Ringing & Migration

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Mark–recapture ringing data from Wicken Fen in Cambridgeshire and Gosforth Park in Newcastle upon Tyne were used to estimate adult survival rates in a southerly and a northerly population of Reed Warblers in England. The computer program MARK was used to estimate survival and recapture rates, adjusted for transient birds, with respect to sexes at each site. Expressed as percentages, survival rates between 1988 and 2004 at the northerly Gosforth Park site were 60.3 ± 6.0 (se) for males and 54.9 ± 10.3 for females. Survival rates at the southerly Wicken Fen site between 1995 and 2004 were 32.9 ± 16.0 for males and 52.0 ± 22.4 for females. Rainfall in the Sahel region of West Africa did not account for variation in survival rates over time at either site and did not correlate with variation in adult Reed Warbler abundance in the UK. At both Wicken Fen and Gosforth Park, Reed Warbler populations increased during the study periods. At Wicken Fen, new recruits due to immigration had a greater contribution to population growth than survival of adults returning to the site, whereas at Gosforth Park the reverse was found.

In the UK, the Reed Warbler *Acrocephalus scirpaceus* has extended its range north and west over recent years (Gibbons *et al* 1993); however, recent analyses have suggested an overall decline in abundance (Clark *et al* 2003). Reedbeds of Common Reed *Phragmites australis* are most extensive in the south, particularly the Norfolk Broads and East Anglia, of which Wicken Fen in Cambridgeshire is one of the largest, with more than 40 ha of reeds (Cadbury 1997). Suitable habitat is less common in the north and small populations of Reed Warblers in these patchy habitats are likely to vary in relation to range expansion, habitat suitability, and reedbed management. In the northeast of England, Reed Warblers are scarce and the largest population is found at Gosforth Park in Newcastle upon Tyne (Redfern & Davidson 2003). Further north, they occur only as sporadic breeders.

An important step towards understanding the reasons behind changes in bird abundance has been the use of bird ringing data to estimate survival rates and productivity (Baillie 1990, 1995). Survival rates are a vital measure of bird populations and monitoring how these vary over time can highlight where conservation effort is needed. For example, British Trust for Ornithology (BTO) ringing data show that decreasing juvenile/first-winter survival explains the decline in Song Thrush

Turdus philomelos numbers from 1975 to 1993 (Thomson *et al* 1997). Survival rates in many species have also been linked to major climatic variables such as precipitation and temperature (*eg* Conroy *et al* 2002). Populations of trans-Saharan migrants such as the Whitethroat *Sylvia communis* (Winstanley *et al* 1974, Hjort & Lindholm 1978), Sand Martin *Riparia riparia* (Jones 1986), and Sedge Warbler *Acrocephalus schoenobaenus* (Peach *et al* 1991) fluctuate in relation to rainfall in the sub-Saharan Sahel region of West Africa. The Reed Warbler is also a trans-Saharan migrant and, although little is known of the wintering areas, recoveries from birds ringed in the UK have shown that they migrate southwest and may winter in West Africa from Senegal to Nigeria (Redfern & Alker 2002).

Bird populations in the UK may also show regional variation in their survival rates and population changes. For example, data from the Constant Effort Sites (CES) project have been used to identify the reasons underlying changes in abundance of Willow Warblers *Phylloscopus trochilus*, a species that within the UK has shown marked declines in southerly populations in contrast to those in the north, with lower adult survival rates reported for declining areas (Peach *et al* 1995). Reed Warblers within the UK may also show regional variation in survival rates.

The aim of this study was to compare adult survival rates and populations of Reed Warblers at two sites in England: a small northern site and a large southern site

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within the core of the UK range. Survival rates were estimated separately for males and females, and correction was made for transient birds, which have been shown to depress estimates of survival in the first year after ringing (Peach *et al* 1991). To investigate whether survival rates vary in relation to conditions on wintering grounds, local survival rates and adult population trends in the UK were compared with indices of Sahel rainfall.

METHODS

Study sites

Wicken Fen Nature Reserve is a Site of Special Scientific Interest (SSSI) located in Cambridgeshire, southern England. The Reed Warbler population is estimated to be 200–600 pairs (Chris Thorne, pers comm), with inaccessible habitats preventing a more precise estimate. Gosforth Park Nature Reserve is a much smaller SSSI located near Newcastle upon Tyne, and the Reed Warbler population there is estimated to be 15–20 pairs. Reed Warblers have been ringed at Gosforth Park since 1988 and at Wicken Fen since the late 1960s, although in this study only data from 1995 onwards were available for Wicken Fen. All adult Reed Warblers caught at Gosforth Park and Wicken Fen over these periods were included in the initial data sets.

