Estimating the contribution of survival and recruitment to large scale population dynamics

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Abstract

Estimating the contribution of survival and recruitment to large scale population dynamics.— At large spatial scales, variation in population abundance results from variation in the survival of reproducing adults and variation in the recruitment of new individuals. Which of these two parameters varies the most and how these parameters are correlated are fundamental questions if we want to understand the large–scale dynamics of such populations. I explore how Pradel's seniority (complement of the proportion of new individuals in the population) may help to answer such questions. I show that the sign of the correlation between temporal variation in seniority and of an independent measure of population growth rate should indicate whether population growth rate is more influenced by variation in survival or by variation in recruitment. Various predictions are proposed for evaluating the degree of regulation in the population (i.e., the existence of a negative correlation between survival and recruitment). Data from the French integrated breeding bird monitoring programme, combining point count surveys, from which population growth rate is estimated, and standardized capture–recapture, allowing the estimation of survival and seniority variation, were used to evaluate the method. Patterns of variation were examined for the four most frequently captured species, using data from 32 trapping sites covering 13 years (1989–2001). For Blackcap and Chiffchaff, the pattern is consistent with population growth rate being under the additive influence of survival and recruitment. For the Reed Warbler, the population appears to be strongly regulated, but with recruitment unable to compensate entirely for survival variation. For the Blackbird, the pattern is more confused and may indicate complex population dynamics, with non–linear relationships between survival, recruitment and population growth rate. Altogether, the method appears extremely promising and is particularly suitable for large scale monitoring of breeding birds by means of ringing.

Key words: Breediing bird survey, Constant effort site, Monitoring, Common bird, Seniority, Regulation.

Resumen

Estimación de la contribución de la supervivencia y del reclutamiento en la dinámica de poblaciones a gran escala.— A grandes escalas espaciales, la variación en la abundancia poblacional se produce como consecuencia de la variación en la supervivencia de los adultos en edad reproductora y la variación en el reclutamiento de nuevos individuos. Para comprender la dinámica a gran escala de estas poblaciones es fundamental conocer cuál de estos dos parámetros varía en mayor medida y de qué modo se correlacionan entre sí. En el presente estudio se analiza cómo el modelo de senescencia de Pradel (complemento del porcentaje de individuos nuevos en la población) puede contribuir a responder estas preguntas. Se demuestra que el signo de la correlación entre la variación temporal en la senescencia y el de una medición independiente de la tasa de crecimiento poblacional debería indicar si la tasa de crecimiento poblacional está más influenciada por la variación en la supervivencia o por la variación en el reclutamiento. Se proponen varias predicciones para evaluar el grado de regulación de la población (es decir, la existencia de una correlación negativa entre la supervivencia y el reclutamiento). Para evaluar este método se utilizaron datos del programa francés de seguimiento integral de aves en edad reproductora, en combinación con estudios de recuento de puntos, lo que permite estimar la tasa de crecimiento poblacional, así como la captura–recaptura estandarizada, que permite estimar la variación en la supervivencia y la senescencia. Se examinaron pautas

de variación para las cuatro especies capturadas con mayor frecuencia, empleando datos de 32 localidades de trampeo a lo largo de un período de 13 años (1989–2001). Para la curruca capirotada y el mosquitero común, la pauta concuerda con una tasa poblacional sujeta a la influencia aditiva de la supervivencia y el reclutamiento. Para el carricero común, la población parece estar fuertemente controlada, si bien el reclutamiento no puede compensar por completo la variación en la supervivencia. Para el mirlo común, la pauta es más confusa, pudiendo indicar una dinámica poblacional compleja, con relaciones no lineales entre la supervivencia, el reclutamiento y la tasa de crecimiento poblacional. En conjunto, el método parece extremadamente prometedor y resulta muy adecuado para el seguimiento a gran escala de aves en edad reproductora por medio del anillamiento.

Palabras clave: Censo de aves reproductoras, Estación de esfuerzo constante, Seguimiento, Passeriformes comunes, Senescencia, Regulación.

