding site and first year effects can be rapidly estimated by Iteratively Weighted Least Squares (IWLS) through fitting Eq. 4 as a generalized linear model (GLM) with k_t' as an offset. Maximum likelihood estimates of the demographic parameters then follow by maximising a combined profile likelihood. In particular, let (θ, η) be the full parameter set, where $\theta = (\phi_{1t}, \phi_{at}, P_t, \lambda) \in \Theta$ is the vector of parameters other than the site effects and y_1, the first year effect, themselves denoted collectively by $\eta = (s_i, y_1) \in H$. Given the joint likelihood of the demographic and survey data,

$$(7) \qquad L_j(\theta, \eta) = L_r(\theta) \times L_c(\theta, \eta)$$

where L_r and L_c denote respectively the demographic and (count or P/A) survey likelihood components, the profile likelihood of θ, given by

$$(8) \qquad L(\theta) = \max_{\eta} L_j(\theta, \eta) = L_j(\theta, \widehat{\eta_\theta})$$

is maximised with respect to θ to provide maximum-likelihood estimates of the parameters. Here $\widehat{\eta_\theta}$ are the MLE of η at a fixed value of θ, obtained by maximising $L_c(\theta, \eta)$ using IWLS. The appeal of maximising over Θ, albeit repeatedly, rather than directly optimising over $\Theta \times H$ is obvious when several hundred parameters are contained in η.

The iterative process is straightforward to implement in modern statistical packages with built-in GLM and generic function optimisation procedures. As the joint log-

likelihood value at convergence is available, it is a simple matter to compute likelihood ratio statistics or Akaike's Information Criteria of different models, though we do not consider model selection here.

Note that as most non-linear maximisation routines optionally return an estimate of the Hessian matrix, calculation of profile-based standard errors and covariances for the arguments of the maximised function, the demographic variables, readily follows. Although the GLM-fitting part of the algorithm also makes available standard errors for the site effects at the final iteration, these of course are not unconditional as they ignore the inherent uncertainty in the demographic parameters which, at each IWLS iteration, are regarded as fixed in the form of the offset. The site-specific parameters are, however, usually of much less ecological interest than their demographic counterparts. Once the latter are calculated, reconstruction of the estimated trend in abundance is also straightforward.

The integrated analyses in this paper were carried out this way in the R programming language (R Development Core Team 2011) using the generalized linear model ('glm') and Nelder-Mead simplex search method ('optim') functions (Nelder and Mead 1965).

Application and simulation studies

UK Bird and Butterfly surveys

The two most widely-monitored taxonomic groups in the UK are birds and butterflies. National monitoring of 'wider countryside' bird species began in the 1960s with the Common Birds Census (CBC) scheme, data from which have formed the subject of most integrated population modelling studies to date. The UK Butterfly Monitoring Scheme (UKBMS) began a little over ten years later (Pollard and Yates, 1993; Roy et al. 2007). Both studies are intensive, consisting of full territory counts and weekly line-transect counts respectively. As a consequence, long-term trends for these taxa are the most accurately estimated, and widely published, of all Britain's widespread terrestrial fauna. For higher taxa such as birds, demographic data are more easily collected, and we base a simulation study in the following section upon data mimicking a combination of count and ring-recovery data. The model of Equation (6) can however be fitted to annual presence-absence data in isolation. We begin by presenting examples based upon UKBMS data, from which we derive annual values C_{it} from sums of weekly counts, making possible a comparison between count-based and P/A-based monitoring.

Count data in isolation

We illustrate relative performance of the procedures using two common butterfly species, the Silver-Washed Fritillary *Argynnis paphia* and the Painted Lady *Vanessa cardui*. These were selected to illustrate different aspects of the modelling; Silver-Washed Fritillary is a localised woodland species, largely restricted to the South-West in the UK and sensitive in its habitat requirements (Asher et al. 2001; Thomas 2007). UKBMS sites that have recorded this species over the period 1980-2007 contain a total of 3531 annual records. In contrast, Painted Lady is a widespread migrant,

arriving from Africa in spring, sporadically in very high numbers (Asher et al. 2001; Thomas 2007). In such years it can be found in all habitats throughout the UK, and produce several broods in favourable conditions, hence exhibiting greater fluctuations between consecutive years than other British species. Over 8000 records from a comparable period are analysed for this species. Estimated population trends under both the Poisson model, fitted to the recorded counts, and the binomial model for data derived by collapsing these into simple records of annual presence/absence, are compared in Figure 1. Trends here are constrained to zero in the opening year, a common device adopted to facilitate easy assessment of decline over the duration of the survey.