Biometrics

Since juveniles of many species have higher mortality rates and are likely to disperse from their natal area, the inclusion of juveniles and first-year Reed Warblers in analyses could substantially bias estimates of adult survival rates. Therefore only adult birds were included in our analyses. At both Wicken Fen and Gosforth Park some birds were sexed in the hand, either when initially ringed or when subsequently retrapped, on the basis of brood patch (BP) or cloacal protuberance (CP) (Redfern & Clark 2001). To increase the sample of sexed birds, some adult Reed Warblers for which no sex was explicitly recorded at the time of ringing or retrapping were sexed using a linear discriminant function. This was calculated using, as predictors, the body mass and wing length of birds caught in both study sites and sexed on the basis of cloacal protuberance or brood patch. Since body-mass data for females were skewed (*ie* non-normal), the data were log-transformed before analysis. To sex birds using the discriminant function, the threshold was a probability of >60 % that the predicted sex was correct. This confidence threshold was chosen to give reasonable confidence that sex was accurately attributed, whilst allowing a good proportion of individuals to be categorised. Discriminant functions were estimated separately for Gosforth Park and Wicken Fen birds using only data for

first encounters to ensure statistical independence. In addition to the discriminant analysis, mean wing lengths were compared between sexes and sites using a two-way ANOVA, with Tukey Simultaneous tests for pairwise comparisons. All analyses were performed using Minitab Release 14. Where appropriate, mean values are given ± standard error (se).

Adult survival and recapture

Mark–recapture data from Gosforth Park (1988–2004) and Wicken Fen (1995–2004) were analysed using the computer program MARK 3.1 (White & Burnham 1999). Cormack–Jolly–Seber (CJS) models were developed using the recaptures-only option, which allows general survival and recapture rates to be modelled with respect to time and groups along with individual covariates (Pollock 2002, Cooch & White 2005). The models that program MARK produces consist of the two standard parameters of survival probability (φ) and recapture probability (p), which can then be allowed to vary between groups and over time. Retrapping took place each year between 24 April and 8 October at Wicken Fen and between 27 April and 16 October at Gosforth Park, with some seasonal variation in the start and end trapping dates. The two sites in this study were analysed separately and sex was modelled as a group variable. At Wicken Fen some projects in addition to the standard ringing effort of the Wicken Fen Ringing Group have been carried out since 1995 and these have increased the ringing effort of the Group. These extra data were included in the analysis because MARK separates out survival and recapture into separate variables, thus taking account of variability in trapping effort (Bearhop *et al* 2003). However, data from the standard ringing visits alone have been used to assess the effect of ringing effort on recapture rates separately (see below).

A common problem with mark–recapture analyses based on mist-netting data is the inclusion of transient birds in the catch. Transients are defined as individuals that permanently emigrate after marking (*ie* birds just passing through) and have an apparent survival rate of zero with respect to the population under study, whereas 'resident' individuals (*ie* those holding territory or nesting in the area) have the potential to be re-encountered. Consequently, the inclusion of transients can substantially depress estimates of local survival (Peach *et al* 1990, Peach 1993, Cooch & White 2005). This also violates one main CJS assumption, that all animals marked on one occasion have an equal probability of survival to the next occasion. Therefore we corrected models in the analyses for transient birds (see Appendix 1 for details of methodology).

For the analysis we first constructed a general model that allowed survival to vary by sex (s) and year (t) for both newly ringed transients and residents (φ1), and previously

ringed residents ($\varphi2$). Recapture rates were allowed to vary between sexes and over time (p_{s*t}), and thus the general model is represented as $\varphi1_{s*t}\ \varphi2_{s*t}\ p_{s*t}$. Estimates of recapture rates are based on birds that are known to have survived (for example from encounter occasions 1 to 3) but which have not been recaptured in the intervening period (for example, encounter occasion 2). Therefore estimates of recapture rates (p) are not influenced by transient individuals since they have all left the sample by the second occasion. To test the fit of the most general models we used 500 bootstrap simulations in MARK. The general models fitted the data adequately for both sites (Wicken Fen: $P = 0.21$, Gosforth Park: $P = 0.23$); nevertheless, some evidence of extra-binomial 'noise' variation was detected, known as 'overdispersion'. To account for this, small adjustments ($\hat{c}$) can be made to the data; a $\hat{c}$ value of 1.0 indicates the model fits the data well, but if $\hat{c} > 1.0$ then there is some degree of overdispersion evident. These $\hat{c}$ adjustments were made for each site in turn. Details on how $\hat{c}$ values were obtained and the methods used are described in Appendix 2.