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Introduction

There is a growing interest in the large–scale monitoring of populations (Yoccoz et al., 2001). One reason for this is global changes which impact biodiversity at large spatial scales. Another reason is the finding that the population dynamics of many species appears to be synchronized over very large geographical areas, leading to a series of emerging scientific questions on the underlying mechanisms. At such scales, and ignoring the age structure of the population, the dynamics of the population may be summarized by the basic equation:

$$N_{t+1} = \lambda_t N_t = (S_t + R_t) N_t \qquad (1)$$

where N is the population size (number of reproducing individuals), λ the population growth rate, S is the survival rate of reproducing individuals and R is the per capita recruitment rate (number of new reproducing individuals produced per reproducing individual per year). Because the biological process influencing survival and recruitment are generally under the influence of different constraints, it is important to determine their relative influence on population dynamics. In other words, which of survival or recruitment variation determine most of the variation in population growth rate (Saether & Bakke, 2000)? For such simple population dynamics, the theoretical sensitivities of these two parameters are equal to 1 (Caswell, 1989), that is variation of 1 unit of survival or 1 unit of recruitment will have the same effect on the population growth rate which will also vary by 1 unit. Hence, what really maters is the amount of natural variation in these two parameters (Gaillard et al., 1998).

A source of such information may come from the estimation of the seniority rate using Pradel's (1996) approach. Seniority rate is a direct measure of the relative contribution of survival and recruitment to the population growth rate, i.e., an analog of elasticity of these two parameters calculated for each time interval (Nichols et al., 2000). This paper explores the use of time–dependent seniority estimates to evaluate whether population growth rate variation is more likely to be due to survival variation, recruitment variation or both. The paper consists of two parts: one is a theoretical analysis of the components of seniority rate and the other is an analysis of data from large–scale ringing–based monitoring undertaken in France (13 years of data from more than 30 sites).

Part 1. Preliminary considerations: temporal co–variation of survival and seniority rates

The seniority rate γ as defined by Pradel (1996) is the estimated proportion of experienced individuals in the population at a given time step. It is obtained by performing a standard survival analysis on reverse capture–recapture histories. $1 - \gamma$ is thus the proportion of new individuals in the population and has been often called recruitment (following Pradel, 1996). This is a bit confusing because $1 - \gamma$ is

generally not equal to recruitment as usually defined by population biologist (i.e., R_t in [1]). Using the parameters from (1), the expected seniority rate may be expressed as a function of survival and recruitment rate:

$$E(\gamma_t) = S_t N_t \,/\, N_{t+1} = S_t N_t \,/\, (S_t + R_t) N_t = S_t \,/\, S_t + R_t \quad (2)$$

From (2), it can be shown that $E(\gamma_t)$ is always between S_t and $1 - R_t$. The quantity $1 - \gamma_t$ is equal to the "true" recruitment only for $S_t + R_t = 1$, i.e., when the population is stable (but then, recruitment can be directly inferred from survival as $R_t = 1 - S_t$). Hence, seniority is a function of recruitment and survival.

In addition to this structural link between seniority and survival expectancies, sampling variation causes a further positive correlation between survival and seniority estimates. Indeed, sampling variation, i.e., the difference between estimated survival in the studied population and the actual survival, affects survival and seniority estimates similarly. In other words, in the absence of actual variation in survival and recruitment, survival and seniority estimates will still be positively correlated.

A logit transformation shows that the actual variation in survival and recruitment contributes equally to variation in seniority rate:

$$\text{logit } (E(\gamma_t)) = \log (S_t) - \log (R_t) \qquad (3)$$

It further shows that temporal variation in seniority should be positively correlated with survival rate variation and negatively correlated with recruitment rate variation. Interestingly, population growth rate as defined in (1) is positively correlated with survival and positively correlated with recruitment rate:

$$\lambda_t = S_t + R_t \qquad (4)$$

Hence, if population growth rate is more influenced by survival variation than by recruitment variation, then population growth rate and seniority rate should be positively correlated, and conversely, if population growth rate is more influenced by recruitment variation than by survival variation, then population growth rate and seniority rate should be negatively correlated. The sign of the correlation between population growth rate and seniority will thus indicate which of survival or recruitment most influence the population dynamics.

When both survival and recruitment rates vary, the prediction depends on the sign of their co–variation:

(1) survival and recruitment variation may be negatively correlated. This may occur when the population is strongly regulated, i.e., when high adult survival limits recruitment of new individuals or, when low adult survival is compensated by high recruitment. If the correlation is very high, then point estimates of seniority rate and survival rate for a given time step should be very similar, that is, $\hat{\gamma}_t \approx \hat{\phi}_t$. Furthermore, population growth rate variation should be much reduced.

