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A capture-recapture model for exploring multi-species synchrony in survival

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Summary

1. Although recent decades have seen much development of statistical methods to estimate demographic parameters such as reproduction, and survival and migration probabilities, the focus is usually the estimation of parameters for individual species. This is despite the fact that several species may live in close proximity, sometimes competing for the same resources. There is therefore a great need for new methods that enable a better integration of demographic data, e.g. the study of synchrony between sympatric species, which are subject to common environmental stochasticity and potentially similar biotic interactions.

2. We propose a mark-recapture statistical model that uses random effect terms for studying synchrony in a demographic parameter at a multi-species level, adapting a framework initially developed to study multi-site synchrony to this novel situation. The model allows us to divide between-year variance in a demographic parameter into a 'synchronous' component, common

to all species considered, and species-specific ‘asynchronous’ components, as well as to estimate the proportion of each component accounted for by environmental covariates.

3. We demonstrate the method with data from three colonially-breeding auk species that share resources during the breeding season at the Isle of May, Scotland. Mark-resight information has been collected since 1984 for Atlantic puffins *Fratercula arctica*, common guillemots *Uria aalge* and razorbills *Alca torda* marked as breeding adults. We explore the relationship between synchrony in the species' survival and two environmental covariates.

4. Most of the between-year variation was synchronous to the three species, and the same environmental covariates acted simultaneously as synchronising and desynchronising agents of adult survival, possibly through different indirect causation paths.

5. *Synthesis and applications.* The model proposed allows the investigation of multi-species synchrony and asynchrony in adult survival, as well as the role of environmental covariates in generating them. It provides insight into whether sympatric species respond similarly or differently to changes in their environment, and helps to disentangle the sources of these differences. The estimated indices of synchrony/asynchrony can facilitate the generation of further hypotheses about similarities/differences in these species’ ecology, such as the potential overlap of wintering areas. The method is readily applicable to other species, ecosystems and demographic parameters.

Keywords: adult survival, Atlantic puffin, Bayesian models, common guillemot, environmental covariates, interspecific synchronisation, partition of variance, random effects, razorbill, WinBUGS.

Introduction

The monitoring of demographic parameters is generating a wealth of valuable information for ecology and conservation and recent decades have seen a corresponding proliferation of statistical models for analysing these types of data. However the potential to integrate different types of data has not been fully exploited, with the majority of these models targeted at analysing single demographic parameters for individual species (Lebreton *et al.* 1992; Williams *et al.* 2002), although some approaches such as integrated population modelling (Besbeas *et al.* 2005) jointly estimate several parameters in a single species analysis. Data from several species have recently been combined in models to study population trends (Sauer & Link (2002)) or species richness (multispecies occupancy models, Dorazio & Royle (2005), Russell *et al.* (2009)) but a move away from single-species single-location to more encompassing approaches is still largely overdue.

Species exist within the context of communities and ecosystems, and when populations of different species are sympatric they are exposed to biotic interactions and the same abiotic environment (Begon *et al.* 2006). Some species may react in a similar way to their common environment, showing synchrony in population trends or in the temporal variation of some demographic parameters such as survival. The underlying cause of synchrony between species is usually not clear, with hypotheses suggesting shared stochastic effects, such as weather (Hawkins & Holyoak 1998) and the response to common predators (Raimondo *et al.* 2004). The study of the species in a community in isolation may lead to only a partial understanding of their ecology or even to incorrect conclusions.

Synchrony between sympatric populations of different species has received less attention compared to synchrony between allopatric populations of a single species (Raimondo *et al.* 2004). The relatively few multi-species examples to date typically address synchrony in abundance through the study of time-series of population size (Swanson & Johnson 1999; Raimondo *et al.* 2004) and are often dedicated to understanding mechanistic predator-prey interactions (New 2009). In general, investigating the mechanisms underlying population change is a difficult task when studying time series of abundance alone, and the incorporation of demographic parameters such as survival, reproductive success and dispersal probabilities is often key in understanding such mechanisms (Loison *et al.* 2002).

We propose a statistical model for studying the variation of a demographic parameter at a multi-species level, through the use of random effects. Between-year variance in the demographic parameter is divided into a ‘synchronous’ component, that represents the common response of all species considered, and ‘asynchronous’ components, specific to each species, and we estimate the contribution of environmental covariates to each of these components. The model is based on that presented by Grosbois *et al.* (2009) for studying the variation of adult survival for a single species at a multi-population scale, although it is conceptually different in its interpretation, and further we relax the variance structure in the model to accommodate differences among species. In this paper, we demonstrate an application of the method to explore synchrony in adult survival using 25 years of individual mark-resight data for three seabird species, the Atlantic puffin *Fratercula arctica* (L.), the common guillemot *Uria aalge* (Pontoppidan) and the razorbill *Alca torda* L., collected at the breeding colony on the Isle of May, southeast Scotland. These three auks (Alcidae) have broadly similar life histories and ecology (Gaston & Jones 1998). Birds from breeding populations on the Isle of May show largely overlapping distributions throughout the year (Wernham *et al.* 2002) and are thus likely to be exposed to similar environmental stochasticity. Consequently we would expect some degree of synchrony in their response in terms of the temporal variation of demographic parameters. Adult survival probabilities for Isle of May puffins, guillemots and razorbills have previously been analysed separately (Harris *et al.* 1997; Harris *et al.* 2000; Crespin *et al.* 2006), but to date no attempt has been made to integrate survival data for these species, and in particular, to look for synchronising and desynchronising agents.

Materials and Methods

Mark-resight data

Mark-resight information was collected for 543 Atlantic puffins (hereafter puffin), 831 common guillemots (hereafter guillemot) and 153 razorbills at the Isle of May (56°11’N, 2°34’W), southeast Scotland. As with many seabirds, annual adult survival probabilities of puffins, guillemots and razorbills are normally high (Harris *et al.* 1997; Sandvik *et al.* 2005). Birds visit land only for breeding and while puffins nest in burrows, guillemots and razorbills lay eggs directly on narrow cliff ledges. Outside the breeding season, auks from the Isle of May disperse over broad areas of the North Sea (Wernham *et al.* 2002), and during the breeding season they eat similar prey, mainly small, lipid-rich, shoaling fish such as the lesser sandeel *Ammodytes marinus* and sprat *Sprattus sprattus* (Daunt *et al.* 2008). Between 1984 and 2007, breeding birds in front of permanent hides were marked with unique colour-rings and resightings of these birds took place each year up to 2008. Once they have bred, individuals of all species rarely breed more than a few metres from where they were marked (MPH, pers. obs.), so resighting effort was mainly focussed on these areas although regular searches were also made in all nearby areas to locate individuals of the three species that had moved.