To test assumptions underpinning CJS methodology, we used the computer program RELEASE, available within MARK, to check whether birds marked at occasion i had an equal probability of survival and recapture to occasion $i +$ 1. This analysis suggested that it was appropriate to include a term for transients in the models at both sites. Akaike's Information Criterion, adjusted for small sample sizes and overdispersion ($QAIC_c$) was used to identify the most parsimonious model from each candidate set (Anderson *et al* 1995, Anderson & Burnham 1999). The model with the lowest $QAIC_c$ and greatest weighting was taken as the best representation of the data. Models were run using the logit link function and all possible combinations of models were tested. Likelihood ratio tests (LRTs) were also used to test whether inclusion or exclusion of effects on survival or recapture rates significantly improved the fit of models. Model averages were then obtained to estimate the overall survival and recapture rates. These values were calculated by averaging over all models with common elements in the parameter structure, weighted by normalised $QAIC_c$ model weights (Cooch & White 2005). This takes into account any uncertainty inherent in the most parsimonious models. Standard errors were calculated across the survival estimates from each model included in the averaging.

Sahel rainfall and local survival rates

An index of yearly (1988–2003) June–October rainfall in the Sahel region of West Africa (5°–20°N, 20°W–5°E) was included in the analyses after initial models had been investigated at both sites; the Sahel effect could then be judged against all other model combinations. This index was calculated as a mean normalised rainfall departure across all stations (Nicholson 1979, 2001, Nicholson & Palao 1993) of which up to 72 were available for this study (obtained from the National Center for Atmospheric Research 2004). The mean normalised anomaly was calculated for individual stations as the difference between observed rainfall in the period June–October and the mean rainfall over the station's history, divided by the standard deviation. This normalised value was then averaged for individual years using all available stations. A covariate of Sahel rainfall was included in Program MARK at both sites. This was conducted by altering the design matrix of the general models once transient birds had been accounted for. This tested the hypothesis that years with less rainfall in the Sahel would have an effect on Reed Warbler survival rates the following breeding season. Overdispersion corrections were applied in the same way as before, and are given in Appendix 2. Linear regression was then used to test for correlations between survival rates at each site and the Sahel index but this was used to assess effect size only. Regression analyses were carried out in Minitab 14.

Ringing effort

A covariate of ringing effort was also included in a separate analysis for Wicken Fen in an attempt to explain variations in recapture rates. Ringing effort data were only available for Wicken Fen Ringing Group (*ie* excluding any extra projects carried out). Therefore, this separate effort analysis excluded any additional ringing and recaptures in the original data set to allow the generation of recapture rates for the Wicken Fen Ringing Group only, which could then be compared with their ringing effort. This effort is described by a unit of 'days' which represents the evening (1600 hrs) until the following morning (1100 hrs), ringing late into the first evening and then at dawn the following day (Chris Thorne, pers comm). Details of the overdispersion adjustment are included in Appendix 2. Linear regression was also used to test for the size of the correlation effect between recapture rates and effort. Strictly speaking, the significance cannot be assessed through linear regression as the annual recapture rates produced by MARK are not strictly independent: therefore the use of regression was limited only to assessing effect size. At Gosforth Park, ringing effort has been more uniform and therefore this covariate was not considered here. Note that since all birds (including extra projects) were included in the analysis of survival in relation to Sahel rainfall at Wicken Fen, an effort covariate could not be included in the Sahel analysis.

Population statistics

To investigate the contributions of different demographic groups to population growth, we estimated the demographic

parameters of population growth rate (λ), seniority (γ), and recruitment rate (*f*) for the Gosforth Park and Wicken Fen populations. The population 'growth' rate indicates whether a population is increasing (λ > 1), decreasing (λ < 1) or in stasis (λ = 1) (Pradel 1996, Nichols *et al* 2000). The seniority parameter is the probability that an animal captured on occasion *t*, was present in the population at time *t* – 1, and the parameter (*f*$_i$), defined in terms of seniority as φ[(1 – γ$_{i+1}$)/γ$_{i+1}$], is analogous to recruitment from immigration and birds returning to the natal area to breed (Pradel 1996, Pradel *et al* 1997, Pradel & Lebreton 1999). The reverse mark–recapture methods of Pradel (1996) were then used to model γ, and *f* in separate analyses, with recapture rate *p*, and survival rate φ, and hence their associated contributions to population growth rate (λ) could then be derived (Pollock *et al* 1974, Nichols *et al* 2000). The value of λ itself was obtained by the formula λ$_i$ = φ$_i$/γ$_i$ but this can also be modelled directly in MARK. In these methods, capture histories are read from the last observation back through time, as opposed to the CJS first observation onwards: thus a capture history of 011010 (where 0 and 1 represent absence or presence, respectively, in each year) reversed becomes 010110. In this analysis, sexes were pooled together as one adult group to increase the sample size. Two separate analyses were performed for each site, one for transients and residents combined, and one for just resident birds. For this analysis it was taken that all assumptions were met, specifically with regard to study area size and boundary configurations. One concern was the increasing area of reedbed over time at Gosforth Park, but this was discounted from the analysis because reedbeds remain within the perimeter boundary which has not changed over the entire period.