Figure 1 shows that the binomial model remains reasonably adept in identifying major population fluctuations, despite the reduction in the informative content of the data. Although the resulting population trends from the two models are very similar in both species, the Poisson model is, of course, predictably more precise in terms of its associated standard errors, especially for the rarer Silver-Washed Fritillary. Here, the binomial confidence limits are particularly large for accurate population assessment. In each case, we have corrected standard errors for lack of fit by applying the standard quasi-poisson and quasi-binomial alternatives with dispersion parameters based upon the residual deviance (Crawley, 2006), rather than attempting here to refine the simple, two-factor model further. With the benefit of a greater number of observations, binomial confidence bounds for the Painted Lady index are much more informative, and partially encompass those from the Poisson model apart from two years where they do not overlap. This suggests that even with such large sample sizes,

count-based surveys still have considerable advantage over P/A surveys in accurately quantifying subtle, short-term changes.

UK butterfly species, with few exceptions, do not survive the winter in the adult state; taxa with greater overlap between generations offer scope to incorporate estimates of survival into the modelling, to inform the estimation of the trend. We investigate this in the next section by means of a simulation study.

Integrated population modelling – A simulation study

For each simulation study, 100 independent sets of ring-recovery and count survey data were generated and combined in pairs for analysis using integrated models for count-survey and ringing data. For comparison, the ring-recovery data were also analysed alone as well as in combination with P/A data obtained by collapsing down the survey data to this form.

The sample sizes and parameter values used to generate the data were selected to reflect values typically encountered in avian population ecology. In particular, three different scenarios were considered, each based on 100 survey sites and 30 years of coinciding survey and bird ringing data. The three scenarios are distinguished by the amounts of data in the census and ringing segments, in which (i) 2500 birds are ringed annually and site effects s_i are obtained by generating 100 random variables from a normal distribution $N(0.5, 0.25)$, (ii) 1000 birds are ringed and $s_i \sim N(0.5, 0.25)$ and (iii) 2500 birds are ringed and $s_i \sim N(1.5, 0.25)$. Thus Scenarios (i) and (ii) correspond to a

lower background count level compared to Scenario (iii) whilst (i) and (iii) feature a higher level of ringing than (ii). Other parameter values throughout were:

(9) $$\log it(\phi_{1t}) = -0.1 + 0.05 \times X_{1t}$$

(10) $$\log(P_t) = -0.4 - 0.06 \times X_{pt}$$

where $\{X_{1t}\}$ and $\{X_{pt}\}$ are two series of simulated values (random variables $\sim N(0,4)$) playing the role of environmental covariates. These two demographic parameters are the most likely to covary with environmental conditions in practice, and for simplicity we assume both ϕ_a (=0.7) and λ (=0.05) are constant in all scenarios, though it is not a modelling requirement that they are so.

For each replicate, the parameters in the integrated count-based and P/A-based models were estimated using the sequence of conditional GLM described above. Note that the simulated values of s_i, X_1 and X_p were kept at the same values within each set of 100 simulations, though these values were reset for (i), (ii) and (iii) and differed between the three scenarios. We have repeated the simulation exercise several times, using e.g. different starting values for the iterative process, and the results presented below are typical of the replicated runs.

In presentation, we concentrate largely upon the estimation of the slopes of the logistic or logarithmic regressions (8) and (9) of ϕ_1 and P on their environmental predictors, as the ecologically significant features of these artificial systems. The mean values and the precision of the slope estimates from the three scenarios are shown in Table 1. The individual slope estimates from the Poisson and binomial models under scenario (i) are shown in Figure 2. We can see that the parameters from the integrated count-based analyses are more precisely estimated, though the

corresponding P/A analyses still perform creditably given the simpler nature of the survey data adopted. There is little difference in estimation bias and precision for the slope of ϕ_1 between the integrated P/A analyses and individual recovery component analyses, but we are also able, when these data are combined, to estimate further important parameters such as productivity. The loss in estimation precision from using P/A as opposed to count data is seen to be greater for the slope of P than for ϕ_1 as expected, as information on P is derived from the survey data alone.