Multi-species synchrony model

Using the standard open population capture-mark-recapture/resight models for estimating apparent survival and recapture/resight probabilities (reviewed in Lebreton *et al.* (1992)), likelihood functions can be constructed individually for each of the species involved in the model. Following standard notation, we denote resight probability in year Y as p(Y) and annual apparent adult survival probability from year Y to Y+1 as Φ(Y). Both resight and survival probabilities can then be modelled to depend on explanatory variables. In order to allow the study of synchrony in survival probabilities, we followed the framework presented by Grosbois *et al.* (2009) and introduced random year effects in the relationship of survival with covariates as follows:

$$\mathrm{logit}\left[\phi_S(\mathrm{Y})\right] = \mathrm{f_S}\left(\mathrm{c_{S1}}(\mathrm{Y}), \ldots, \mathrm{c_{Sn_s}}(\mathrm{Y})\right) + \delta(\mathrm{Y}) + \varepsilon_{\mathrm{S}}(Y)\,. \qquad \text{(eqn 1)}$$

$\Phi_S(Y)$ is the apparent adult survival from year Y to Y+1 for species S. Survival is related to covariates and random effects through the logit link function, although alternative link functions are possible. The relationship with covariates is handled through $f_S(.)$, a species-specific function of n_s covariates c_{Si}. The function could be for example a linear regression or a nonparametric relationship. For the year random effects, $\delta(Y)$ is a random term which is common to all species considered and only depends on the year, and $\varepsilon_S(Y)$ is a random term that depends on the year and species. The δ and ε_S terms are assumed to be independent and have distributions $\delta(Y) \sim N(0, \sigma_\delta^2)$ and $\varepsilon_S(Y) \sim N(0, \sigma_s^2)$ respectively, with no correlation between terms. We extend the approach of Grosbois *et al.* (2009) so that the 'year x species' random terms can have different variances for the different species (i.e. σ_s^2 are species-specific) and so the between-year variance in survival unexplained by the covariates can be differently partitioned for different species. The δ term corresponds to the amount of between-year variation (unexplained by the covariates, if present) that is synchronous to all species considered, while the ε_S terms characterise the species-specific ('asynchronous') components. Note also that Grosbois *et al.* (2009) use a single common covariate that takes different values for each colony, while in this study each common covariate has the same value for all the species considered (as the geographical area is the same), but each species might have a different combination of covariates.

Assuming independence between the data for the different species, the overall likelihood function for all species together can be written as the product of the individual likelihoods. This is similar to the way in which likelihood components corresponding to different demographic parameters are combined for a single species in an integrated population modelling framework (Besbeas *et al.* 2005). In the proposed model, the species-specific likelihood components share at least one parameter, the variance of the common random term δ.

Once the model parameters have been estimated, a species-specific intra-class correlation coefficient can be calculated based on the variances of the random terms as an index of synchrony in adult survival:

$$\mathrm{ICC}_s = \frac{\hat{\sigma}_\delta^2}{\hat{\sigma}_\delta^2 + \hat{\sigma}_s^2}. \quad \text{(eqn 2)}$$

This quantity represents the synchrony of species S with the rest of the species: the amount of between-year variance for species S (either total or unexplained by the covariates, if present in the model) that is accounted for by the common random term δ(Y). When $\hat{\sigma}_\delta^2$ is large compared to $\hat{\sigma}_s^2$, then ICC_S is large and the between-year variation for that species is then mostly synchronous with the other species.

In order to evaluate the effect of the environmental covariates in generating synchrony and asynchrony between species survival, two models are compared, following the method in Loison *et al.* (2002) and Grosbois *et al.* (2009). Both models include random effects δ(Y) and $\varepsilon_S(Y)$ but one of them does not have covariates (only a separate intercept for each species). We can define the residual variance of δ, $\hat{\sigma}_\delta^2(\mathrm{res})$, for the model with covariates, and the total variance, $\hat{\sigma}_\delta^2(\mathrm{total})$ when there are no covariates but only random effect terms. The same can be done for each species for the variance of the ε_S term: $\hat{\sigma}_s^2(\mathrm{res})$, $\hat{\sigma}_s^2(\mathrm{total})$. Based on these values, a set of coefficients can be calculated:

$$C_\delta = 1 - \frac{\hat{\sigma}_\delta^2(\mathrm{res})}{\hat{\sigma}_\delta^2(\mathrm{total})}. \quad \text{(eqn 3)}$$

$$C_s = 1 - \frac{\hat{\sigma}_s^2(\mathrm{res})}{\hat{\sigma}_s^2(\mathrm{total})}, \text{ for each species S.} \quad \text{(eqn 4)}$$

C_δ and the C_s coefficients measure the contribution of the environmental covariates to the interspecific synchronous δ and asynchronous ε_s components of the between-year variances, respectively.

Environmental covariates for survival

Environmental covariates are known to influence demographic parameters in many species (Stenseth *et al.* 2003), and have been shown in some cases to be responsible for interspecific synchrony (Hawkins & Holyoak 1998). In the case of North Atlantic seabird survival probabilities, studies often include covariates related to two oceanographic factors, the North Atlantic Oscillation (NAO) and the temperature at the sea surface (SST).

The winter NAO index is a well-known indicator of climatic conditions over north-western Europe and has been shown to influence ecological processes (Stenseth *et al.* 2003). Winter NAO with various time-lags have been related to survival of Atlantic puffins, common guillemots and razorbills (Harris *et al.* 2005; Sandvik *et al.* 2005; Grosbois *et al.* 2009). For this study, we used the station-based extended winter (December to March) North Atlantic Oscillation index ('wNAO'), obtained at http://www.cgd.ucar.edu/cas/jhurrell/indices.html. Following Sandvik *et al.* (2005) and Harris *et al.* (2005), we used both wNAO without time lag ('wNAO_0'), that reflects the direct effect of weather harshness on survival, and wNAO with a 1-year time lag ('wNAO_1'), that reflects the indirect effect of climate, possibly through the food chain.