(2) Survival and recruitment variation may be positively correlated. This may occur when the same environmental factor affects adult survival and recruitment of new individuals (for example, winter weather may strongly determine both adult and juvenile survival variation). This will result in low variation in the seniority rate (because variation in the number of experienced individual will be hidden by the same variation in the number of new individuals).

Other tests may help to discriminate between these different situations. Three appear particularly useful: (i) the correlation between population growth rate and survival (predicted to be positive if survival variation affects population growth rate variation); (ii) comparison of the importance of temporal variation between survival and seniority (see prediction in table 1); (iii) the partial correlation between seniority rate and estimates of both survival rate and population growth rate (table 1).

Part 2. Case study: estimating temporal variation in survival and recruitment from nation–wide capture–recapture monitoring

In many countries, volunteer ornithologists monitor the abundance of common breeding birds by means of extensive surveys. Such monitoring is based on counts of individuals undertaken using a standardized method, at fixed points, transects or sites. The repetition of these counts year after year by the same observer at a given place makes it possible to estimate variation in abundance. These schemes, known as the Breeding Bird Survey in North America or the Common Birds Census in the U.K. were started as early as the 1960s. More recently, besides these traditional censuses using direct counts, amateur ringers have been involved in breeding bird population monitoring by a growing number of ringing schemes. Such programmes, known as the CES (Constant Effort Site, in Britain and Ireland, started in 1983, and subsequently in a growing number of countries in continental Europe; Peach et al., 1996) or MAPS (Monitoring Avian Populations for Productivity and Survival, in North America, started 1994; DeSante et al., 1999) are based on standardized mist–netting of breeding populations of small birds at a number of sites, repeated year after year. Date and number of capture occasions, as well as the numbers and locations of mist–nets are kept as constant as possible from one year to the next for a given site.

The French breeding bird monitoring programme

In France, both a BBS–like and a CES–like programme were initiated in 1989 (Julliard & Jiguet, 2002). For the BBS type of survey, individuals were counted on permanent plots during a fixed period of 5 minutes, counting both visible individuals and singers. To be valid, the counts must be repeated at approximately the same date (± 7 days within April

to mid June), at the same time of day (± 15 minutes within 1 to 4 hours after sunrise), by the same observer. Between 1989 and 2001, 3,000 points were surveyed over an average six years per site. Survey plots usually comprised groups of 10–15 points, with at least 200 m between each point. Such groups of points were not spread homogenously over France. However, clusters of groups were found in the North, Normandy, Auvergne and Languedoc, i.e., regularly scattered on a north–south gradient. This data set makes it possible to estimate changes in the abundance of the various species considered, using a standard log–linear analysis with a site effect included (e.g., Julliard et al., 2004).

The basis of the French CES protocol is the same as that used by other CES schemes: mist–nets are erected at the same place, year after year and capture sessions are conducted at nearly the same dates each year. However, compared to other CES schemes, more nets are erected per site (12–50 12m–long nets), and there are usually only three trapping sessions per year between mid–May and mid–July, instead of 9–12 visits between May and August. Nets are concentrated on a small area to ensure a high density of nets (3–5 nets per ha) in order to maximize capture rates. As in other CES schemes, all individuals are ringed. Nets are visited every 30–60 minutes, and birds are immediately released near the net after data have been taken. All recaptures, even those from the same day, are recorded. For all species, plumage features provide good criteria for age determination, allowing accurate distinction between adults and young of the year (Svensson, 1992).

The goal of this analysis was to compare temporal variation in survival and seniority, and to analyze how temporal variations in these parameters were correlated with variations in population growth rates estimated from the point count survey. Note that no point counts were run on CES sites.

Data selection and parameter estimation

Throughout the analysis, juveniles are ignored. The analysis was repeated for the four most abundant species: Blackcap *Sylvia atricapilla* (6,272 individuals), Blackbird *Turdus merula* (3,446 individuals), Reed Warbler *Acrocephalus scirpaceus* (3,205 individuals), and Chiffchaff *Phylloscopus colybitta* (2,722 individuals). All sites with at least three consecutive years of captures between 1989 and 2001 were selected. On average, each site was operated for eight years giving a total of 258 site–years. For three sites, the data set was split into two parts due to major changes in the number of nets. For any given site, only species with at least five individuals captured and at least one individual recaptured were selected.