UK adult population trends and Sahel rainfall

An index of adult Reed Warbler abundance within the UK derived from the BTO Constant Effort Sites scheme (CES) was compared with Sahel rainfall in the preceding wet season. CES data may offer a better measure of population change for Reed Warblers than other survey methods (Crick *et al* 2004). The Sahel rainfall index and the CES population data both exhibited autocorrelation (Box & Jenkins 1976), showing that successive observations were correlated through time. This was examined using the Box–Jenkins time series ARIMA modelling procedure (Box & Jenkins 1976) in Minitab 14. To test for a correlation between population size and Sahel rainfall, an ARIMA model was used to produce and cross-correlate the residuals of the two series (see Peach *et al* 1991). These are the differences between the modelled and actual observations and the use of this method avoids spurious significant correlations that may arise when simply producing a direct correlation, and can provide a robust way of testing for significant relationships between two time-series. A first-order auto-regressive model provided an adequate fit to the CES index series, although the time-series was shorter than recommended for such an analysis. The Sahel index was best fitted by inclusion of a moving average term as well as an autoregressive term; this improved the fit of the model as the Ljung–Box statistics gave non-significant *P* values indicating that the residuals were uncorrelated.

Local population trends and Sahel rainfall

Seasonal captures, defined as the number of birds captured per season, were also examined as trends over time and in relation to the Sahel rainfall index using regression analysis in Minitab 14. Ringing effort was used to adjust the number of birds captured by the Wicken Fen Ringing Group to remove the effect of this variable, and to test for correlations with Sahel rainfall in the absence of any effort bias. This was calculated by dividing the number of individuals captured by the ringing effort for the same respective season, thus giving a unit of birds captured per ringing day. At Gosforth Park, ringing effort has been more uniform and no corrections were applied to captures. Gosforth Park showed no autocorrelation for the number of captures per season, and Wicken Fen showed no autocorrelation for the number of captures per ringing day.

RESULTS

Biometrics and discriminant function analysis

For wing length, there was a significant difference between the sexes (two-way ANOVA, effect of sex: $F_{1,853}$ = 250.3, $P < 0.001$), and between Gosforth Park and Wicken Fen ($F_{1,853}$ = 12.4, $P < 0.001$), with a significant interaction between sex and site ($F_{1,853}$ = 7.9, $P = 0.005$). There was no significant difference in wing length between females at Gosforth Park (64.4 ± 0.2 [se] mm, n = 84) and Wicken Fen (64.4 ± 0.1 mm, n = 289; Tukey Simultaneous Test, $P = 0.981$), but the mean wing length for males at Wicken Fen (66.7 ± 0.1 mm, n = 379) was significantly greater than males at Gosforth Park (66.0 ± 0.1 mm, n = 138; Tukey, $P < 0.001$). For body mass, there was also a significant difference between males and females (effect of sex: $F_{1,853}$ = 40.9, $P < 0.001$), and also a near-significant effect between Wicken Fen and Gosforth Park birds (effect of site: $F_{1,853}$ = 3.6, $P = 0.056$) but with no significant interaction between sex and site ($F_{1,853}$ = 0.3, $P = 0.560$). The mean body masses for Wicken Fen birds were 11.74 ± 0.07 g for females (n = 270) and 11.32 ± 0.03 g for males (n = 365), and at Gosforth Park the mean body masses were 11.94 ± 0.14 g for females (n = 84) and 11.39 ± 0.05 g for males (n = 139).

A linear discriminant function (D) calculated using wing length and body mass for birds sexed on the basis of brood patch or cloacal protuberance accurately predicted the sex of 77.4% of the birds at Wicken Fen (males: D = 27.95wing + 7.96mass – 972.81; females: D = 27.11wing + 8.69mass – 926.24; n = 252), and 79.3% of the birds at Gosforth Park (males: D = 24.03wing + 5.34mass – 823.28; females: D = 23.20wing + 6.64mass – 784.70; n = 188). For Wicken Fen, the discriminant score ranges that defined each sex were -0.123 to 3.938 for males and -4.205 to -0.145 for females. At Gosforth Park, these ranges were -0.143 to 3.762 for males and -3.636 to -0.191 for females. When the respective discriminant functions were applied to the unsexed birds, 29 birds out of a total of 316 were rejected at Wicken Fen and 4 out of 14 birds at Gosforth Park, based on 60 % probability that the assigned sex was correct. These 'uncertain' birds were excluded from the survival analyses. At Wicken Fen, some birds had been sexed by other means such as tarsus length, so these were excluded from the initial analysis to focus solely on birds with BP and CP information recorded, but were still accepted in the final survival analyses.