Several different indices based on SST averaged over different areas and seasons have been used in relation to the three species considered here (Harris *et al.* 1997; Harris *et al.* 2005; Sandvik *et al.* 2005; Grosbois *et al.* 2009). For this study, monthly values were obtained from http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.monthly/.sst and averaged for an area of 10 cells around the Isle of May, on a grid of 1°x1°. The first SST covariate considered was the average over January to May, following Harris *et al.* (2005). We denote this variable as 'SST_0' (no time lag). This period of the year coincides with the spawning season and larval period of the sandeel, the auks' main prey species during the breeding season. We also included its 1-year time lag 'SST_1', that is, the average over January to May of the previous year (Harris *et al.* 2005).

Heterogeneity in resight probability

Before fitting the data in combination, we assessed the goodness of fit (GOF) of the general fully time-dependent Cormack-Jolly-Seber (CJS) model {Φ(t)p(t)} with program RELEASE (Burnham *et al.* 1987), for each species individually. In this model, both survival and resight probabilities are allowed to vary from year to year. The GOF was very similar for all species studied. The general CJS model fits the data poorly, due mostly to the 2.C component (guillemot: χ^2=173.49, df=22; puffin: χ^2=129,9, df=22; razorbill: χ^2=55.35, df=17; all p-values < 0.001), which indicates heterogeneity in resight probability (‘trap dependence’), an effect that has been reported already for puffins at the Isle of May (Harris *et al.* 2005). Component 3.SR fitted well for all 3 species (p-values > 0.9), therefore showing no evidence of individual heterogeneity in survival probability, as noted in previous analysis of these species from the Isle of May (Harris *et al.,* 2000; Harris *et al.,* 2005; Grosbois *et al.,* 2009).

The trap-dependence in resight probability detected for the three species was taken into account in the synchrony models by adding a 1-year trap-dependence structure as follows:

$$\mathrm{logit}[p_S(i,Y)] = \log\left(\frac{p_S(i,Y)}{1-p_S(i,Y)}\right) = r_S(Y) + a_S \cdot T_S(i,Y). \quad \text{(eqn 5)}$$

For each species *S*, the resight probability for individual i in year Y, $p_S(i,Y)$, depends through a logit link on a year-specific resight probability $r_S(Y)$ and an additive term a_S that is only included if the individual was resighted in the previous occasion. This is achieved by using the indicator function $T_S(i,Y)$ that can be seen as an individual covariate for each capture occasion. Thus $T_S(i,Y)=1$ if bird *i* was caught in year *Y-1*, and zero otherwise. The species-specific terms a_S represent the amount of 1-year trap-dependence for each species studied.

Analysis of the auk data

We applied the method outlined above to investigate the amount of synchronisation in the variation of adult survival for the three auk species at the Isle of May, by jointly analysing their mark-resight data. For simplicity, we used the same covariates for all three auk species, but this is, in general, not a restriction and as mentioned above, species-specific covariates could be considered. The vector cov = {c1,c2,c3,c4} = {wNAO_0, wNAO_1, SST_0, SST_1} in the models hereafter refers to the four covariates together. All covariate time series, between 1984 and 2008, were standardised prior to inclusion in the models by subtracting the mean of the series and dividing by its standard deviation. We verified that the covariates do not have high correlation. For adult survival, we considered a logit link function and a linear regression, with the aforementioned set of four standardised covariates c_j and corresponding species-specific regression coefficients β_{jS}:

$$\operatorname{logit}[\phi_S(Y)] = \left\{\beta_{0S} + \sum_{j=1}^{4}\left(\beta_{jS} \cdot c_j(Y)\right)\right\} + \delta(Y) + \varepsilon_S(Y)\,. \quad \text{(eqn 6)}$$

All models considered in the following sections had fully time-dependent resight probability with 1-year trap-dependence modelled as explained in eqn 5 and these are denoted ‘p(t+a)’.

As the Bayesian approach is more flexible for handling random effects than the classical maximum likelihood framework (Barry *et al.* 2003), we conducted our study within a Bayesian framework with MCMC sampling. All models were programmed in WinBUGS (Spiegelhalter *et al.* 2003). The WinBUGS code used to fit the models can be found in the online Supplement. After a burn-in period of 100000 samples, the MCMC chains were run for 150000 iterations (with a thinning of 3 to reduce the amount of data stored). Convergence was assessed with the Gelman-Rubin statistic calculated as modified by Brooks and Gelman (1998), after starting 3 chains with dispersed initial values for all variables. The statistic suggests that convergence had been achieved after 100000 samples. Uninformative priors were used for all variables (regression coefficients $\beta_{iS} \sim U(-5,5)$; standard deviation of the δ and ε random terms $\sigma_x \sim U(0,3)$; year-specific component of resight probabilities $r_S(Y) \sim N(0,10^{-4})$; trap-dependence coefficients $a_S \sim U(-5,5)$). We conducted a prior sensitivity study for the random effect variances by specifying conventionally used vague inverse-gamma priors as an alternative to uniform priors.

Starting from the full model {Φ(cov+δ+ε)p(t+a)} we constructed all of the eight combinations of up to three of the arguments of survival (covariates, ‘year’ random term δ, ‘year x species’ random terms ε_S), or none at all. In the cases when covariates were removed, a species main effect was kept through a species-specific intercept. For brevity we did not attempt a formal model-reduction exercise in terms of reducing the number of individual covariate terms required. We fitted each of the resulting eight models (Table 1) to the auk mark-resight data. The models were ranked in terms of their Deviance Information Criterion (DIC), a Bayesian analogue of AIC (Spiegelhalter *et al.* 2002) that balances model fit and complexity. It is calculated as $DIC = D(\theta) + 2p_D$, where $D(\theta)$, the deviance when using the mean of the posterior distribution of the parameters, is penalised by twice the effective number of estimated parameters p_D. DIC is available directly in WinBUGS, with the best model being the one with the lowest DIC value. Although its use is controversial in the context of hierarchical models (Spiegelhalter *et al.* 2002; Barry *et al.* 2003; Millar 2009), note that the model ranking does not affect the analysis of synchrony.

Simulation study

We used simulation to study the performance of the proposed method in fitting a set of data derived from known parameters. We selected the full model structure $\{\Phi(cov+\delta+\varepsilon)p(t+a)\}$ from the previous section and chose parameter values based on the best model obtained in the Isle of May auk study, in order to stay within ecological realism. Mark-resight data were generated 20 times (the processing time required for the MCMC sampling is prohibitive for a much larger simulation study), matched to values estimated for the three auk species, with the same number of animals as in the real data set. For each species, each of these data sets differed only in the value of the survival rates, as the random effect terms (both common and species-specific) that were added to the linear relationship were generated independently with same variance for each simulated data set. The rest of the parameters were kept unchanged. The model $\{\Phi(cov+\delta+\varepsilon)p(t+a)\}$ was fitted to the 20 data sets using WinBUGS (50000 MCMC iterations after a burn-in of 100000). We used the medians of the posterior distributions for each parameter to calculate the bias, and then averaged over the 20 data sets.

