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Disentangling the sources of variation in the survival of the European dipper

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ABSTRACT   *The population growth rate of the European dipper has been shown to decrease with winter temperature and population size. We examine here the demographic mechanism for this eﬀect by analysing how these factors aﬀect the survival rate. Using more than 20 years of capture-mark-recapture data (1974-1997) based on more than 4000 marked individuals, we perform analyses using open capture-mark-recapture models. This allowed us to estimate the annual apparent survival rates (probability of surviving and staying on the study site from one year to the next one) and the recapture probabilities. We partitioned the variance of the apparent survival rates into sampling variance and process variance using random eﬀects models, and investigated which variables best accounted for temporal process variation. Adult males and females had similar apparent survival rates, with an average of 0.52 and a coeﬃcient of variation of 40%. Chick apparent survival was lower, averaging 0.06 with a coeﬃcient of variation of 42%. Eighty percent of the variance in apparent survival rates was explained by winter temperature and population size for adults and 48% by winter temperature for chicks. The process variance outweighed the sampling variance both for chick and adult survival rates, which explained that shrunk estimates obtained under random eﬀects models were close to MLE estimates. A large proportion of the annual variation in the apparent survival rate of chicks appears to be explained by inter-year diﬀerences in dispersal rates .*

1 Introduction

Predicting the future dynamics of population in the face of environmental changes requires reliable estimates of demographic parameters, their variability through

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time, as well as covariances among them and the sources of their variability (Caswell, 1989; Sugihara *et al.*, 1990; Van Tienderen, 1995). Obviously, the limiting factor in this context is the amount and quality of data available to estimate the parameters and infer the types of processes underlying their variability (Sæther *et al.*, 1998; Gaillard *et al.*, 2000; Tufto *et al.*, 2000). The analysis of time series based on estimates of population size contributes to the evaluation of the relative impact of density-dependent and density-independent factors on the fluctuation of population size (e.g. Sugihara & May, 1990; Ellner & Turchin, 1995; Engen *et al.*, 1998; Sæther *et al.*, 2000a,b). However, focusing on population size alone limits our insights into mechanisms (Coulson *et al.*, 2000), the study of which requires investigation of parameters such as survival, reproductive, immigration and emigration rates.

The development of capture-mark-recapture models facilitated investigation of survival rates and permitted tests for an influence of age and other factors, such as for example sex, climate or density on survival rates (Lebreton *et al.*, 1993). However, a large sampling variance makes identification of the biological processes underlying the variability in survival difficult (Burnham *et al.* 1987; Link & Nichols, 1994). The introduction of random effects models (Burnham in review), which allow decomposing a series of point estimates into a sampling variance and a process variance, provided a new tool for estimating the characteristics of biologically interesting processes.

The dynamics of the population of the European dipper (*Cinclus cinclus*) of the Lygna river in Norway has been shown to be driven by an interaction of density and winter weather (Sæther *et al.*, 2000a). Annual variation in winter climate accounted for about half of the temporal variance in the population growth rate. These results, based on population censuses performed from 1977 to 1997, focused on net recruitment rate (log-transformed multiplication annual rate λ) and immigration rate, that were both density-independent and positively correlated with winter temperature. Here, we addressed the demographic mechanisms underlying those fluctuations in population size using a long-term data set on marked birds. More specifically, we focused on temporal variation in age-specific survival rates, which in small passerine birds often varies in both space and time (e.g. Clobert *et al.*, 1988; Gould & Nichols, 1997; Ringsby *et al.*,1999), explaining a large proportion of the temporal variance in population growth rates of Sæther & Bakke (2000). We disentangled the respective influence of density and winter climate on variation over time in survival. We focused on the true process variance, which can be estimated by decomposing the total variance using random effects models (Burnham *et al.*, 1987).

2 Study area and population

The study area was located in the lower part of the Lygna river in the county of Vest Agder in southern Norway (58°15′N, 7°15′E). It extended for 60 km from the mouth of the river to the inland. The same study area was surveyed from 1974 to 1997.

Dippers have been captured and marked every year since 1974. Chicks were captured in the nest while older dippers were caught using nets. All individuals were marked with colour rings (breeding birds) or metal rings (chicks), measured and released. Sex can be determined only for birds 1-year-old. Age is known exactly when birds are caught for the first time as chicks or yearlings. In other

TABLE 1. Number of dipper marked as chicks, 1 year-old and 2 year-old marked in Lygna river and included in the analysis. Note that only chicks that have been recaptured when 1 year-old or older could be sexed. Thirteen individuals classified as $\geqslant 1$ year-old when captured (8 females and 5 males) have not been included in the analysis because they could not be put into the age class categories considered here

Age at capture	Chick	1-year-old	2-year-old	Total
Males	113	309	197	619
Females	100	402	180	686
Undetermined	3355	0	0	3355
Total	3568	715	377	4660

cases, individuals were classified as adults. A total of 4660 birds were marked during the period, 3568 of which were caught for the first time as chicks, 715 as 1-year-old and 377 as adults (older than 1 year) (Table 1).

The size of the breeding population in year t has been estimated from 1978 onwards by searching the banks of the river several times during the breeding season for occupied nest sites (Fig. 1). The size of the breeding population was expressed in terms of number of breeding pairs. The dipper is territorial and only nests along rivers (Wilson, 1996). Locating nests and determining whether a breeding pair occupies them are therefore facilitated by this linearity and territoriality characteristic of the dipper's ecology. It was not possible to obtain an estimate of the population size using capture-mark-recapture models (e.g. through a robust design approach, Pollock *et al.*, 1990) because the protocol had not been planned to perform such an analysis. However, the estimates of the number of breeding pairs were unlikely to be related to variation in the capture and recapture effort, because the counting of occupied territories was an independent process from capturing and marking birds. Data on population size were not available for the first 4 years of the study (1974-1977).