For the most widespread species, there were 31 data sets each of which included up to 13 years of data. The full time dependent model, including all possible combinations of years and sites, thus re-

Table 1. Prediction of the effects of the actual temporal co–variation of survival (*S*) and recruitment (*R*) on the outcome of modeling temporal variation in estimated survival (ϕ) and seniority rates (γ). $\lambda_t = S_t + R_t$, is the population growth rate: (v). Variable; (c). Constant; + Positive correlation; – Negative correlation; [1] Due to sampling correlation; [2] Adjusted effect more significant than main effect; NS. Test should be statistically not significant.

*Tabla 1. Predicción de los efectos de la covariación temporal real de la supervivencia (*S*) y el reclutamiento (*R*) en los resultados de la modelación de la variación temporal en la supervivencia estimada (v) y los índices de senescencia (c). k_t = S_t + R_t, es la tasa de crecimiento poblacional: (v). Variable; (c). Constante; + Correlación positiva; – Correlación negativa; [1] Debido a la correlación de la muestra; [2] Efecto ajustado más significativo que el efecto principal; NS. El test debería ser estadísticamente no significativo.*

	S_t(v), R_t(c)	S_t(c) R_t(v)	S_t(v) R_t(v) uncorrelated	– correlated	+ correlated
LRT time dependence	$\phi > \gamma$	ϕ (NS) $< \gamma$	unpredictable	$\phi \approx \gamma$	$\phi \gg \gamma$
Sign of the correlation between γ_t and λ_t	+	–	unpredictable	λ not varying much	γ not varying much
Partial correlation between γ and ϕ_t and λ_t	ϕ_t + λ_t NS	ϕ_t + [1] λ_t – [2]	ϕ_t + [2] λ_t – [2]	ϕ_t + λ_t NS or –	ϕ_t + [1] λ_t NS or –

quires 744 parameters to be defined. Such large numbers of parameters pose several problems. A minor one is that MARK (White & Burnham, 1999) is unusable if the analysis has to be done in a reasonable amount of time. I thus relied on SURGE (Reboulet et al., 1999). This may solve the issue of computing time but there are still problems of convergence. Local likelihood maxima were detected in many of the model runs. Being interested in models with common temporal variation in survival across sites, and not being willing to make unrealistic assumptions of constancy of capture probability over time or sites, I first planned to use the model [$\phi_{site+year}$; $p_{site*year}$], i.e., additive effect of year and site for survival and full time and site variation for capture probability, as a baseline model (notation as in Lebreton et al., 1992). A way to decrease the rate of presumably bad convergence was to constrain all capture parameters corresponding to year–site combinations that were not monitored to be equal. This represents about 1/3 of the capture parameters. This has the other advantage of checking that no mistakes occurred when the data set was being built: the estimated values for all of these parameters should be 0. Yet, there were still several cases of bad convergence. One of the symptoms was that the last survival (or seniority) estimate was equal to 1. Another sign of bad convergence in the case of models including external variables was that the ratio (estimated slope/standard error) differed substantially from the LRT for constancy of the parameter. Unfortunately, changing initial values was usually inefficient when the model included a large number of parameters.

In order to reduce the number of parameters to be estimated, I used the mean number of within–season recaptures as a proxy for the efficiency of capture rate for a given species in a given site. Many individuals are captured several times within a CES season. The average number of captures per captured individual calculated for each year, each species and each site was used as an external variable for modelling capture probability. For each data set, six models of capture rate variation were used [$p_{site*year}$], [p_{c*site}], [p_{c+site}], [p_{site}], [p_c], [$p.$] where *c* represents the external variable as defined above. The AIC of model [p_c] was generally far smaller than the AIC values of models with other parameterizations of capture rate, whatever the model for survival or seniority. LRT tests for the significance of the external variable [p_c] <> [$p.$] varied between 15 and 30 (1 df) indicating that the variable was able to retrieve much of the variation in capture probability, both between and within sites. This result appears to be extremely useful because capture probability could be modelled with only two parameters without making assumptions of constancy over time or sites.

Results

For each species considered, I ran the various tests proposed in table 1.

For all species, statistically significant temporal variation in survival and seniority were detected (table 2, fig. 1). Survival was clearly more variable than seniority in two cases (Blackbird & Chiffchaff, table 2). In the other two cases, the amount of temporal variation in survival and seniority were similar. For three cases out of four, the different tests fitted more or less with one of the scenarios described in table 1.