Results

Data analysis

According to the DIC values (Table 1), the best of the eight possible models fitted was the full model $\{\Phi(cov+\delta+\varepsilon)p(t+a)\}$, where survival depended on the set of covariates but had also common (δ) and species-specific (ε_S) random terms. As expected, the models with covariates outperformed the corresponding models with only species main effect (intercept). In both cases, with and without covariates, the inclusion of any kind of random effects gave a substantial improvement in terms of DIC, and having both common and species-specific random terms was better than having either in isolation.

Prior sensitivity was tested for the best model using alternative priors. In particular, the use of inverse-gamma priors for the random effect variances appeared to be slightly more informative than specifying uniforms for their standard deviation, and the posterior distributions were sensitive to the choice of the gamma distribution parameters, as it has been noted in previous studies (Royle 2008). This was particularly the case for razorbills, the species with least data. These results support the selection of uniform priors for these parameters.

[Table1_about_here]

Concentrating on the full model {Φ(cov+δ+ε)p(t+a)}, estimated survival probabilities (Fig. 1) differed substantially for the three species, although most values remained relatively high (above 0.8 or even above 0.9 for puffins and guillemots), as is typical for long-lived seabirds. Note that the size of the 95% credible intervals reflected the amount of data available for each species, being wider for razorbill (153 birds) and very narrow for guillemots (831 birds). Survival was relatively stable over the years for guillemots, showed wider variation for razorbills, with pronounced peaks in a few particular years, while estimates for puffins were intermediate.

[Figures1&2_about_here]

The trap-dependence coefficients (a_S in eqn 5) were all positive for the three species and therefore the probability of seeing a bird was higher if it was seen the previous year. Using the estimates of a_S and r_S we calculated the estimated resight probabilities for the three species, for the case when a bird was seen the year before, and for when it was not (Fig. 2). Notice that resight probability is 1 for the three species in the last year. When the study was repeated excluding 2008, this effect appeared again associated to the last year, in this case 2007. We conclude that, as with the Cormack-Jolly-Seber model in which the final year's survival and recapture probability are not identifiable, the survival estimates for the last year should be discarded, as they are biased low due to the artificially high recapture probability. In the case of razorbill, four other years had resight probabilities estimated to be 1. The number of marked razorbills was substantially lower than for the two other species, and these estimates reflect years for which all birds known to be alive the previous year were either seen or never seen again. Regarding the boundary estimates in later years, note that the future resight of even one bird alive but missed in these years will remove the estimates from the boundary, and the correlated survival rates will rise as a consequence.

Table 2 shows the regression coefficients for the full model, {Φ(cov+δ+ε)p(t+a)}. Most of the point estimates were below zero, denoting a negative relationship between adult survival and the covariate represented. Note that some of the 95% credible intervals spanned both sides of 0. In the particular case of 1-year time-lagged SST for razorbill, the corresponding beta was very close to zero, indicating a lack of strong influence of that covariate on razorbill survival. The fact that some of the regression coefficients corresponding to the time-lagged versions of wNAO and SST were far from zero indicated that they also had an indirect effect on adult survival, acting possibly through the food chain (Harris *et al.* 2005; Sandvik *et al.* 2005).

[Table2_about_here]

Interspecific synchrony (ICC_S) and the fraction of variation accounted for by the covariates for each species (C_δ and C_s terms) were calculated from the estimates of the full model {Φ(cov+δ+ε)p(t+a)} and the 'species main effect' model {Φ(S+δ+ε)p(t+a)} (Table 3).

[Table3_about_here]

For the model with covariates, the residual variances of the species-specific random terms $\hat{\sigma}_s^2(\mathrm{res})$ were all substantially lower than that of the common random term $\hat{\sigma}_\delta^2(\mathrm{res})$ which is also noticeable when looking at the estimates of the random terms for each year of the study (Fig. 3). As a result, all three ICC_S values were high. These values suggested that for puffin, guillemot and razorbill, most of the variation unexplained by the environmental covariates used in this study was synchronous to the three species.

[Fig.3_about_here]

In the ‘species main effect’ model, all $\hat{\sigma}_s^2(\text{total})$ and $\hat{\sigma}_\delta^2(\text{total})$ variances increased compared to the model with covariates, to accommodate the extra variation created by the lack of covariates. The species-specific variances increased more, in proportion, and therefore the ICC_S terms decreased to below 80%.

The fraction of the synchronous variance accounted for by the set of covariates (C_δ) was around 26%, that is, about one fourth of the variation that is synchronous to the three auk species was explained by components of the climate related to wNAO and SST. Climate is acting to some extent as a synchronising agent in the survival of puffins, guillemots and razorbills but there is still about 75% of synchronous variation among species that is not explained by these covariates. The environmental covariates were also responsible for a large part of the asynchronous variation, as shown by the values of the C_s coefficients. For puffins and razorbills, the values were very high (≈81% and 60% respectively), implying that most of the between-year variation asynchronous to the other auk species was related to these climatic covariates. For guillemots on the other hand, less than half of the asynchronous variation in adult survival was explained by these covariates. Thus it appears that the same climatic factors can act simultaneously as synchronising and desynchronising agents for adult survival of these species at the Isle of May. There is some indication that both wNAO and SST can act indirectly on survival (Harris *et al.* 2005). It is therefore possible that the oceanographic effects reflected in wNAO and SST can act through different indirect causation paths, some of them affecting the three species in synchrony, some others affecting them differently or only affecting some of the species.

Simulations

We obtained the average over the 20 simulated data sets of the median value of each parameter (Table 4).

[Table4_about_here]

Bias was calculated as the average over the 20 simulations of the absolute value of the difference between the point estimate (median) and the true value. It was generally small for the regression and trap-dependence coefficients. The largest values appeared with the estimation of the variance of the random effects. In relation to the species-specific random terms, it is worth noting that as expected the largest bias was associated with the species with least data (razorbill, 153 marked individuals) while the smallest corresponds to guillemots (with 831 birds). These differences disappeared when the simulations were repeated with 831 individuals for each of the three species. Bias in survival estimates was in almost all cases below 3% and was again in general largest for razorbills (smallest data set) and smallest for guillemots (largest data set).