Winter is a critical stage for the survival of dipper in Europe (Galbraith & Tyler, 1982; Sæther *et al.*, 2000a). We used three different indices of winter harshness, all available from 1974 onwards. Mean winter temperature (denoted 'win')
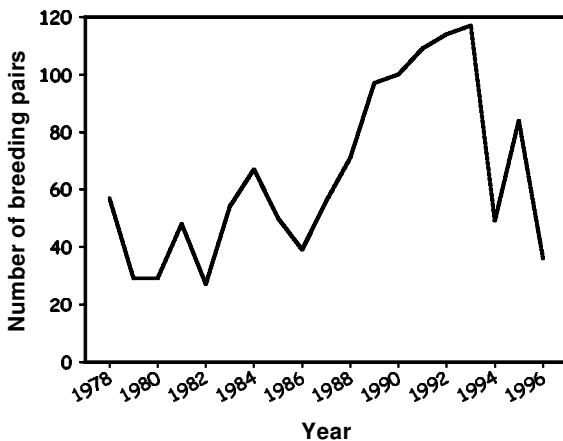

FIG. 1. Number of breeding pairs of dipper along the river Lygna from 1978 to 1996.

corresponded to the mean temperature from January to March and was recorded at the Konsmo weather station by the Norwegian Meteorology Institute. The number of days with ice (denoted 'ice') on the lake Lygna at the river's upper end has been recorded every year since 1974 by local representatives of the Norwegian Water Resources and Electricity Directorate. As an additional index of winter climate, we also considered the North Atlantic Oscillation Index (denoted 'NAO'), which is an index of large-scale fluctuations in atmospheric mass between the subpolar Atlantic and the subtropic regions (Hurrell, 1995). As a general pattern, high positive values of the NAO index tended to be associated with warm and rainy or snowy winters in coastal regions of the European northern Atlantic (Mysterud *et al.* 2000). Winter temperature, NAO and the number of days with ice on the river are highly intercorrelated (see below) and were therefore not included together in the same model. All these variables were standardized before analysis.

3 Statistical analyses

We used capture-mark-recapture/resighting models to estimate apparent survival, and recapture probabilities (see Lebreton *et al.*, 1992, for a review). Apparent survival (Φ) was estimated on a yearly basis (from one summer to the next) and corresponded to the probability of surviving and staying on site. If the true survival is denoted S and the dispersal probability d, then $\Phi = S(1 - d)$. Recapture probability (p) is the probability of capturing or resighting a marked bird during summer. Notations follow advice given by Lebreton *et al.* (1992) for the first data set and were similar to Catchpole *et al.* (2000) for the second data set (see below).

We performed analyses on two separate data sets. The first data set was based on all birds of known sex, i.e. captured at least once when 1 year-old. For all these birds, sex was determined. We could therefore test both sex differences and the variation of apparent survival through time. Dippers breed in pairs but some level of polygyny is sometimes observed (Wilson, 1996; Yoerg, 1998), whereby sex-specific survival rates could be expected. Sex and time effects were designated by 'sex' and 't' between parentheses with '$\star$' for interacting effects and ' $+$ ' for additive effects (e.g. $\Phi(\text{sex} + t)$ meant that apparent survival varied with the main effects of sex and time, with no interaction). Covariates were placed between brackets and as subscripts ($\Phi_{[n]}$ means that apparent survival is a linear function of population size on a logistic scale, see Table 2 for more details).

The second data set was based on all birds of known age, i.e. captured as chicks or 1 year-old. We considered three age-classes: chicks, 1 year-old birds and 2 year-old birds. Although individuals can reproduce as yearlings, their reproductive success is lower than in older birds (Wilson, 1996). We therefore checked whether they also differed in their apparent survival rates. We tested for age and time effects in the apparent survival rates, and then focused on chick apparent survival. Because models can become quite complicated to write when age, time and covariate can interact, we adopted the notation used by Catchpole *et al.* (2000). The apparent survival had a subscript for age (e.g. Φ_c for chick survival, $\Phi_{\geqslant 1}$ for the survival of $\geqslant 1$ year-old birds). Time variability was indicated between parentheses and covariates between brackets. When time had an additive effect on the survival of two different age-classes, survival for these age classes was grouped between parentheses (e.g. $(\phi_c, \Phi_{\geqslant 1})(t)$ indicates that the survival rates of chick and of $\geqslant 1$ year-old birds covaried in parallel over time on a logistic scale, see Table 4 for details).

The analysis followed three steps. In the first step, we assessed the fit of models

used as a starting point in the analyses. Goodness-of-Fit tests (GOF) were performed using (1) program RELEASE (Burnham *et al.*, 1987) and (2) Monte Carlo tests (500 simulations) implemented in program MARK (White & Burnham, 1999). For the first data set (i.e. adult birds), we evaluated the fit of the Cormack-Jolly-Seber (CJS) model stratified by sex (model $\Phi_{sex\star t}$, $p_{sex\star t}$). As this step did not provide evidence of an effect of sex (see results), we then assessed the fit of the non-stratified CJS model with a Monte Carlo test. For the second data set, which involved three groups dependent on the age at first capture (chicks, yearlings, adults), we pooled the various components of the GOF test of the CJS model stratified by group obtained using program RELEASE. However, as we expected a lower chick apparent survival, we did not include the Test 3. SR component of the chick group (see Gaillard *et al.* 1997 for a similar approach). We performed the Monte Carlo test using model $\Phi_c(t)\Phi_1(t)\Phi_2(t)p_c(.)p_1(.)p_2(.)$, which was a reasonable global model to start with (see results). We also checked for overdispersion using both the χ^2 value of the GOF test and the result of the Monte Carlo test. In the first case, we estimated the overdispersion index, $\hat{c}$ as χ^2 divided by the number of degrees of freedom of the RELEASE GOF test. In the second case, $\hat{c}$, was estimated as the ratio of the observed deviance of the test model divided by the mean deviance of simulated models.