Table 2. Modeling temporal variation in seniority (γ) and survival (ϕ). Changes in deviance between nested models (i.e., LRT) are presented (changes in AIC could be obtained as changes in deviance – 2df). For every species and model, capture probability was modeled with a site–, year– and species–specific capture efficiency index (see methods). (The sign is the sign of the slope of the external variable of interest.)

Tabla 2. Modelación de la variación temporal en la senescencia (γ) y la supervivencia (ϕ). Se indican los cambios de desviación entre los modelos anidados (es decir, LRT) (los cambios de AIC podrían obtenerse como cambios de desviación – 2df). Para cada especie y modelo, la probabilidad de captura se modeló con un índice de eficiencia de captura dependiente del lugar, el año y la especie (ver métodos).

Test	Df	Chiffchaff	Blackcap	Reed Warbler	Blackbird
LRT $[\phi_t]$ vs $[\phi_.]$	11	45.48	31.36	35.04	35.50
LRT $[\gamma_t]$ vs $[\gamma_.]$	11	19.78	36.36	31.97	19.99
LRT $[\phi_\lambda]$ vs $[\phi_.]$	1	15.63 (+)	6.56 (+)	6.67 (+)	4.25 (+)
LRT $[\gamma_\lambda]$ vs $[\gamma_.]$	1	2.25 (−)	0.99 (−)	14.32 (+)	0.01
LRT $[\gamma_\phi]$ vs $[\gamma_.]$	1	5.51 (+)	8.31 (+)	22.00 (+)	0.01
LRT $[\gamma_{\lambda+\phi}]$ vs $[\gamma_\phi]$	1	10.74 (−)	5.94 (−)	3.90 (+)	0.02
LRT $[\gamma_{\lambda+\phi}]$ vs $[\gamma_\lambda]$	1	14.00 (+)	13.26 (+)	11.57 (+)	0.01

Chiffchaff and Blackcap

For the Chiffchaff, survival variation was strongly positively correlated with to population growth rate variation (15.53 units of deviance from the 45.48 units for temporal variation; table 2). Seniority was slightly negatively correlated with population growth rate variation (2.25 units of deviance from the 19.78 units for temporal variation; table 2). However, after adding survival estimates as a second external variable, the test for the effect of population growth rate jumped to 10.74 units of deviance (table 2). The two variables explained almost all of the temporal variation in seniority (16.25 units of deviance explained with 2 df and 3.23 units of deviance unexplained with 9 df left; table 2).

For the Blackcap, a similar tendency was detected, but the proportion of temporal variation explained was lower (table 2).

Altogether, for these two species, the pattern of variation fitted well with population growth rate being determined concomitantly by variation in both survival and recruitment.

Reed Warbler

For the Reed Warbler, time–dependent seniority estimates were very similar to the time–dependent survival estimates (fig. 1). Both seniority and survival were positively correlated with population growth rate. Even after introducing the survival estimates as an external variable for modeling seniority variation, the estimated slope for population growth rate remained positive (table 2).

This pattern is close to the one predicted for a strongly regulated population with recruitment variation compensating for survival variation. In addition, the fact that seniority was rather strongly positively correlated with population growth rate suggested that population growth rate was more influenced by survival rate than by recruitment rate. Altogether, the observed pattern of variation suggests that variation in recruitment imperfectly compensated for variation in survival.