Under Scenario (ii) the scale of the survey data is unchanged but there are now fewer ring-recoveries compared to Scenario (i). As a consequence survival parameters are now less precisely estimated from the recovery analyses, resulting in turn in less precise estimation of population trend and demography by the integrated analyses. Indeed Figure 3 shows that both integrated models perform less well for estimating change in survival and productivity than in Scenario (i). In agreement with (i), the use of P/A data as opposed to counts results in greater precision loss for the slope of P (s.e. = 0.0041 as opposed to 0.0019) than for ϕ_1 (s.e. = 0.0027, versus the Poisson 0.0019). However the two integrated analyses provide similar precision values for the remaining parameters, including the intercept of P (not shown). We show in Figure 4a the individual estimates of the slope of ϕ_1 estimated three ways. We can appreciate from the off-diagonal offsets of the estimates that both types of survey data provide information on this parameter, resulting in a reduction in standard error from data combination compared with using the recovery data alone (see Table 1).

The third scenario however reveals an interesting difference. Here the survey counts are (on average) higher than in Scenario (i) but the information in the demographic

data is the same. The simulation results from this scenario are shown in Figure 5. We can see that the higher count level has improved the performance of the integrated count-based method, however the performance of the corresponding P/A method has deteriorated, especially for estimating change in P. This is because the effects of population change manifest more at high count levels, but these higher levels imply a smaller frequency of absences for the P/A method. As a result, a greater proportion of sites are expected to produce records of presence throughout, or almost throughout the series, making little or no contribution to the analysis. The effects of this are found to be more serious for productivity than for survival in our analyses (Table 1), as we do not incorporate direct demographic information on this parameter. The graph of the individual estimates for the slope of ϕ_1 is given in Figure 4b. The higher concentration of the integrated P/A estimates near the diagonal compared with the corresponding count-based estimates is striking, indicating the limited capacity of the P/A data to influence estimation in this case.

The relative efficiency of using P/A data compared with count information is, however, improved if a parameter is constant, rather than varying with a covariate. For illustration, we repeated the analyses of Scenarios (i)-(iii), but with the slope for productivity set to zero in both the data generation and the model-fitting. In this case, the (constant) productivity rate was well-estimated by both integrated analyses throughout, with the standard error from the P/A analyses only (i) 4.6% or (ii) 4.3% higher than that from their count-based counterparts at the two low count level scenarios. While this increased to 21.0% under Scenario (iii), this increase is still substantially lower than the almost 7-fold increase observed for the slope of P in Table 1(iii).

Discussion

Integrated analyses of disparate datasets have the potential to increase the flexibility and precision with which we can estimate changes in abundance, demographic parameters and the relationship between them. Recent developments permitting the models to be fitted directly to data collected from spatially separated sites, rather than to an index of abundance derived from them, extend the potential still further. The models arising however have potentially enormous numbers of nuisance parameters, but we have shown how exploiting an inherent conditional linearity permits relatively rapid fitting and comparing of models.

Integrated population methods have relied up to now upon the use of count-based survey information. For survey data arising from multiple sites, the approach based on modelling the counts directly offers greater flexibility not just by permitting different distributions for data of this kind, but for incorporating data of an entirely different nature. The CBC, which has so far formed the basis of IPM for British bird species, was an intensive volunteer-based survey. Encounters with birds were mapped on 10-12 summer visits to each site, then carefully translated into likely territories - both painstaking procedures. When this procedure was superseded in 2000 by the BTO/JNCC/RSPB Breeding Bird Survey, a simpler record of birds counted along 1 km transects just twice a year, the number of sites surveyed increased enormously, and coverage in remote regions especially improved (Freeman et al. 2007a). See also Roy et al. (2007) for a discussion on reduced-effort surveys for British butterflies. In

general, the simpler the data are to gather, the more are likely to be available. It is, for instance, very much easier to gather data in the form of simple lists of species encountered – binary 'presence/absence' data (Roberts et al., 2007), and we have shown how such data could be analysed either in isolation or as part of an integrated approach. The need to develop optimal methods for population monitoring from such data is especially great in many circumstances: in those regions where high biodiversity does not coincide with ample availability of the substantial resources necessary to monitor it (Balmford et al. 2003; Roberts et al. 2007), and historical count data at least are lacking, or for species/habitat combinations in which detection is largely via calls or indirect signs hard to convert to counted individuals. The approach proposed in this paper provides a first step to achieving this goal. While we assume a species is absent where not recorded, and adopt the 'presence/absence' nomenclature for convenience, it is acknowledged that this assumption may fail in practice. We return to this issue at the end of the paper.