Adult survival rates and transient models

The final sample sizes included in the total analyses each year at both sites are presented in Table 1. For the northerly Gosforth Park site, the best model was one that specified separate survival rates for $\varphi 1$ (transients and residents) and $\varphi 2$ (resident survival rate only), with an additional sex variation in $\varphi 1$ (denoted $\varphi 1_s$) (Appendix 3, Table i). There was less certainty that the effects included in model $\varphi 1_s$ $\varphi 2 p$ were the 'best' representation of the data under the QAIC approach. The weighting given to this model was 0.30, with the next model in the list showing a similar 0.20 $QAIC_c$ weighting; the top three models did not differ by a threshold $QAIC_c$ value of > 2.0, hence any of these three models could be a suitable representation. LRTs showed that including a sex effect on resident survival gave no significant improvement (χ^2_1 = 1.3, P = 0.286) indicating male and female survival rates were similar. The effect of time on resident survival gave no model improvement (χ^2_{11} = 17.2, P = 0.103): therefore this parameter was largely time invariant at Gosforth Park. Including a sex effect for recapture also gave no significant improvement of model fit (χ^2_1 = 0.3, P = 0.582), which was also true for the effect of time on recapture rates (χ^2_{13} = 10.1, P = 0.688). Resident survival rate estimates were obtained by model averaging using models that included common parameters. These showed parity between the sexes: females 54.9 ± 10.3 (se) %, males 60.3 ± 6.0 %. Recapture rates for resident birds at Gosforth Park were 70.2 ± 10.9 % for females and 74.1 ± 5.8 % for males, therefore showing no sex differences.

Table 1. The number of known-sex birds (including those from the discriminant-analysis sexing), either newly ringed (N) or recaptured (R), that were included in Program MARK models at both sites: Gosforth Park 1988–2004, Wicken Fen 1995–2004.

	Sex Retrap	Gosforth Park				Wicken Fen			
		Male		Female		Male		Female	
		N	R	N	R	N	R	N	R
Year	2004	12	11	9	4	15	4	14	4
	2003	11	14	7	1	31	3	22	2
	2002	11	17	9	4	20	3	19	3
	2001	18	12	8	5	22	7	27	2
	2000	9	8	9	1	65	8	60	0
	1999	8	8	5	4	30	2	22	0
	1998	8	6	7	1	20	1	9	1
	1997	10	3	3	3	13	2	17	0
	1996	7	4	8	2	26	1	17	2
	1995	5	4	4	1	80	4	64	3
	1994	6	2	2	0				
	1993	4	3	2	0				
	1992	4	4	0	0				
	1991	4	4	1	1				
	1990	6	3	3	0				
	1989	3	2	4	1				
	1988	13	0	6	0				

Despite time not improving MARK models at Gosforth Park, there was some evidence for a slight linear increase over time in model average estimates (Fig 1); the sexes were equal in their fluctuations over time.

At the southerly Wicken Fen site, the most parsimonious model included a transient/resident effect on survival rate, a sex effect on transient survival ($\varphi 1_s$), a sex effect on resident survival ($\varphi 2_s$), and no effect on recapture rates ($\varphi 1_s$ $\varphi 2_s$ p; Appendix 3, Table ii). The $QAIC_c$ weighting given for this model was 0.17, with the next-best model showing a similar 0.16 $QAIC_c$ weighting. Since the best model fit was < 2.0 $\Delta QAIC_c$ to the next five models in the list, each could represent the data sufficiently; however, LRTs revealed that including a sex effect on resident survival ($\varphi 2_s$) improved the fit significantly (χ^2_1 = 3.6, P = 0.053), which was also true for transient survival (χ^2_1 = 4.6, P = 0.033). Likewise, there was a significant improvement in models with a sex effect on recapture rates (χ^2_1 = 4.4, P = 0.036), despite this effect being excluded from the top model. The highest model (by $QAIC_c$) that included annual time effects and a group interaction on resident survival ($\varphi 2_{s*t}$) showed near significance (χ^2_5 = 9.7, P = 0.084) compared to the next highest with a sex effect only ($\varphi 2_s$); this raises the possibility of small differences between males and females in their survival rate variation over time. Time on its own showed no significance for survival
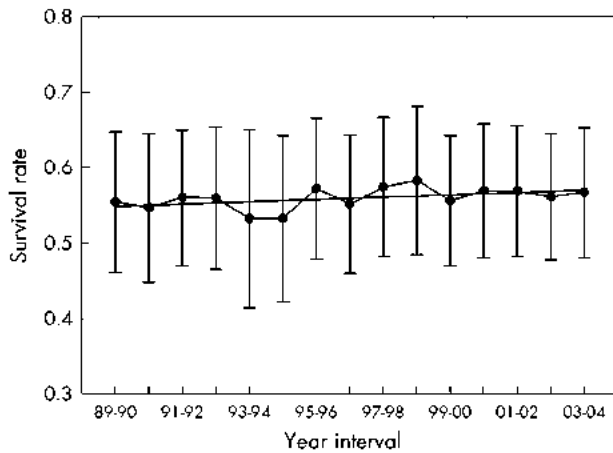
Figure 1. Resident survival rates averaged across both sexes at Gosforth Park (1989–2004) ± 95% confidence intervals. Model averaged estimates were produced using Program MARK (White & Burnham 1999). No resident survival rate was available for the period 1988/89 due to the constraint applied for transient individuals. The line is a linear regression of survival rate against time; this trend just failed to reach significance ($r_{14} = 0.48$, $F_{1,13} = 3.90$, $P = 0.070$) and models including time effects in Program MARK gave no statistical improvements to the analysis.