Blackbird

For the Blackbird, few correlations were found: survival was to a small extent correlated with population growth rate (4.25 units of deviance from the 35.50 units for temporal variation). Seniority was neither correlated with population growth rate nor with survival (0.03 units of deviance explained from the 19.99 units for temporal variation). Yet, inspection of figure 1 suggests that seniority and survival co–varied in some years but not in others. A plot of seniority estimates against population growth rate revealed a possible non–linear relationship (fig. 2). Indeed, the square of population growth rate (λ^2) was significantly related to seniority (7.40 units of deviance). The main effect of population growth rate was still not significant indicating a symmetric relationship around zero. The slope for λ^2 was negative. Hence, seniority tended to be positively correlated with λ when the population was decreasing and negatively related to λ when the population was increasing. This could indicate that variation in Blackbird sur-
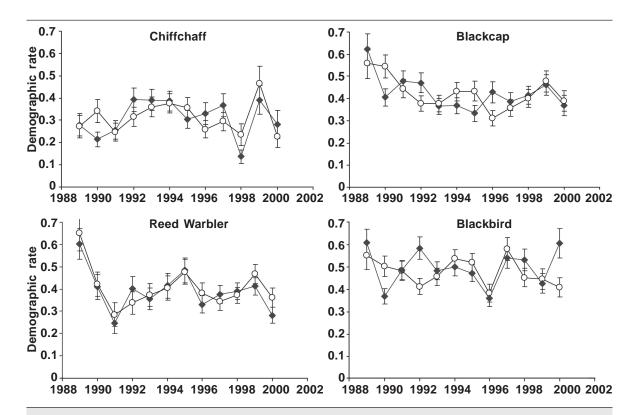
Fig. 1. Temporal variation in survival (black diamonds) and seniority (open circles) for four common passerines: vertical bars ± 1 SE. (Data from the French Constant Effort Site scheme.)

Fig. 1. Variación temporal en la supervivencia (rombos negros) y la senescencia (círculos blancos) para cuatro Paseriformes comunes: barras verticales ± 1 EE. (Datos extraídos del programa francés Constant Effort Site.)

vival is mainly responsible for population declines while population recovery is mostly under the control of recruitment.

General discussion

Data quality

As almost everywhere else, the French point count survey was not based on an explicit sampling framework. Instead, observers were asked to choose their survey sites. Hence, there is no guarantee that population variation measured by such a scheme is representative of the actual population variation. Yet, previous analyses have shown fairly high similarities between population variation from this scheme and from comparable surveys in neighboring countries (Julliard et al., 2004).

In addition to the lack of a sampling framework for the survey sites, using mist–nets added constraints to the choice of sites. The scrub layer has to be well developed to ensure efficient trapping. Hence, there is a further bias toward particular habitats amongst the sites used for mist–netting. Yet, population size variation (measured as the number of adults caught) estimated from capture data is very similar to population variation measured from point count surveys for many species (R. Julliard, unpublished analysis). This was the case in particular for Blackbird, Blackcap and Chiffchaff, but not for the Reed Warbler.

Altogether, this means that finding relationships between population growth rates estimated with one survey and demographic parameters estimated with another, is in itself an important results. Indeed, few studies have demonstrated the usefulness of CES/MAPS ringing monitoring. This is partly due to the young age of such schemes (the French one is among the oldest), and partly due to the difficulty of the analysis (dealing with data from so many sites is rather time consuming).

Robustness of the approach

For Blackcap and Chiffchaff, the approach suggests that both survival and recruitment variation
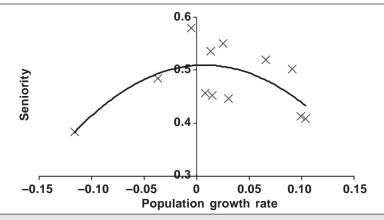
Fig. 2. Relationship between seniority and population growth rate for the Blackbird showing a possible nonlinear relationship. Seniority estimated from the French Constant Effort Sites data; population growth rate estimated from the French Breeding Bird Survey.

Fig. 2. Relación entre la senescencia y la tasa de crecimiento poblacional del mirlo común, indicando una posible relación no lineal. La senescencia se ha estimado a partir de los datos del programa francés Constant Effort Site; la tasa de crecimiento poblacional se ha estimado a partir de los datos del censo francés de aves reproductoras.

shape the population growth rate. Although such a claim may appear trivial, it is probably the first time it is supported by such convincing results at this spatial scale. The main limitation of previous studies of the contributions of different demographic parameters to population growth rates is that the population growth rate estimate and demographic parameter estimates came from the same data sets (e.g., Saether & Bakke, 2000; Saether et al., 2002).

For the Reed Warbler, the results suggest that survival rather than recruitment is the main driver of population growth rate. In addition, there was evidence for some compensation between recruitment and survival. This suggests that Reed Warbler populations are strongly regulated (the level of recruitment is dependent of the level of survival), but that variation in survival is too large to be compensated by recruitment, leading to further population variation.