Discussion

This paper presents a model, fitted using Bayesian methodology, for studying synchrony in adult survival between several species, and the contribution of environmental covariates as synchronising and desynchronising agents, adapting the framework used for a multi-population study by Grosbois et al. (2009) to the multi-species situation. This method does not directly shed light into the typically complex mechanisms that underlie the observed synchronisation or desynchronisation between different species, but it can be used to provide insight into community dynamics and to point out further avenues of investigation in terms of environmental covariates.

Auk survival at the Isle of May

The survival estimates obtained in our study with the best model {$\Phi(cov+\delta+\varepsilon)p(t+a)$} are consistent with previous analyses of the three species individually (Harris *et al.* 2000; Harris *et* *al.* 2005; Reynolds *et al.* 2009). However estimates of a species' survival from a more integrated study have the potential for borrowing strength from the rest of the ensemble, with the consequent gain in precision. In this study, some of the regression coefficients seem to point to the existence of indirect environmental effects, possibly through the food web, as noted in Sandvik *et al.* (2005): regression coefficients were negative for SST with no delay and others with 1-year lag were not zero. Some of the estimated regression coefficients were low and had 95% credible intervals that included zero, possibly pointing to a lack of a strong influence of the corresponding environmental covariates on that particular species' survival. We did not attempt a systematic covariate selection process prior to the modelling as the primary aim at this stage was to develop the statistical model for studying multi-species synchrony and demonstrate the potential of this framework.

There was a significant proportion of variance not explained by our set of four covariates, which indicates that there is scope for further investigation. This may include the existing environmental covariates with longer time lags (Harris *et al.* 2005) or averaged over different periods of the year or broader areas in which auks overwinter (Sandvik *et al.* 2005). Biotic covariates, like prey stock estimates (Harris *et al.* 1997) could also be considered, as well as non-linear or non-parametric relationships with the covariates (Gimenez *et al.* 2006) These covariates will be the object of further exploration of this data set, with a focus on the ecology of these auk species. Our study lays the methodological groundwork for this.

Future developments of the framework

A number of interesting generalisations can be considered for the framework presented by Grosbois *et al.* (2009) for the multi-colony case and extended in this study for multi-species synchrony. Firstly, the framework of using species-specific and common random effect terms could be adapted to other demographic parameters, as already suggested by Grosbois *et al.* (2009) for the multi-population situation. The natural next step would be to consider synchrony in several demographic parameters by analysing them together and potentially incorporating time-series of abundance, in an integrated population modelling framework (Besbeas *et al.* 2005). The joint likelihood of such analysis would extend over demographic parameters as well as over different species, an analysis that to our knowledge has not been done to date. Apart from the inherent benefits of the integrated modelling, the partition of variation into synchronous and asynchronous components could be carried out for each of the demographic parameters used, in the same fashion as was done here for adult survival. The synchrony/asynchrony of the response to the environmental covariates could be simultaneously assessed across species for different life history traits. Conversely, synchrony in different demographic rates could be studied for a single species, investigating for example if juvenile and adult survival are synchronous and if climate contributes to this effect.

Few studies address spatial and temporal synchrony simultaneously (but see Swanson & Johnson (1999)). For survival, such a situation could be tackled with a multi-species multi-population framework, combining the model proposed by Grosbois *et al.* (2009) with that of ours:

$$\mathrm{link}[\phi_{\mathrm{SP}}(\mathrm{Y})] = \mathrm{f}_{\mathrm{SP}}\left(\mathrm{c}_{\mathrm{SP1}}(\mathrm{Y}), \ldots, \mathrm{c}_{\mathrm{SPn_{SP}}}(\mathrm{Y})\right) + \delta(\mathrm{Y}) + \lambda_{\mathrm{S}}(\mathrm{Y}) + \gamma_{\mathrm{P}}(\mathrm{Y}) + \varepsilon_{\mathrm{SP}}(\mathrm{Y}) . \quad \text{(eqn 7)}$$

Survival $\Phi_{SP}(Y)$ from year Y to Y+1 for species S in site P would be related through the logit link function to a species-and-site-specific function $f_{SP}(.)$ of a set of n_{SP} environmental covariates $c_{SPi}(Y)$ and random effects. In this case, these would include an overall common term $\delta(Y)$, terms specific to species $\lambda_S(Y)$ and sites $\gamma_P(Y)$, and finally species-and-site-specific terms $\varepsilon_{SP}(Y)$. The number of parameters to be estimated increases compared to the multi-species or multi-colony cases, and we can expect the requirements in terms of amount of data needed to be able to estimate the parameters to increase.

The alternative parameterisation proposed as a generalisation of the multi-population model (Grosbois *et al.* 2009, eqn 1) can also be adopted in the multi-species framework we present, allowing the incorporation of covariates into the species-specific partition of variance between synchronous and asynchronous components. When mechanistic hypotheses about interspecific relations exist, it could be worth considering applying the framework presented here to models that take into account these interactions explicitly (see New (2009) for an example of state-space multi-species model with predator-prey interaction).

Finally, the application of random effects to study multi-species synchrony could be explored for other types of data beyond mark-recapture. One example is occupancy models (MacKenzie *et al.* 2006) where detection/non-detection data of an unmarked species are used to estimate the percentage of sampled sites where the species is present, taking into account imperfect detection. In a similar fashion to that in eqn 1, data from several species sampled at the same sites could be modelled together, adding common and species-specific random effects terms to account for the between-site variation not accounted for by a set of covariates:

$$\mathrm{logit}\left[\Psi_S(\mathrm{i})\right] = \mathrm{f}_S\left(\mathrm{c}_{S1}(\mathrm{i}), \ldots, \mathrm{c}_{Sn_s}(\mathrm{i})\right) + \delta(\mathrm{i}) + \varepsilon_S(\mathrm{i}) . \qquad \text{(eqn 8)}$$

In this case, $\Psi_S(i)$ (the probability of site i being occupied by species S) depends through a logit link function on a set of covariates $c_{Sj}(i)$ and two random terms. The variance σ_δ^2 of the common terms $\delta(i)$ represents the variation of occupancy across sites that is synchronous to all species considered, while the variances σ_s^2 of the species-specific terms $\varepsilon_S(i)$ correspond to the asynchronous components. The derivation of indices of synchrony and the contribution of the covariates in synchronising and desynchronising occupancy across sites is then straightforward. The number of sites is usually large compared to the number of years available in typical mark-recapture studies, facilitating the characterisation of the random effect variances. We note that multispecies occupancy models have already been proposed to study communities (e.g., Russell et al. 2009) although not specifically targeted to investigate synchrony in occupancy.