We do not, of course, advocate the use of P/A data over count-based information; where the latter can be taken in sufficient quantity such data will always be the preferred option. In some cases, however, simple lists of species present (or at least 'recorded') may be all that can be collected. We have shown that where sufficient data are available these can still yield acceptable population trends. This is especially so if additional, compatible demographic data are incorporated, which then gives rise to the possibility of identifying ecological influences upon survival and productivity. Furthermore, when data are limited, the addition of independent P/A information may improve estimation precision for survival. It is, as ever, essential to exercise caution in the amalgamation of datasets this way. Clearly P/A records need to be either complete

species lists or to arise in some standardised form, say from a search within a fixed time period, to ensure that apparent changes reflect demography rather than search intensity. As we have seen (Figure 5), such changes in status at a site are critical. Sites at which a species is merely known to have been present throughout intuitively offer little in the way of insight, and this is borne out by deteriorating performance in the binomial model of Figure 5, as average numbers are increased. Confidence that separate datasets sample from effectively the same population is of course essential to any integrated analysis. As demonstrated, greater precision arises from count data than from P/A data of similar scale and design. However, a trade-off exists, in that in many circumstances the latter may be easier to gather in bulk, and precision loss may be compensated for by increased sample size.

An appealing feature of IPM is that a wide range of alternative models and data sources can be incorporated in the analysis. The integrated approach here is equally applicable under a negative binomial distribution for count data, as this merely requires an alternative form of the likelihood for these. We have deliberately considered in this work the case in which direct information on productivity is not available, and estimation of this parameter is entirely dependent upon the indirect information contained in the survey data and the validity of the population model. We have seen that even in this case a reasonable picture of population and demographic change can be derived under appropriate circumstances. If, in addition, data explicitly quantifying components of productivity are incorporated, it seems reasonable to expect that the performance of the integrated P/A model will be improved (c.f. Reynolds et al. 2009; Cave et al., 2010). The methods of the present paper have assumed no movement of individuals between sites but a useful extension would relax

this assumption, at least for neighbouring sites. Borysiewicz et al (2009) and McCrea et al (2010) provide promising directions for incorporating movement into IPM, although the number of sites currently considered is small.

We note finally that in practice both counts and simple species lists might be available from entirely different sources, and thus a combined likelihood incorporating both types of survey data might be formed. This raises the possibility that, for species too rare or elusive to be covered in sufficient number by a scheme such as the CBC, BBS or UKBMS, augmentation by additional P/A data much more simply gathered in quantity may profoundly increase our confidence in estimates of their population levels, with or without additional demographic data. Although not considered here, possible extensions of the approach to wider contexts include models for presence-only data (Ward et al. 2009), or relaxing the assumption of closure to estimate immigration (Abadi et al. 2010). Employing repeated visits within a season and estimating separately the probabilities of a species being present, and those of its being detected (MacKenzie et al., 2006; Royle and Nichols, 2003), also appears to be a promising line of future research. Variation in detectability is clearly a potential source of bias in population monitoring (Kéry et al. 2009), meriting particular consideration. Although the combination of likelihoods remains equally straightforward, the simplicity of model-fitting adopted in the present paper is, however, likely to be lost.

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Table 1. Average estimated slopes of relationships between first-year survival and productivity and appropriate covariates. Standard errors from 100 simulations in parentheses.

Scenario	Poisson model		Binomial model		Ringing data alone
	ϕ_1	P	ϕ_1	P	ϕ_1
(i)	0.052 (0.0016)	-0.060 (0.0019)	0.052 (0.0018)	-0.071 (0.0037)	0.051 (0.0018)
(ii)	0.051 (0.0019)	-0.062 (0.0019)	0.053 (0.0027)	-0.070 (0.0041)	0.051 (0.0031)
(iii)	0.051 (0.0010)	-0.060 (0.0008)	0.051 (0.0014)	-0.075 (0.0053)	0.051 (0.0014)

Legends for Figures.

Figure 1. Estimated population trend, log-transformed (y_t) for (a) Silver-Washed Fritillary and (b) Painted Lady. Estimates from binomial model (lines) and Poisson model (symbols), with 95% Confidence Limits. In each case y_t is estimated relative to a value of zero in 1980.