Figure 2. Resident survival rates for males (•) and females (o) at Wicken Fen (1996–2004) ± 95% confidence intervals. Model-averaged estimates were produced using Program MARK (White & Burnham 1999). No resident survival rates were available for the period 1995/96 due to the constraint applied for transient individuals. The lines are linear regression plots of survival rate against time and these trends showed no significance for either males ($r_7 = 0.33$, $F_{1,6} = 0.71$, $P = 0.433$), or females ($r_7 = 0.51$, $F_{1,6} = 2.11$, $P = 0.196$). There was some evidence for variation in survival rates between the sexes over time (φ_{s*t}), derived from the analysis using MARK, however this effect just failed to improve significantly the fit of models to the data.

($\chi^2_5 = 5.9$, $P = 0.314$) and was not an important effect for recapture rates either ($\chi^2_8 = 8.8$, $P = 0.357$). Model averages revealed that resident survival rate estimates for Wicken Fen were 52.0 ± 22.4 % for females and 32.9 ± 16.0 % for males, showing that male birds had a much lower survival rate than females. Recapture rates were 27.3 ± 14.6 % for females and 40.1 ± 17.3 % for males, suggesting that males were more likely to be recaptured. The model-average adult estimates at Wicken Fen showed a near-significant linear increase over time ($r_{14} = 0.65$, $F_{1,6} = 4.28$, $P = 0.084$), but individual sexes showed less of a correlation (Fig 2).

There was considerable overlap between the 95% confidence intervals for the resident survival rate estimates from Program MARK (Gosforth Park: 41.7–72.3%; Wicken Fen: 13.5–73.4%). However, the yearly survival rate estimates were significantly higher for Gosforth Park than Wicken Fen over the time period 1995–2004 (ANOVA: $F_{1,14} = 1038.27$, $P < 0.001$). This was also the case for recapture rates (95% confidence intervals: Gosforth Park: 53.6–85.3%; Wicken Fen: 11.1–67.2%) which were also higher each year at Gosforth Park (ANOVA: $F_{1,14} = 1382.07$, $P < 0.001$). The power of the analysis suffered slightly due to the transient correction; however, this was a problem at the outset since the Gosforth Park analysis had a low sample size and the Wicken Fen data spanned fewer years.
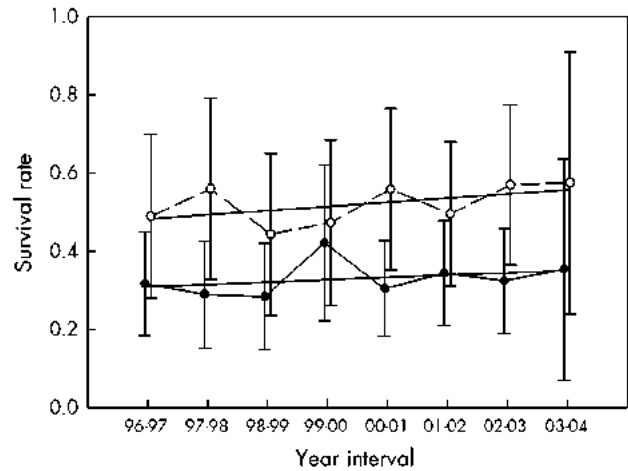
Sahel rainfall and local survival rates