Conclusion

Improved understanding of how the environment synchronises and desynchronises demographic parameters can be of great value in generating ecological hypotheses, especially when coupled with biological knowledge of these species. Links between demography and environmental conditions are complex, with variables acting simultaneously as synchronising and desynchronising agents. For example, in the case of the auks considered here, it is likely that to understand the processes involved, more information will have to be incorporated. The results of synchrony could be related to similarities in wintering grounds, as new research clarifies the picture of where these birds spend the winter months (Harris *et al.* 2009). Models like the one presented by Grosbois *et al.* (2009) for multi-populations and its adaptation for multi-species introduced in this paper represent new steps towards more integrative approaches to study demographic parameters. Methods to study multi-species relations are urgently needed given the changing environmental conditions and may play an important role in increasing our understanding of how climate change may affect communities' composition, as sympatric species react in similar or different ways to changes in their environment.

Acknowledgements

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Tables

Table 1. DIC values for the different models compared. ‘cov’ refers to the set of four covariates (wNAO_0, wNAO_1, SST_0 and SST_1). ‘S’ refers to species main effect (intercept only). ΔDIC is the DIC increment compared to the model with lowest DIC.

Model	DIC	ΔDIC
Φ(cov+δ+ε)p(t+a)	1104.2	0
Φ(S+δ+ε)p(t+a)	1105.1	0.9
Φ(cov+δ)p(t+a)	1108.3	4.1
Φ(cov+ε)p(t+a)	1110.6	6.4
Φ(S+ε)p(t+a)	1111.7	7.5
Φ(S+δ)p(t+a)	1139.8	35.6
Φ(cov)p(t+a)	1153.6	49.4
Φ(S)p(t+a)	1202.2	98.0

Table 2. Median (and 95% Credible Intervals) of the marginal posterior distribution of the regression and 1-year trap-dependence coefficients of model $\{\Phi(cov+\delta+\varepsilon)\ p(t+a)\}$

	puffin	guillemot	razorbill
β_o (intercept)	2.51 [2.22,2.81]	2.68 [2.39,2.97]	2.36 [2.02,2.76]
β_1(wNAO_0)	-0.14 [-0.47,0.18]	0.15 [-0.16,0.45]	0.27 [-0.13,0.67]
β_2(wNAO_1)	-0.19 [-0.56,0.18]	0.08 [-0.27,0.43]	-0.43 [-0.91,0.03]
β_3(SST_0)	-0.47 [-0.93,0.02]	-0.11 [-0.55,0.31]	-0.46 [-1.06,0.11]
β_4(SST_1)	-0.31 [-0.75,0.11]	-0.4 [-0.81,-0.01]	-0.04 [-0.58,0.48]
a	1.86 [1.54,2.18]	2.94 [2.54,3.35]	1.81 [1.22,2.41]

Table 3. Estimated residual and total variance of the common (δ) and species-specific (ε_S) random effect terms, and Inter-class correlation (ICC_S) coefficients. The fraction of between-year variance in survival accounted for by the climatic variables (C_δ and C_S) were calculated based on the estimated variances. 'Species 1' refers to the Atlantic puffin, 'species 2' to the common guillemot and 'species 3' to razorbill. 95% Credible Intervals are shown in brackets.

	Interspecific synchronous variance component $\hat{\sigma}^2_\delta$	Species-specific asynchronous variance component $\hat{\sigma}^2_s$	Inter-class correlation ICC_S
Model Φ(S+δ+ε)p(t+a) (total variances)	$\hat{\sigma}^2_\delta$ =0.386 [0.066,0.885]	$\hat{\sigma}^2_1$ =0.191 [0.017,0.628]	ICC_1 =0.667 [0.173,0.965]
		$\hat{\sigma}^2_2$ =0.137 [0.008,0.487]	ICC_2 =0.735 [0.245,0.982]
		$\hat{\sigma}^2_3$ =0.202 [0.005,0.849]	ICC_3 =0.665 [0.117,0.987]
Model Φ(cov+δ+ε)p(t+a) (residual variances)	$\hat{\sigma}^2_\delta$ =0.288 [0.091,0.711]	$\hat{\sigma}^2_1$ =0.036 [0.000,0.346]	ICC_1 =0.894 [0.304,0.999]
		$\hat{\sigma}^2_2$ =0.079 [0.001,0.377]	ICC_2 =0.787 [0.350,0.996]
		$\hat{\sigma}^2_3$ =0.082 [0.001,0.660]	ICC_3 =0.785 [0.205,0.998]
Fraction of variation accounted for by the climatic covariates	C_δ = 0.256	C_1 = 0.810	
		C_2 = 0.425	
		C_3 = 0.595	

Table 4. Mean over 20 simulated mark-resight data sets of the median value of the MCMC samples for all simulation parameters. For each data set, 50000 MCMC samples were obtained with WinBUGS using the full model $\{\Phi(cov+\delta+\varepsilon)p(t+a)\}$ after a burn-in of 100000 samples. Also shown is bias (in respect to the true value used for generating the simulated data sets), as absolute value and as percentage of the true values. 'Species 1' refers to the Atlantic puffin, 'species 2' to the common guillemot and 'species 3' to razorbill.

	True value	mean of medians	SE of medians	Bias	Bias(%)
a(Sp1)	1.9	1.95	0.23	0.051	2.7%
a(Sp2)	2.9	2.99	0.23	0.094	3.3%
a(Sp3)	1.8	1.72	0.26	-0.077	-4.3%
β_0(Sp1)- intercept	2.50	2.60	0.14	0.098	3.9%
β_0(Sp2)- intercept	2.70	2.74	0.15	0.043	1.6%
β_0(Sp3)-intercept	2.40	2.52	0.14	0.123	5.1%
β_1(Sp1)-wNAO_0	-0.10	-0.09	0.16	0.006	-5.7%
β_1(Sp2)-wNAO_0	0.10	0.12	0.15	0.017	16.7%
β_1(Sp3)-wNAO_0	0.30	0.32	0.21	0.025	8.2%
β_2(Sp1)-wNAO_1	-0.20	-0.19	0.23	0.007	-3.6%
β_2(Sp2)-wNAO_1	0.10	0.10	0.22	0.001	1.2%
β_2(Sp3)-wNAO_1	-0.40	-0.36	0.26	0.036	-9.1%
β_3(Sp1)-SST_0	-0.50	-0.55	0.28	-0.049	9.8%
β_3(Sp2)-SST_0	-0.10	-0.08	0.21	0.022	-21.8%
β_3(Sp3)-SST_0	-0.40	-0.36	0.29	0.036	-8.9%
β_4(Sp1)-SST_1	-0.30	-0.30	0.20	0.000	0.1%
β_4(Sp2)-SST_1	-0.40	-0.43	0.19	-0.031	7.8%
β_4(Sp3)-SST_1	0.04	-0.03	0.27	-0.067	-167.8%
σ^2_δ	0.300	0.338	0.13	0.038	12.8%
σ^2_1	0.040	0.070	0.07	0.030	76%
σ^2_2	0.080	0.094	0.06	0.014	17.6%
σ^2_3	0.080	0.149	0.12	0.069	86%