Figure 2. Estimates of the slopes of the relationships between (a) φ_1 and (b) P and their respective covariates, estimated via binomial (y-axis) and Poisson (x-axis) models, from 100 sets of data matching simulation Scenario (i)

Figure 3. As Figure 2, but from data matching Scenario (ii).

Figure 4. Estimated slopes of the relationship between first-year survival and covariate X_1 using integrated analysis (y-axis) and individual recovery component analysis (x-axis). IPM estimates from Poisson (circles) and binomial (squares) models under (a) Scenario (ii) and (b) Scenario (iii).

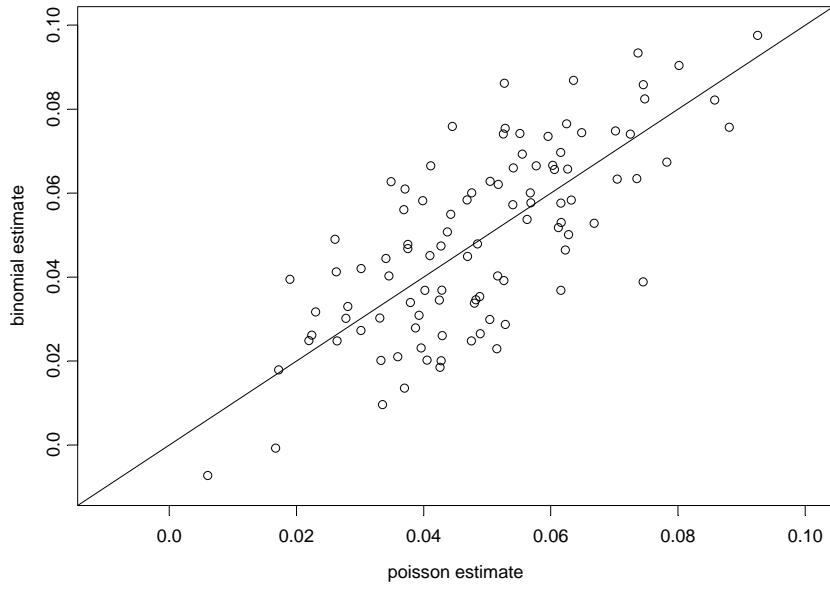**Figure 5.** As Figure 2, but from data matching Scenario (iii)
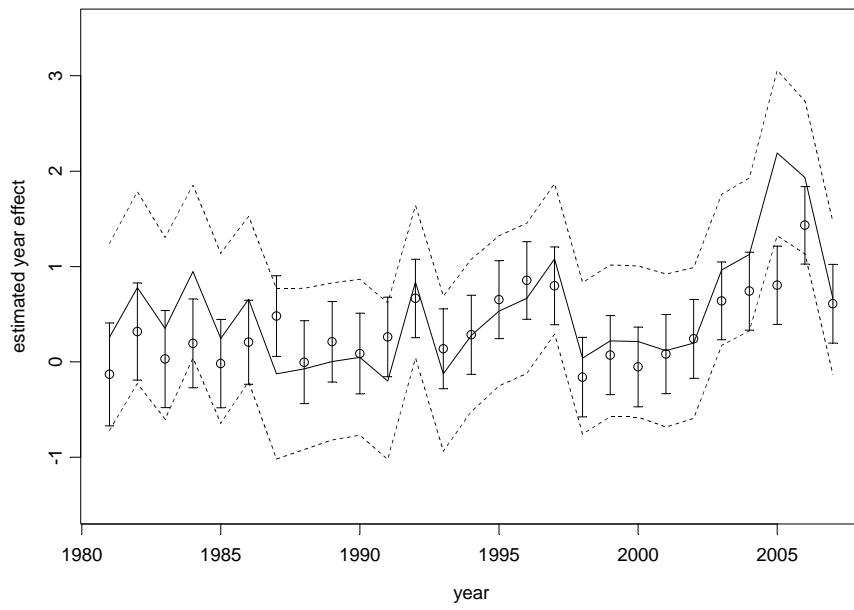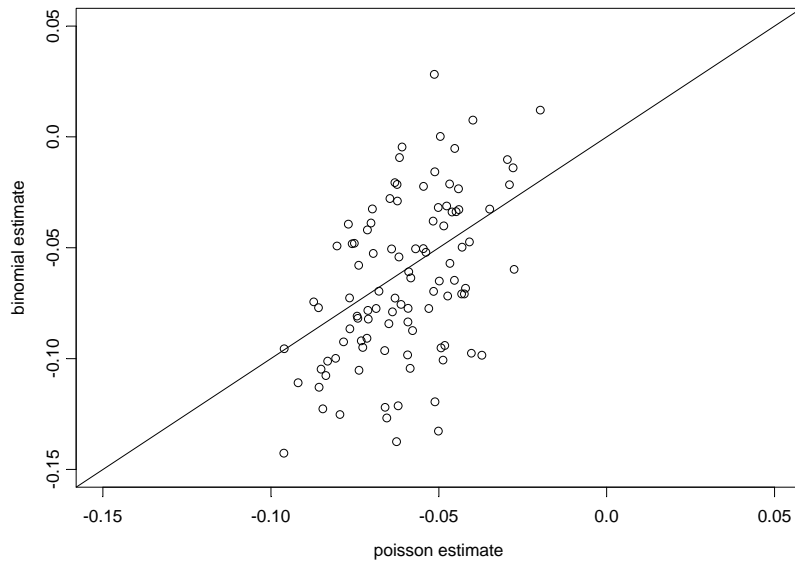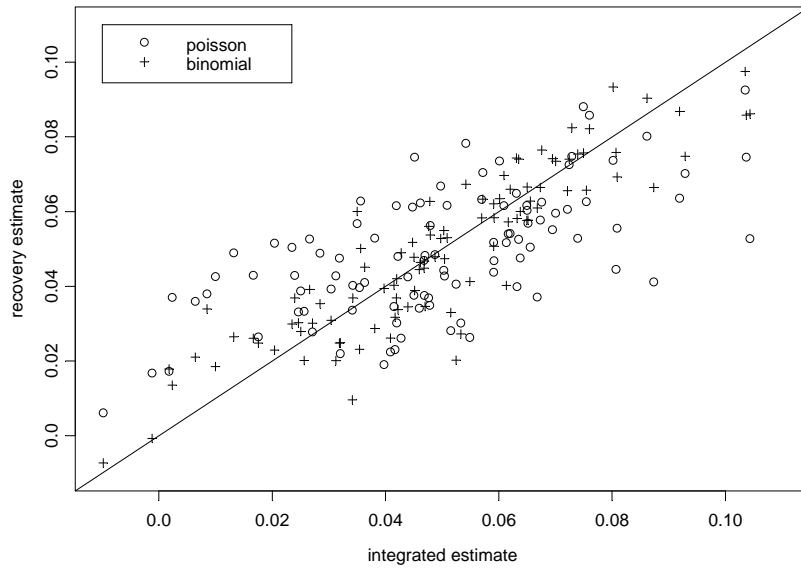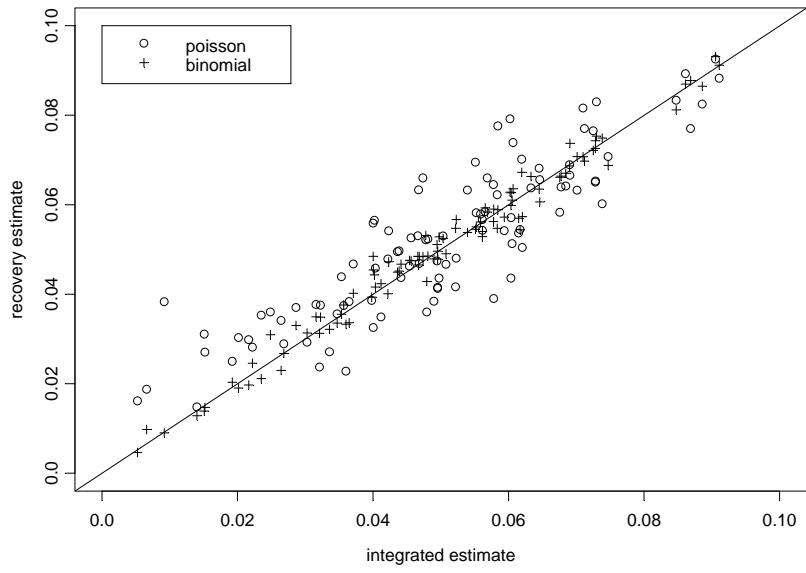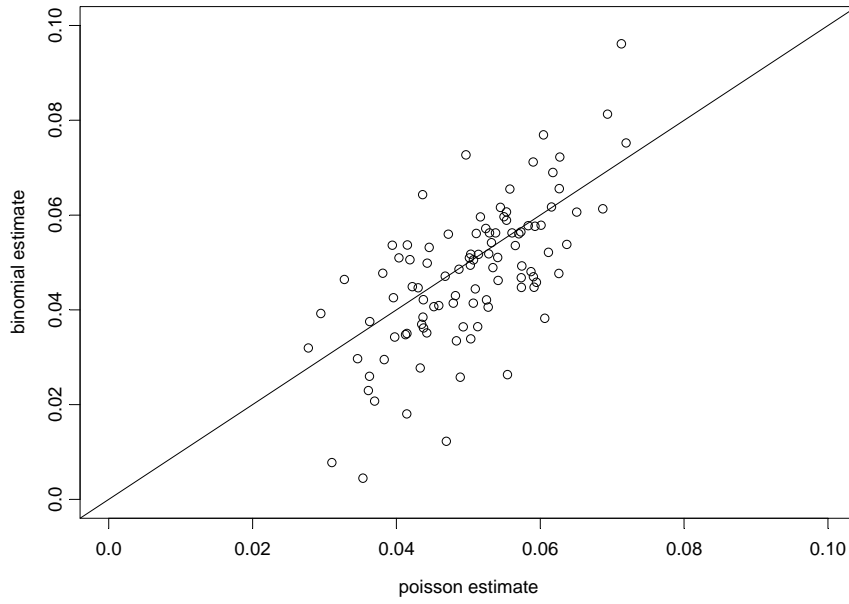
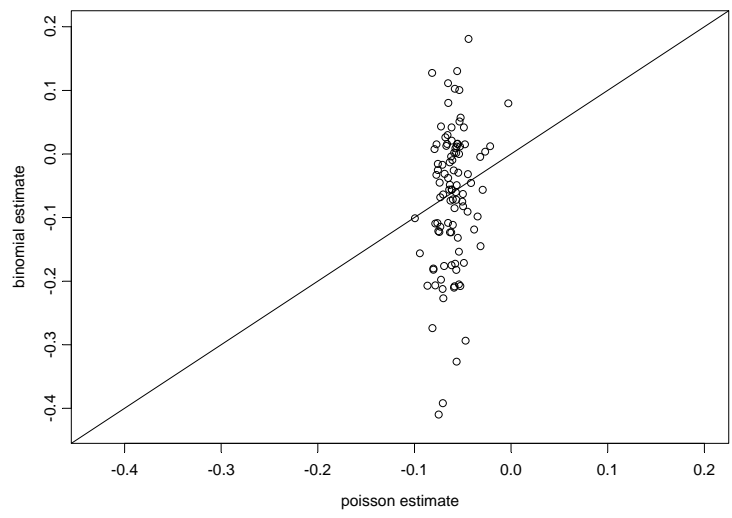Figure 1a