The second step involved a test for sex (first data set) and age (second data set) effects, along with time effect on apparent survival rates and recapture probabilities. We used the random effects models in order to get an estimate of the process variance underlying the temporal variability in apparent survival rates. Indeed, the total variation over time in a series of parameters includes two components: the process, or 'true' variation (σ^2), and the sampling variation (σ_s^2) which depends on the sample size of marked animals. The principles underlying random effects models in capture-mark-recapture are presented online as part of the description of program MARK (http://www.cnr.colostate.edu/class_info/fw663/Mark.html). We therefore only recall the information needed to follow our analysis. Within the framework of open capture-mark-recapture models, where maximum likelihood (MLE) apparent survival rates are estimated along with a sampling variance, it is possible to estimate the total variance (σ_{tot}^2, variation over time estimated with the MLE apparent survival rates) and the sampling variance (σ_s^2 based on the sampling variance of each apparent survival estimates). Knowing the total and sampling variation, process variation can be obtained as $\sigma^2 = (\sigma_{tot}^2 - \sigma_s^2)$. Performing a decomposition of the variance assumes that the apparent survival rates are the realization of a random variable from a distribution with mean and variance equal to the process variance. Based on the estimation of this mean value and from the process variance, one can recalculate the expected value of the apparent survival rates at any time step. Because these values are always shrunken towards the global average (or the values predicted by external covariates; see below) compared to the MLE estimates, there are called 'shrunk' estimates (see Louis & Shen, 1999, for a recent discussion). The degree of shrinkage depends on the variance component proportion (σ^2/σ_{tot}^2).

For both apparent survival for 1 year-old birds (first data set) and chicks (second data set), we calculated the estimated process variance, the shrunk estimates, the degree of shrinkage, the coefficient of variation over time of these estimates and the mean value of the shrinkage coefficient over the series of apparent survival rates. Because the analyses of the effects of covariates were performed on the period 1978-1996 (the 18 years for which all covariates were available), we calculated the process variance and coefficient of variation over this period.

In the third and final step of the analyses, we sought the external variables that best explained the variability over time of $\geqslant 1$ year-old and chick apparent survival, respectively. Following Lebreton *et al.* (1992), we used a logit link between each covariate and the apparent survival rates. We selected whether the external variables were accounting for the variation in survival rates based on AICc values. Then we calculated the percentage of the process variation explained by each of the co-variates, in the framework of random effects models. The principle was first to fit the random effects model assuming a constant mean to obtain the process variance $\hat{\sigma}^2$ and, second, to fit the random effects model assuming that the mean depends on one of the covariates and so obtain the residual variance σ_{res}^2. The percentage of the variance explained by the covariable is then calculated as $(\hat{\sigma}^2 - \sigma_{res}^2)/\hat{\sigma}^2$.

The model selection was based on AICc values throughout the analyses (Burnham *et al.*, 1995, Burnham & Anderson, 1998). All the analyses were performed using MARK (White & Burnham, 1999).

4 Results

4.1 Testing for sex effects and analysis of adult apparent survival

Goodness of fit tests. The goodness of fit of the CJS model tested with RELEASE was satisfactory (sex pooled $\chi^2 = 65.787$, df $= 83$, $P = 0.918$, males: $\chi^2 = 40.342$, df $= 39$, $P = 0.411$, females: $\chi^2 = 25.445$, df $= 44$, $P = 0.989$) and did not indicate overdispersion ($\hat{c} = 0.793$). The use of the Monte Carlo test on the CJS model with no sex effects resulted in the same conclusion, as the mean deviance of the simulated CJS models was 392.579 for an observed deviance of 378.333, leading to a $\hat{c}$ of 0.964. The probability of obtaining a value at least as high as the observed deviance under CJS was 0.66, indicating a good fit of the data set to the CJS model. We therefore proceeded in our analyses without any correction factor for overdispersion.

Testing for sex differences. Given the low difference in AICc between models $\Phi(\text{sex} + t)p(t)$ and $\Phi(t)p(t)$ and between models $\Phi(t)p(\text{sex} + t)$ and $\Phi(t)p(t)$, we concluded that there were no sex differences in either apparent survival or recapture probabilities respectively (Table 2). We therefore performed all the remaining analyses with data from the two sexes pooled.

Temporal variability. The model (M5, Table 2) with the lowest AICc was the time dependent model in both apparent survival and recapture probabilities. The mean of recapture probabilities over time was 0.952 (s.e. $= 0.015$). Two years with low recapture probabilities appeared to account for this variability, as the recapture probability was 0.656 (s.e. $= 0.183$) in 1976 and 0.589 (s.e. $= 0.113$) in 1994. Decomposing the variance of apparent survival rates into a process variance and a sampling variance, we found that the process variance was 0.0439 (s.e. $= 0.210$), with a mean of 0.524 (s.e. $= 0.051$). The coefficient of variation of the shrunk estimates was 40.1%. In contrast, the mean sampling variance was 0.0036, which was one order of magnitude lower than the process variance. The degree of shrinkage was therefore close to 1 (0.96). Thereby, the shrunk estimates and corrected standard errors are close to the values obtained by maximum likelihood estimation procedures (Fig. 2).