Figures

Figure 1: Estimated apparent adult survival from model {Φ(cov+δ+ε)p(t+a)} for a) Atlantic puffin, b) common guillemot and c) razorbill at the Isle of May. The point estimates are the median of the MCMC samples for each variable, obtained with WinBUGS. Vertical bars show 95% credible intervals. Survival rate estimates from the fully time-dependent model {Φ(t)p(t+a)}, estimated with WinBUGS for each species separately, are shown as a dotted line.

Figure 2: Estimated resighting probabilities for a) Atlantic puffin, b) common guillemot and c) razorbill at the Isle of May, according to model {Φ(cov+δ+ε)p(t+a)}. The point estimates are the median. Solid lines represent the values when the animal has been resighted the year before; the opposite case is shown with dashed lines. Vertical bars show 95% credible intervals.

Figure 3. Value of the random effect terms (on the logistic scale) estimated for each year by the best model {Φ(cov+δ+ε)p(t+a)}. Both common random terms δ(Y) (a) and the species-specific random terms $\varepsilon_S(Y)$ for each species (b) are shown. Note the different scales in a) and b). The estimates are not shown for the last year of the study.

Figure 1

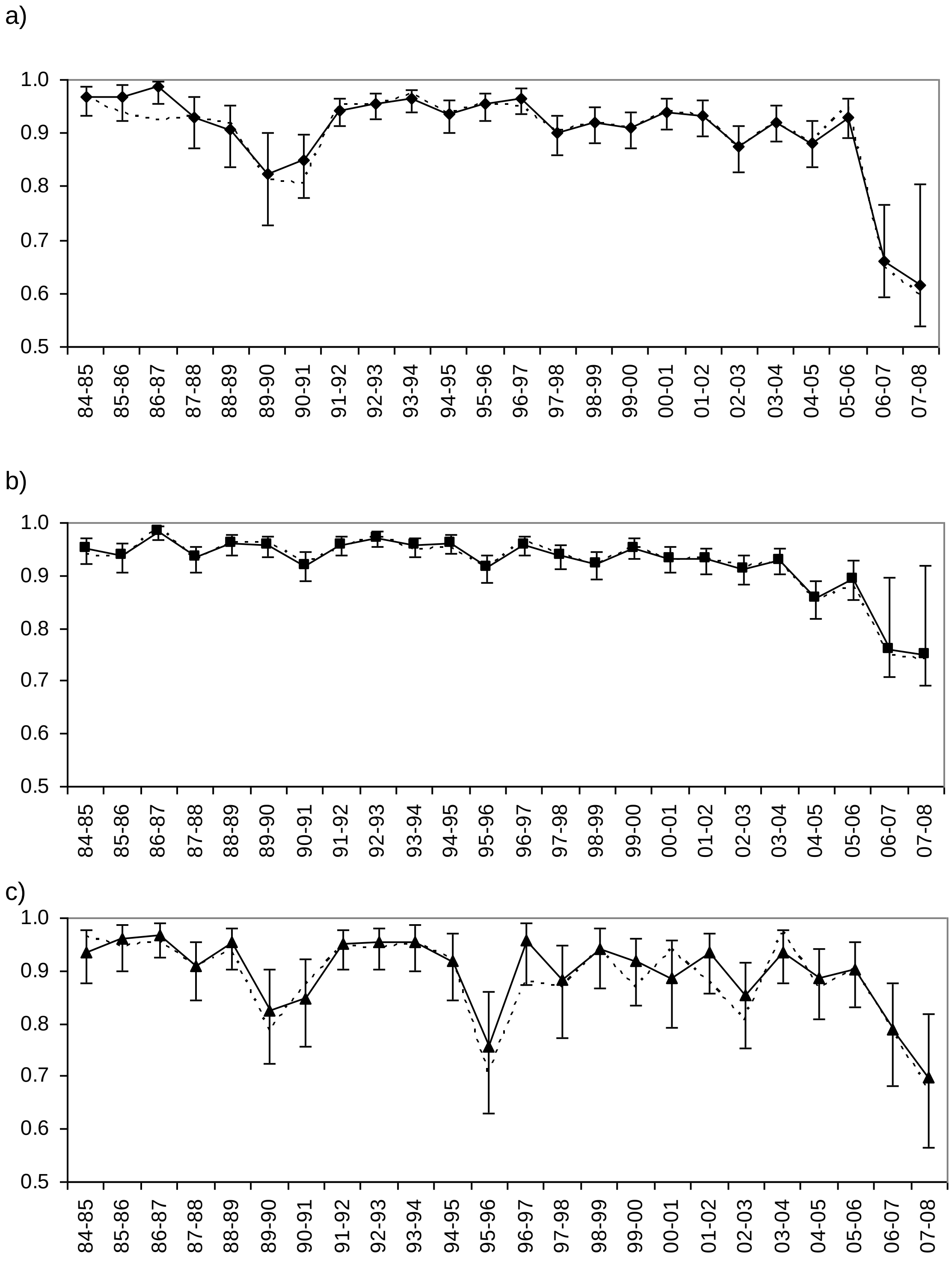
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Figure 2