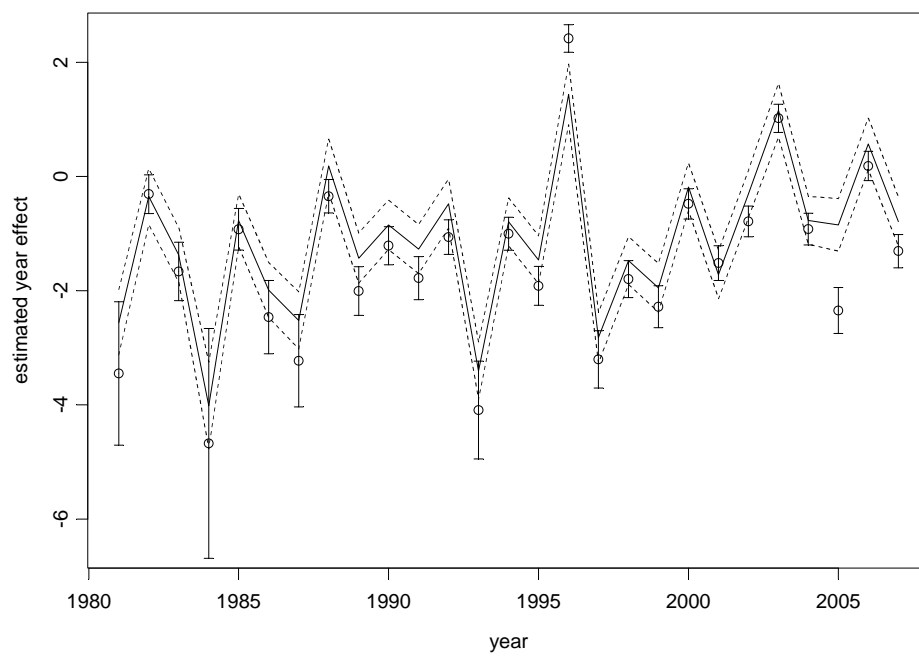
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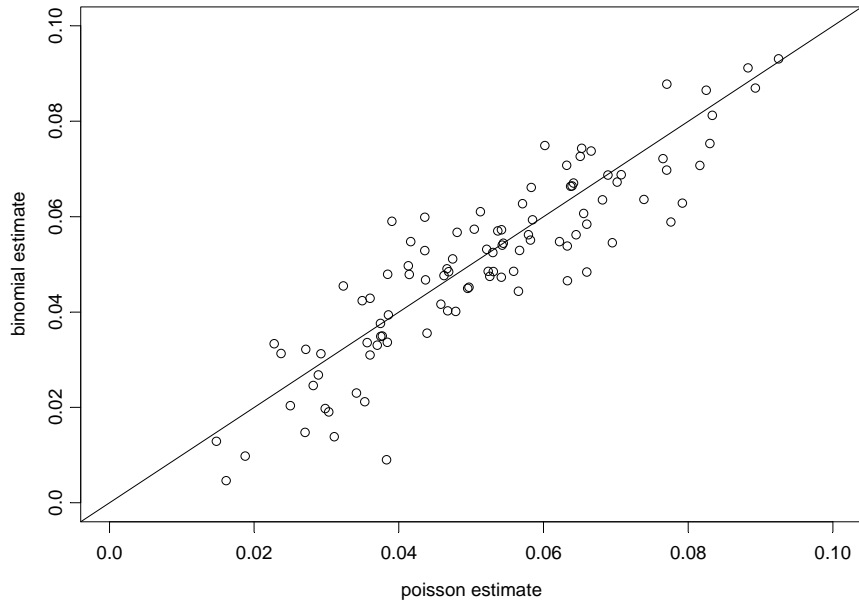
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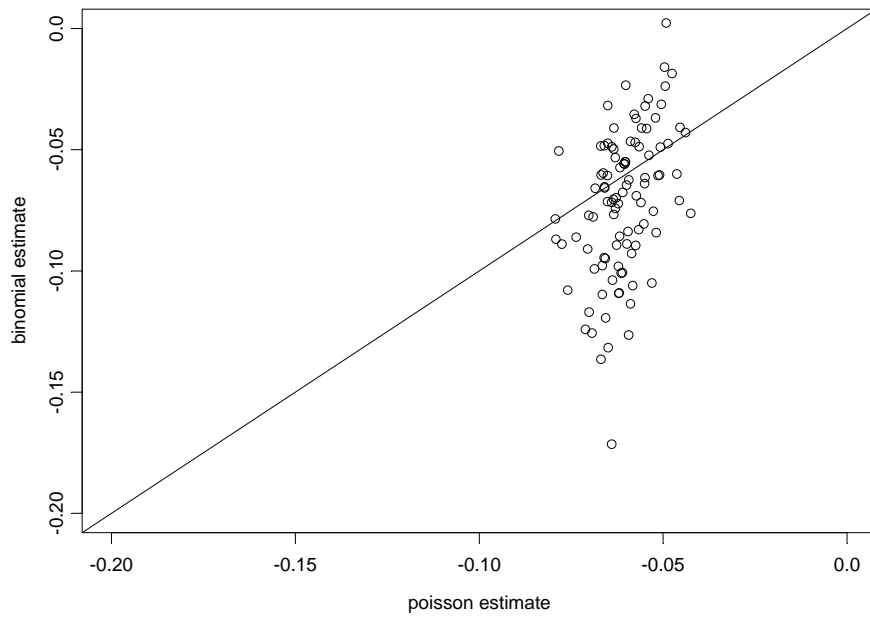
Figure 2b

Figure 3a

Figure 3b

Figure 4a

Figure 4b

Figure 5a

Figure 5b