TABLE 2. Capture-mark-recapture models and their AICc for the adult file (1 year of age). The ΔAIC column corresponds to the difference between the AIC of each model and the AIC of the selected model. Φ is the apparent survival, *p* the recapture probabilities, *t* stands for the year effect, 'sex' for the sex effect, 'win' for winter temperature, 'ice' for the number of days with ice on the river, 'NAO' for the North Atlantic Oscillation index and '*n*' for population size. Models are ranked by increasing deviance. The selected model is in bold

	Model	AICc	ΔAICc	Par	Dev
M1	$\Phi(\text{sex}\star t)p(\text{sex}\star t)^{\#}$	3411.69	74.84	90	345.350
M2	$\Phi(\text{sex}+t)p(\text{sex}+t)$	3339.68	2.83	41	377.020
M3	$\Phi(t)p(\text{sex}+t)$	3338.13	1.28	40	377.540
M4	$\Phi(\text{sex}+t)p(t)$	3338.59	1.73	40	377.997
M5	$\boldsymbol{\Phi(t)p(t)^{\#\#}}$	**3336.85**	**0.00**	**39**	**378.333**
M6	$\Phi(t)p(.)$	3346.31	9.46	24	418.615
M7	$\Phi_{[\text{win}+\text{n}]}p(t)$	3354.18	17.32	24	426.479
M8	$\Phi_{[\text{win}]}p(t)$	3444.16	107.30	21	522.576
M9	$\Phi_{[\text{NAO}]}p(t)$	3461.57	124.72	18	546.098
M10	$\Phi_{[\text{ice}]}p(t)$	3473.86	137.00	20	554.314
M11	$\Phi_{[\text{n}]}p(t)$	3562.03	225.18	24	634.331
M12	$\Phi(.)p(t)$	3567.30	230.45	19	649.793
M13	$\Phi(.)p(.)$	3694.13	357.28	2	810.939

[#]Model on which the GOF test was performed using RELEASE
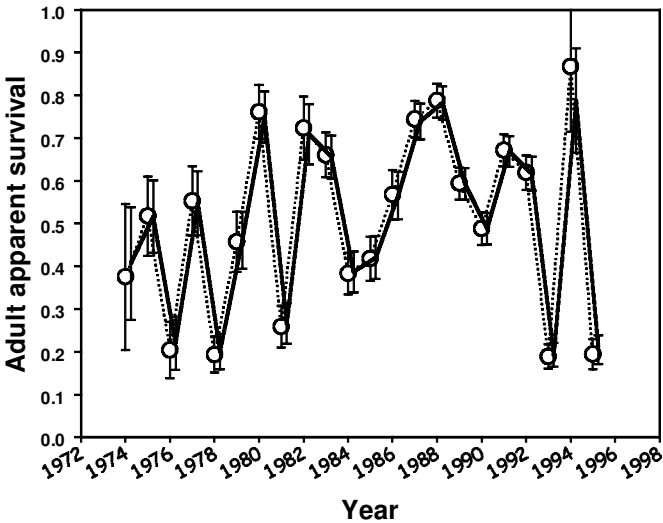[##]Model on which the GOF test was performed using Monte Carlo tests in MARK

FIG. 2. Adult (≥ 1 year-old) apparent survival estimates (± s.e.) from 1974 to 1997. Both the maximum likelihood estimates (points and dashed line) and the estimates obtained under the random effect models (bold line) are plotted.

Explaining temporal variability by external variables. The temporal variation was best explained by population size and winter temperature (model M7, Table 2). Indeed, these two variables explained 88% of the total temporal variability (Table 3, Fig. 3). The slope of the relationship between winter temperature and apparent survival was 0.193 (s.e. = 0.021), and between population size and apparent survival was − 0.130 (s.e. = 0.024, Fig. 4).

TABLE 3. Percentage of the temporal variance in adult apparent survival explained by temperature in winter, number of days with ice on the stream, the NAO index and population size. We considered apparent survival estimates from 1978 to 1996, because this interval corresponds to the time interval during which all variables were available

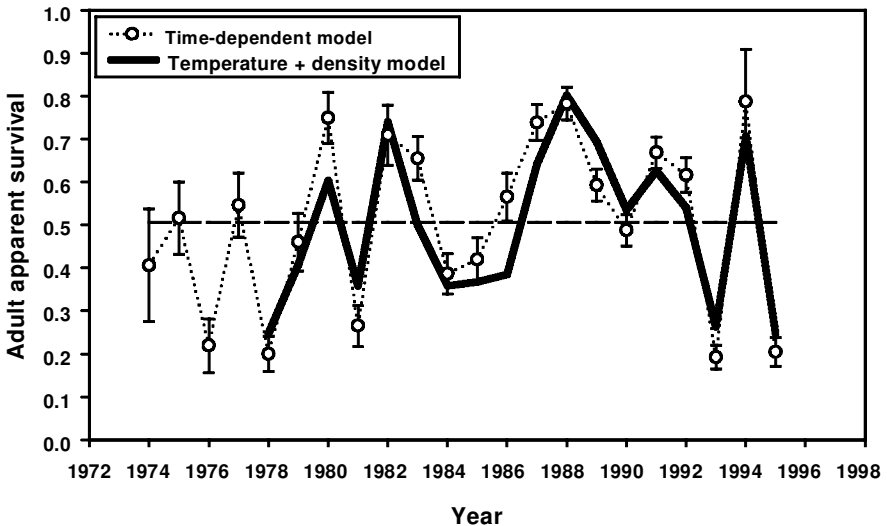| Model	Residual variance	Variability explained
$\Phi(t)$	0.044	
$\Phi[win]$	0.020	54.5%
$\Phi[ice]$	0.031	29.5%
$\Phi[NAO]$	0.026	40.9%
$\Phi[n]$	0.045	0.0%
$\Phi[win + n]$	0.005	87.9%

FIG. 3. Apparent survival for the adult age-class ($\geqslant$1 year-old), as estimated from the time dependent model (M5, Table 2, with $\pm$ s.e.) and from the model where adult apparent survival depends on winter temperature and population size (M7, Table 2). Estimates were obtained under random effect models and are therefore shrunk estimates.