When Sahel rainfall was included as a covariate in the MARK analysis of Gosforth Park data (Appendix 3, Table iii), after correction for transient birds, this did not explain any variation in survival rates over time (LRT: $\chi^2_1 = 0.4$, $P = 0.554$). Likewise, at Wicken Fen this covariate did not improve upon the best model ($\chi^2_1 = 0.1$, $P = 0.869$). Resident survival rates were, therefore, uncorrelated with the Sahel rainfall index at both sites. Survival rates of resident adults also showed little correlation with the Sahel rainfall index (Fig 3): the slopes of linear regression lines were not significantly different from zero either for Gosforth Park ($r_{14} = 0.08$, $F_{1,13} = 0.08$, $P = 0.787$), or Wicken Fen ($r_7 = 0.20$, $F_{1,6} = 0.25$, $P = 0.637$), and this remained the case when the data were reanalysed after removing the autocorrelation within the rainfall series (Gosforth Park $r_{14} = 0.12$, $F_{1,13} = 0.21$, $P = 0.658$; Wicken Fen $r_7 = 0.12$, $F_{1,6} = 0.09$, $P = 0.776$). Since Wicken Fen birds also showed some differences between sexes in how survival varied over time, males and females were examined separately in relation to the Sahel index; as with averaged survival rates, no correlation could be found for either sex either before (females: $r_7 = 0.43$, $F_{1,6} = 1.32$, $P = 0.294$; males: $r_7 = 0.53$, $F_{1,6} = 2.33$, $P = 0.177$) or after autocorrelation had been accounted for (females: $r_7 =$
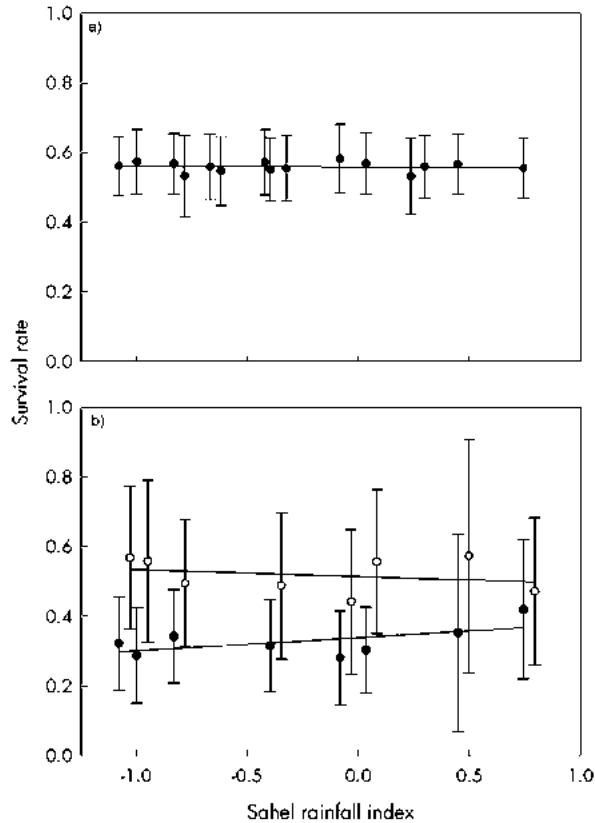
Figure 3. Estimated annual resident survival rates of (a) adult Reed Warblers at Gosforth Park (1988–2004) and (b) male (•) and female (o) Reed Warblers at Wicken Fen 1995–2004, plotted against an index of annual rainfall for the preceding wet season (June–October) in the Sahel region of West Africa. Survival rates are model-averaged estimates of the appropriate resident parameters produced using Program MARK (White & Burnham 1999). At Gosforth Park the effect of sex on resident survival (φ_s) gave no significant model improvement in MARK, whereas at Wicken Fen a significant improvement was observed. Error bars are ± 95% confidence intervals, and in (b) data for males and females have been offset slightly with respect to the *x*-axis so that error bars are distinct.

0.44, $F_{1,6}$ = 1.43, P = 0.276; males: r_7 = 0.56, $F_{1,6}$ = 2.42, P = 0.127). The survival-rate time series did not exhibit autocorrelation at either site. These regression analyses utilise survival rates that are correlated through time and so should be interpreted with caution, preferably to assess the effect size only.

Ringing effort at Wicken Fen
When ringing effort was included as a MARK covariate in the analysis of the Wicken Fen Ringing Group data, this improved the fit of models to the data set. The most parsimonious model was one that included a sole effort effect on recapture rates (*p*) and the inclusion of this effect was significant (LRT: χ^2_1 = 4.1, P = 0.042; Appendix 3,

Table iv). Recapture rates were 20.7 ± 10.5 % which showed no significant differences across sexes (χ^2_1 = 0.3, P = 0.610). Regression analysis also showed that ringing effort was significantly correlated with numbers of birds recaptured (r_{10} = 0.74, $F_{1,9}$ = 10.61, P = 0.010).

Local population demographics
At Gosforth Park, the estimated rate of population change for resident birds (λ_r) was 1.06 ± 0.02 (SE) suggesting an increasing population ($\lambda_r > 1$); transient birds made little difference to the analysis. At Wicken Fen, the population change estimate was 1.03 ± 0.07, which also indicated an increasing population, and inclusion of transient birds here substantially lowered this estimate ($\lambda_{t/r}$ = 0.91 ± 0.01) demonstrating the importance of their exclusion. At Gosforth Park, the seniority parameter (γ_r) was estimated as 0.54 ± 0.04 and the recruitment rate (f_r) was 0.49 ± 0.04, whereas at Wicken Fen γ_r was 0.44 ± 0.07 and f_r was 0.59 ± 0.09. This suggests that, at Gosforth Park, the survival of adult residents from the previous occasion was more important to population growth than new recruits, in contrast to Wicken Fen where new recruits of resident birds not previously seen were most important.