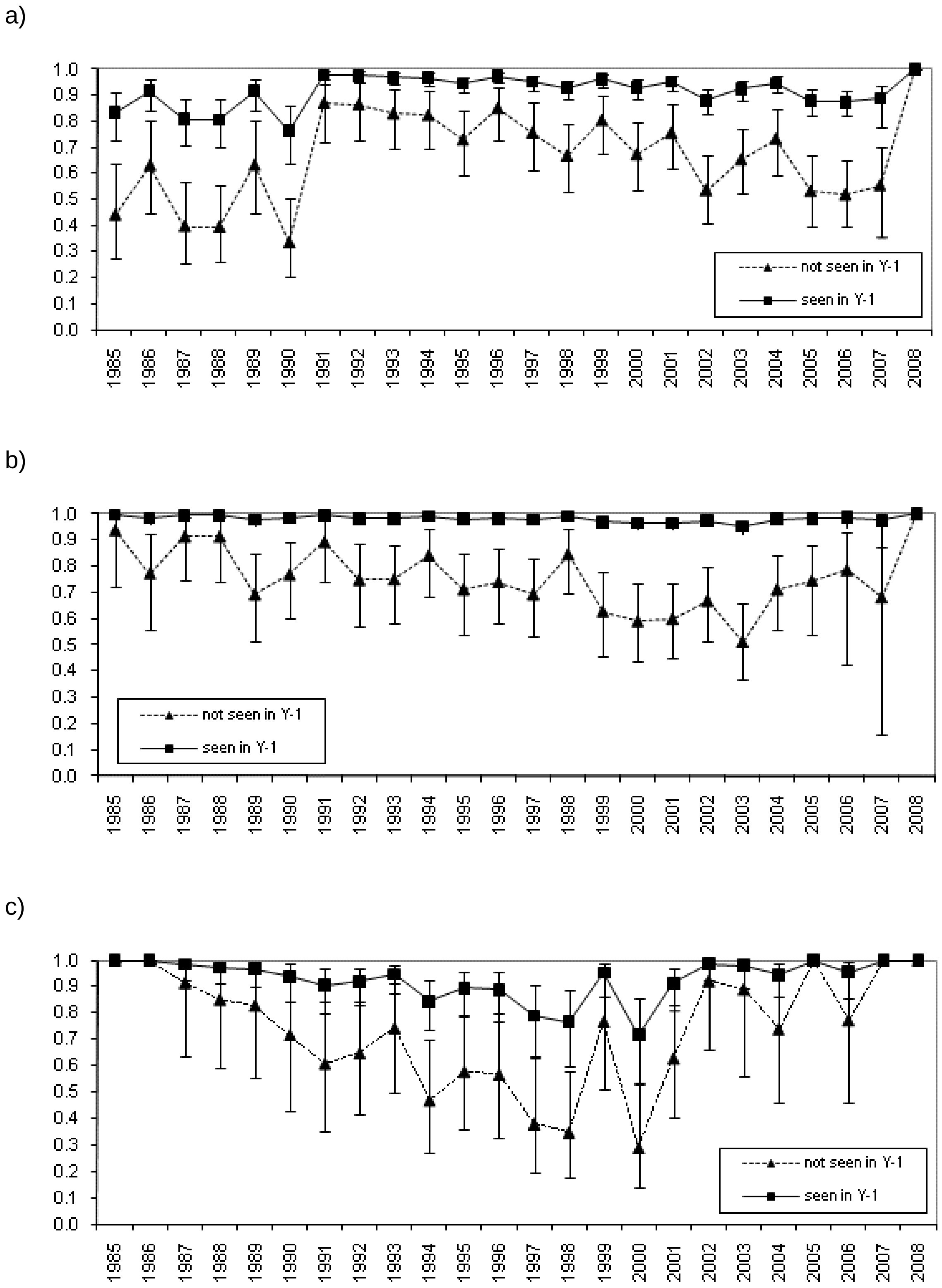
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Figure 3

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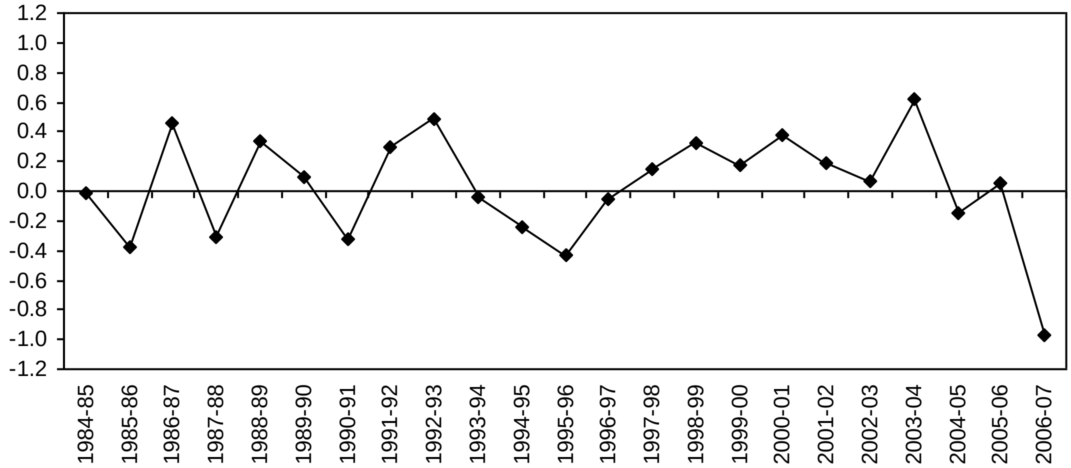
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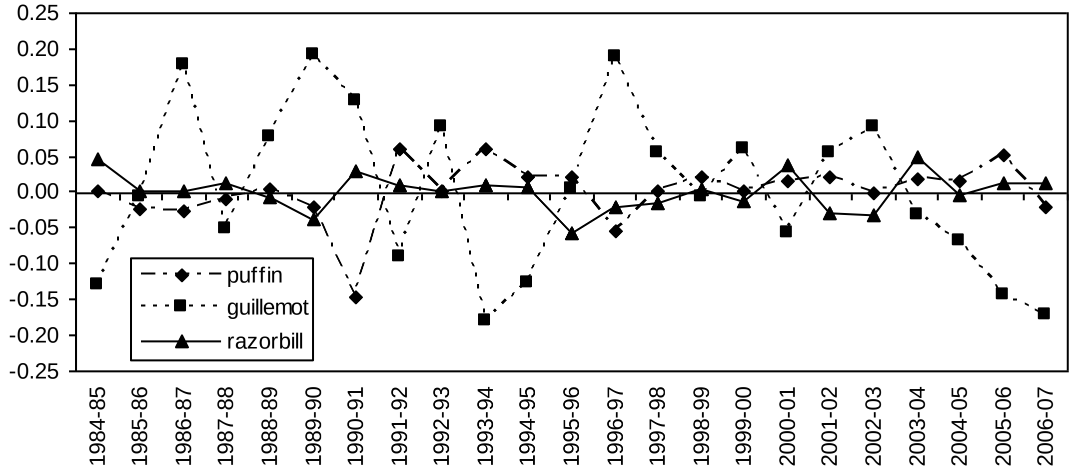
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