4.2 Testing for age effects and analysis of chick apparent survival

Goodness of fit tests   The GOF test of the CJS model by group was not significant ($\chi^2 = 111.691$, df $= 109$, $P = 0.415$) once the Test3.SR component of the chick group was removed. Using this result, $\hat{c}$ was 1.024, a value that indicates no overdispersion. We performed the Monte Carlo test on the $\Phi_c(t)\Phi_1(t)\Phi_2(t)$ $p_c(.)p_1(.)p_2(.)$ model (M2, Table 4), which had a deviance of 656.638. The mean deviance of the 500 simulated models was 636.968 and the probability of having a deviance larger than 656.638 was 0.48. This indicated a good fit of the $\Phi_c(t)\Phi_1(t)\Phi_2(t)p_c(.)p_1(.)p_2(.)$ model and a $\hat{c}$ value of 1.034. Again, this did not lead us to suspect any substantial overdispersion. We therefore proceeded with the model selection procedure without a correcting factor for overdispersion.
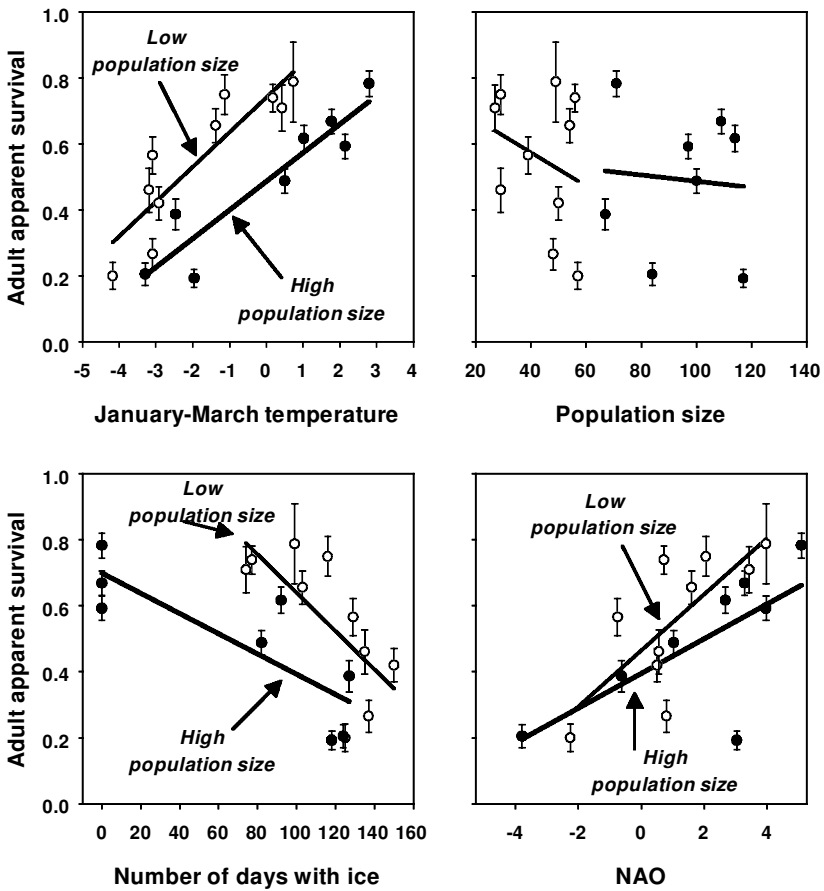
Fig. 4. Adult apparent survival (shrunk estimates obtained under the random effect model, ± s.e.) as a function of winter temperature, population size, the number of days with ice on the river and the NAO index. For illustrative purposes, two regression lines are shown, the bold line corresponding to above-average values of population size and the thin line to below-average values of population size.

Testing for age differences.   The selected model had age-specific recapture probabilities. The model with three age-classes in recapture probabilities had a lower AIC than the model with two age-classes (M6 versus M7, Table 4). The mean recapture probability over time was 0.515 (s.e. = 0.042) for birds marked as chicks, 0.862 (s.e. = 0.021) for birds marked as yearlings and 0.909 (s.e. = 0.014) for birds marked as 1 year old. As we found varying recapture probabilities in the analyses of the adult-only data set, we checked again for this variability in the age-structured data set. The model with varying recapture probability for birds marked as chicks was not selected (see for example model M9 versus M11, Table 4), while the model with varying recapture probabilities for older birds had similar AICc (M8) to the model with constant recapture probabilities (M11). For the sake of power and because we are focusing on the patterns in chick apparent survival rates only in this part of the analysis, we chose to keep the recapture probability constant in all age-classes. There was no detectable difference in 1-year-old and ⩾2-year-old dippers' apparent survival rates (lower AICc value for model M6 compared with model M2, Table 4). The average survival rates over time were indeed 0.510

TABLE 4. Capture-mark-recapture models and their AICc for the complete file including birds marked as chicks, yearling and adult. Models are ranked according to deviance values. Because the notation for age-specific models are complex when age, time and covariates can interact, we specified the survival and recapture components of the models in two separate columns. The table cells where either the survival component of the model or the recapture component of the model is the same as in the selected model are in bold. The age structure is indicated as subscript to apparent survival or recapture probabilities: 'c' for chicks, '1' for yearling, '$\geqslant 1$' for yearlings and older, '2' for adults $\geqslant 2$ year-old.