It should be noted that the method described here makes it possible to clearly separate negatively correlated survival and recruitment (regulated populations) from positively correlated survival and recruitment (due for example to similar climatic effects). The adult survival of Reed Warblers may partly depend on rainfall in their African winter quarters, as has been found for the con–generic Sedge Warbler *A. schoenobaenus* (Peach et al., 1991). It is plausible that juvenile survival is also under the influence of the same climatic variable, in which case survival and recruitment should be positively correlated. Although this may be true, the results clearly indicate that regulation totally obscures any

such relationship, reversing the sign of the expected relationship between recruitment and survival.

The results for the Reed Warbler highlight another aspect of the patterns for Chiffchaff and Blackcap. The fact that the effect of recruitment on population growth rate was detectable (negative relationship between seniority and population growth rate) suggests weak, if any, regulation by recruitment in these species. As noted in the preliminary analysis, perfect compensation between recruitment and survival should lead to equality between point estimates of seniority and survival for a given time step. As a consequence, the slope relating seniority and survival estimates should be equal to 1. Without such compensation, the relationship should be blurred by independent variation in recruitment, and the slope should be below 1. Hence, it might be possible to estimate the compensation between survival and recruitment by estimating the slope between seniority and survival. Further studies along these lines may be useful, although one has to keep in mind that sampling variation is likely to weaken the approach.

Another interesting aspect would be to evaluate the relative contributions of survival and recruitment variation to population growth rates. The relevant information is reflected in the relative importance of temporal variation of survival and seniority and in the strength of the relationship between seniority and population growth rate. Again further studies are needed, and again, the sampling correlation between seniority and survival may reduce the chances of obtaining a clear answer. In this study we have already found contradictory results for the Chiffchaff

where survival was found to be much more variable than seniority (suggesting more variation in survival than in recruitment) but the slope relating seniority to population growth rate was negative (suggesting a stronger influence of recruitment than survival).

For the Blackbird, the method failed to identify a simple scenario. Although the possibility that the data set for this species was too biased cannot be ruled out, there is no reason why it should be more biased than those for the other species. In particular, Blackbirds have relatively high survival and capture rates. I suggested that the absence of simple patterns of variation in the parameters considered is due to non–linear effects of survival and recruitment on population growth rate, with survival variation being responsible for population decrease and recruitment variation being responsible for population increase. Although this interpretation is appealing at first glance, the biological mechanism that might bring about such a scenario is unclear. Furthermore, it is not entirely clear whether such a scenario would indeed result in the observed pattern. Again further work is needed. Yet, the fact that the method may allow the detection of non trivial patterns of population dynamics is particularly exciting.

Suitability of data for such analyses

It must be stressed that the method presented here depends on the availability of independent estimates of population growth rates. It is obvious that population growth rate estimated from the same CMR data using Pradel's (1996) approach is unsuitable. Similarly, population growth rates estimated by other means, that are not independent of the number of captured individuals (e.g., number of nests in a study population for which the capture rate is high) are also likely to lead to spurious results, because of the strong sampling correlation between all of the estimated parameters.

The other limit comes from the use of seniority. The general case where it is used here is noticeably different from the particular case where it has mostly been used previously, that is, to study age–specific accession to reproduction (Pradel & Lebreton, 1999). Indeed, in the case studied here, it is essential that the same technique is used to catch unmarked individuals and to recapture individuals: the capture rate, estimated from the sequence of recaptures, must apply to unmarked individuals. In particular, all data based on resightings do not satisfy this requirement, since the resighting probability cannot be assumed to be equal to the capture probability of unmarked individuals.

Implication for CES/MAPS monitoring

As stated above, this study considerably strengthens the case that CES/MAPS monitoring is capable of measuring temporal variation in recruitment and survival. In addition, it demonstrates the value of catching as many adults as possible instead of maximizing both adult and juvenile captures. This has implications for the optimal number of trapping occasions. The 9–12 trapping occasions recommended by most schemes aims to cover the reproductive season as completely as possible. However, because the adult population is constant, the number of new adults caught is continuously decreasing from one trapping occasion to the next throughout the season. If there is a trade off at the scale of the country between the number of sites monitored and the number of trapping occasion within a site, then in order to maximize the number of adults caught, the optimal number of trapping occasions may be much lower than 10. In France, where the requested number of trapping sessions is 3 (ringers are allowed to do more), the number of sites reached 90 in 2003. In the U.K., there are about 120 CES, but about 10 times more ringers than in France.

Acknowledgments

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