	Survival model	Recapture model	AICc	ΔAICc	Par	Dev
M1	$\Phi_c(t)\Phi_1(t)\Phi_2(t)$	$p_c(t)p_1(t)p_2(t)$	5098.38	79.44	134	585.337
M2	$\Phi_c(t)\Phi_1(t)\Phi_2(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}^{\#\#}$	5037.09	18.15	69	658.638
M3	$\boldsymbol{\Phi_{c[win]}\Phi_1}(t)$	$p_c(t)(p_1,p_2)(t)$	5036.12	17.18	63	669.940
M4	$\Phi_c(t)\Phi_{\geqslant1}(t)$	$p_c(t)p_{\geqslant1}(t)^{\#}$	5105.96	87.02	90	684.352
M5	$\Phi_c(t)(\Phi_1,\Phi_2)(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5025.42	6.47	48	689.809
M6	$\Phi_c(t)\Phi_{\geqslant1}(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5023.38	4.44	47	689.810
M7	$\Phi_c(t)\Phi_{\geqslant1}(t)$	$p_c(.)p_{\geqslant1}(.)$	5025.37	6.42	46	693.827
M8	$\boldsymbol{\Phi_{c[win]}\Phi_{\geqslant1}(t)}$	$p_c(.)(p_1,p_2)(t)$	5019.31	0.36	44	691.823
M9	$\boldsymbol{\Phi_{c[win]}\Phi_{\geqslant1}(t)}$	$p_c(t)p_1(.)p_2(.)$	5035.10	16.16	46	703.561
M10	$\Phi_{c[win+n]}\Phi_{\geqslant1}(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5023.15	4.20	31	722.004
M11	$\boldsymbol{\Phi_{c[win]}\Phi_{\geqslant1}(t)}$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5018.94	0.00	27	725.882
M12	$(\Phi_c,\Phi_1,\Phi_2)(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5027.24	8.30	28	732.160
M13	$(\Phi_c,\Phi_{\geqslant1})(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5025.23	6.28	27	732.164
M14	$\Phi_{c[ice]}\Phi_{\geqslant1}(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5026.56	7.62	27	733.500
M15	$\Phi_{c[NAO]}\Phi_{\geqslant1}(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5027.29	8.34	30	734.225
M16	$\Phi_{c[n]}\Phi_{\geqslant1}(t)$	$\boldsymbol{p_c(.)p_1(.)p_2(.)}$	5033.62	14.68	30	734.500
M17	$\Phi_c(t)\Phi_{\geqslant1}(t)$	$p(t)$	5180.61	161.67	69	802.160
M18	$\Phi_c(.)\Phi_1(.)\Phi_2(.)$	$p_c(.)p_1(.)p_2(.)$	5398.82	379.88	6	1148.005
M19	$\Phi(t)$	$p(t)$	6876.25	1857.3	46	2544.706

[#] Model on which the GOF test was performed using RELEASE
[##] Model on which the GOF test was performed using bootstraps in MARK

(s.e. $= 0.020$) for yearlings and 0.509 (s.e. $= 0.042$) for $\geqslant$2-year-old dippers. We therefore pooled these two age-classes in all the following analyses of apparent survival rates.

Temporal variability. Based on the model with time-dependent chick apparent survival rates (M6, Table 4), the mean and variance of the chick apparent survival rates estimated with random effects models were 0.0571 (s.e. $= 0.008$) and 0.000599 (s.e. $= 0.0245$), respectively . The coefficient of variation was therefore 42.9%, quite similar to the coefficient of variation recorded for adult apparent survival rates (40.1%). With a mean sampling variance of 0.000533, the degree of shrinkage was 0.76, and the gain in precision of the shrunk estimates compared to the maximum likelihood estimates was therefore higher than for the adult series of apparent survival rates (Fig. 5).

The difference in AICc values between the model with additive time and age-class effects (M13) and the model with interactive time and age-class effects (M6) was smaller than 2, suggesting that the variability of apparent survival of chicks and $\geqslant$1-year-olds is partly determined by the same factors.

Explaining temporal variability by external variables. The best model among the set of models fitted (Table 4) was the model where the chick apparent survival was accounted for by mean winter temperature (M11, Fig. 6). Forty-eight percent of the variation in apparent survival was explained by this variable (Table 5). The
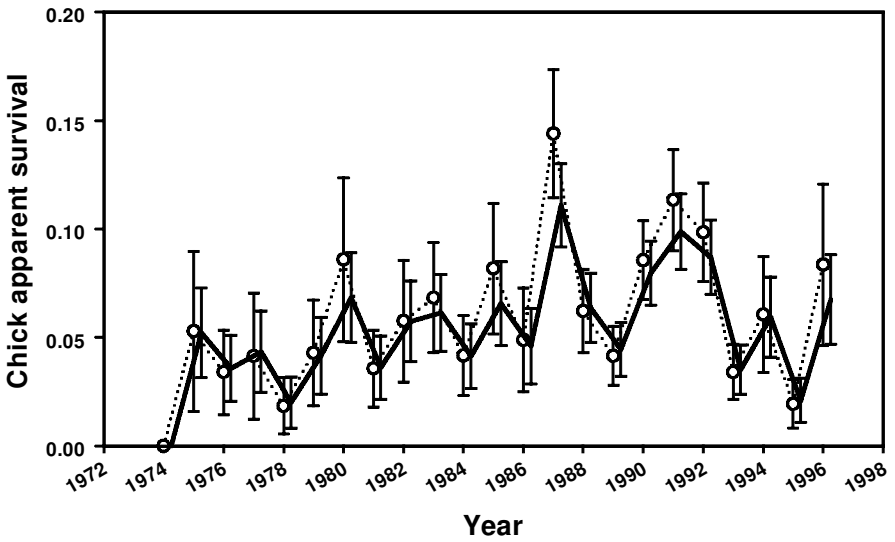
FIG. 5. Chick apparent survival estimates ($\pm$ s.e.) from 1974 to 1997. Both the maximum likelihood estimates (points and dashed line) and the estimates obtained under the random effect models (bold line) are plotted.
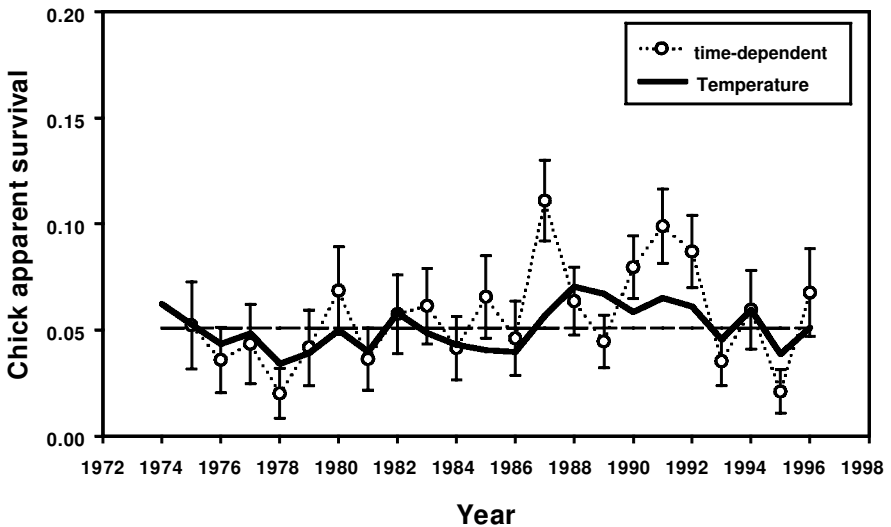

FIG. 6. Apparent survival for the chick age-class, as estimated from the time-dependent model (M6, Table 4, with $\pm$ s.e.) and from the model where chick apparent survival depends on winter temperature (M11). Estimates were obtained under random effect models and are therefore shrunk estimates.

slope of the relationship between apparent survival and temperature was 0.0158 (s.e. $= 0.0057$, Fig. 7). This slope was significantly lower than the slope found for adults ($Z = 8.072$, $P < 0.001$).

5 Discussion

The comparative analysis of chick and adult apparent survival highlighted a very high variation in these demographic parameters. This is in agreement with the

TABLE 5. Percentage of the temporal variance in chick apparent survival explained by temperature in winter, number of times there was ice on the stream, the NAO index and population size. We considered apparent survival estimates from 1978 to 1996, because this interval corresponds to the time interval during which all variables were available

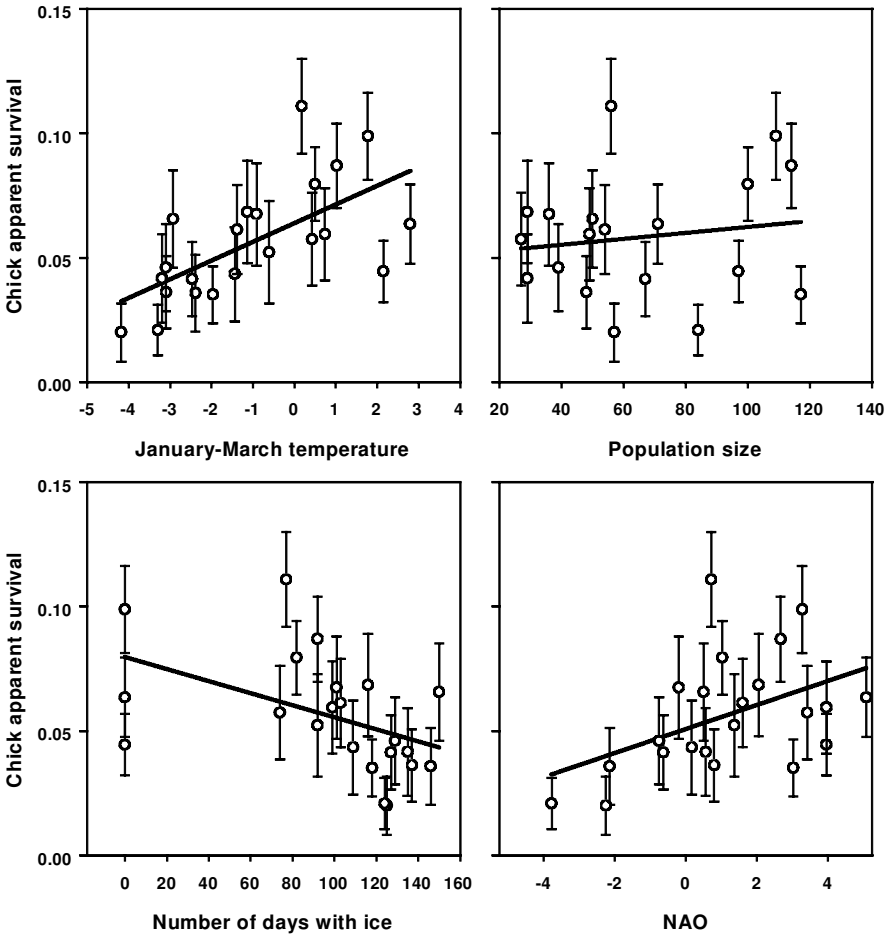| Model	Residual variance	Variability explained
$\Phi(t)$	0.00060	
$\Phi(win)$	0.00031	48.3%
$\Phi(ice)$	0.00052	13.3%
$\Phi(NAO)$	0.00048	20%
$\Phi(n)$	0.00065	0.0%
$\Phi(win + n)$	0.00034	43.3%

FIG. 7. Chick apparent survival (shrunk estimates obtained under the random effect model, ± s.e.) as a function of winter temperature, population size, the number of days with ice on the river and the NAO index

variation in population size observed in some dipper populations, which can vary three- to six- fold over a few decades (Sæther *et al.*, 2000a; Wilson, 1996). This variation in apparent survival rates exceeds the sampling variance, which explains the moderate difference between 'shrunk' estimates and maximum likelihood estimates, especially in adults (Fig. 1). The recapture/resighting probabilities were high but still not equal to 1 (only about 50% for chicks and 90% for adults). It is therefore highly recommended to use estimates based on capture-recapture instead of 'raw' estimates from direct observations for studying apparent survival and recruitment.

The absence of sex effect on apparent survival was expected from former studies of dipper populations (e.g. Lebreton *et al.*, 1992) and from the fact that dippers are monomorphic, are only slightly polygynous and breed in pairs (Wilson, 1996). Unfortunately, we were not able to test for sex effects in chick apparent survival, because the chick's sex could not be determined. As explained in the statistical analyses section, the apparent survival rates estimated here for adults and chicks were including a dispersal component. These apparent survival rates are relevant for explaining the local dynamics of our population as one component of the population multiplication rate, but they do not allow a direct understanding of the underlying mechanisms.

Post-natal dispersal is common in dippers: in a UK population, Tyler *et al.* (1990) indeed documented up to 30% of post-natal dispersal (the dispersal rate being then about $d = 0.30$). As dippers can disperse far from their birthplace (up to 1055 km, Hegelbach & Koch, 1994), and as it is virtually impossible to check all the rivers, this dispersal rate is probably underestimated. In our population, the average proportion of chicks surviving and staying on the study site was equal to 0.57. As far as we know, no other study has quantified this 'surviving × philopatry' rate in other dipper populations, limiting the possibility for comparison. If we assume a similar rate of post-natal dispersal rate as in Tyler *et al.*'s (1990) study, the mean true survival rate of chicks could be as low as $S = \Phi(1 - d) = 0.08$. The post-natal dispersal rate is, however, probably partly site- and year-specific, and should be estimated as such in our studied population. Indeed, dispersal rate is obviously dependent on the size and shape of the study area, and the justification of using dispersal rates from one site to the other is therefore weak.

With a high contribution of the dispersal component to chick apparent survival, the relationship of the 'true' survival with population size or winter temperature may be strongly biased. This may explain why the best model with external variables only explained 48% of the variability in chick apparent survival whereas the corresponding figure was 88% in adults (Table 5). This may also explain the lack of relationship between population size and chick apparent survival. Indeed, we could have expected the level of philopatry to depend on population size, i.e. on the number of available territories. To disentangle the role of dispersal from the survival, two independent analyses would be necessary: a multi-site approach (Nichols & Kendall, 1995) and the combination of models estimating chick survival (this paper) and models estimating recruitment rates (Pradel, 1996). This approach should provide reliable estimates of immigration rates (Loison *et al.*, unpublished analyses).

Breeding dispersal is usually not as substantial. For instance, Tyler *et al.* (1990) found that only 3.6% of monitored adults ($n = 138$) dispersed ($d = 0.036$). The mean apparent survival rate found here (about $\Phi = 0.52$) may therefore be increased to a 'true' survival of about $S = \Phi/(1 - d) = 0.54$ to account for breeding dispersal. This level of survival corresponds to results found elsewhere (e.g. apparent survival

of 0.60 in France, Lebreton *et al.*, 1992; true survival of 0.55-0.60 in the UK, Galbraith & Tyler, 1982). The large variability highlighted here exemplifies the need for long-term studies of adult survival, before inferring general patterns about the sources of variability of adult survival for this species. Even with a relatively limited CMR data set, Lebreton *et al.* (1992) reported a strong effect of catastrophic events in the river (flood) on survival in a 7-year study. To be able to make predictions on the future dynamics of the population, empirical studies have to be long enough to permit investigation of the relationship between survival events and environmental variability (Sæther *et al.*, 2000a), even for a species with such a relatively short life span as the dipper.

The temporal variability in adult apparent survival rates was surprisingly well accounted for by only two variables, population size and winter temperature, as expected from the results of Sæther *et al.* (2000a). Mean winter temperature appeared to be the best of the three indexes of winter severity to account for variation in survival. The correlation found with the NAO index however should prove useful to predict the dynamics of this dipper population in the future, as the NAO index fluctuates with some known patterns (decadal trends, Davies *et al.*, 1997; Hurrell *et al.*, 1995) and could reflect global warming. There was no indication of an interaction between population size and winter severity, even though a high population size often magnifies the effect of environmental variation on demographic parameters (Portier *et al.*, 1998). This assumption of a possible interaction between population size and winter temperature however relies on the assumption of competition for food, which could decrease adult condition and thereafter, survival during harsh winters. Alternatively, the negative effect of population size on apparent survival could also reflect increasing dispersal.

In the analysis of the data set based on known-age birds, the age effect does not appear to extend beyond yearlings (see also Ringsby *et al.*, 1999). The data set composed of adults only is therefore suitable for use of the Pradel (1996) set of models, which permit estimation of recruitment (or alternatively λ) and its process variance. As mentioned earlier, combining estimates of recruitment, chick apparent survival rates, and reproductive rates (number of young produced per adult) would also give access to the immigration rates, even without a multi-site approach (Loison *et al.*, unpublished analyses).

Our results show that apparent chick and adult survival rates were partly determined by the same factors, i.e. at least winter temperature. There is therefore a covariation through time of these two parameters. To be able to build projection models and predict the future dynamics of the dipper population (e.g. under different scenarios of climatic change as in Sæther *et al.* 2000a, or as a part of an Environmental Impact Analysis), the covariation among the different demographic rates over time should be investigated as well. Although the covariation terms can dramatically change the outcome of demographic models, there has been no way so far—as far as we know—to estimate the temporal covariance of two series of parameters estimated by capture-mark-recapture models. Similarly, we have overlooked the possible covariation that may occur between survival rates and population size and the temporal autocorrelation in the series of population size. Further developments of random effects models and of models combining time series analysis and CMR models should render the approach of covariation among rates and between rates and covariates feasible in a short time (Burnham, personal communication; Besbeas *et al.*, under revision), giving biologists access to important components of life history strategies from field data.

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