In terms of actual captures of adult birds each season (including transients), there was a significant increase observed at Gosforth Park from 1988 to 2004 (r_{16} = 0.81, $F_{1,15}$ = 31.14, P < 0.001). This was also the case if just resident birds were considered (r_{16} = 0.75, $F_{1,15}$ = 19.23, P = 0.001; Fig 4). Wicken Fen showed no significant changes in the number of adult birds captured in each season (1995–2004) whether all birds (r_9 = 0.31, $F_{1,8}$ = 0.85, P = 0.383), or just residents (r_9 = 0.35, $F_{1,8}$ = 1.08, P = 0.329; Fig 4) were considered.

Sahel rainfall and UK adult population
The CES index (1983–2003) showed no significant correlation to the Sahel rainfall index (r_{20} = 0.06, $F_{1,19}$ = 0.08, P = 0.781) (Fig 5), and this was also true when the effects of autocorrelation were removed by comparing the residuals from both series (r_{20} = 0.34, $F_{1,19}$ = 2.55, P = 0.127). This suggested that the UK abundance of Reed Warblers in the breeding season was not correlated with amount of rainfall in the preceding wet season in the Sahel over the CES time series used.

Sahel rainfall and local population trends
Data for both Gosforth Park and Wicken Fen showed no autocorrelation for the number of captures of adult Reed Warblers per season. The number of adults captured each year at Gosforth Park showed no correlation with the Sahel rainfall in the previous wet season with respect to either residents (r_{16} = 0.05, $F_{1,15}$ = 0.02, P = 0.877) or both
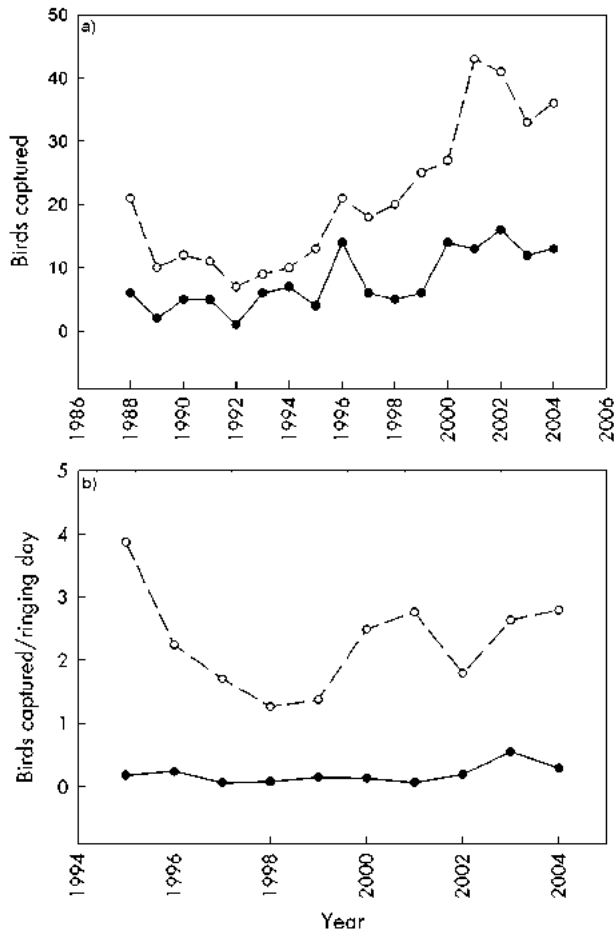
Figure 4. Total numbers of birds, and numbers of resident birds captured during April–September at (a) Gosforth Park (1988–2004), and (b) Wicken Fen (1995–2004). Transient and resident delineation was based on whether individuals were recaptured again after more than 10 days from the initial encounter in the first year of capture, and therefore transients identified in one year may take up residency in another year. Wicken Fen data were divided by the effort of the Ringing Group giving a scale of birds captured/ringing day. Solid lines represent residents only and dashed lines represent both residents and transients combined.

transients and residents combined (r_{16} =0.05, $F_{1,15}$ = 0.04, P = 0.850), and this was also true when the residuals were compared to correct for autocorrelation in the Sahel rainfall indices (r_{16} = 0.06, $F_{1,15}$ = 0.30, P = 0.591 for residents, and r_{16} = 0.18, $F_{1,15}$ = 0.54, P = 0.476 for transients and residents combined). This was also the case for captures (adjusted for ringing effort) at Wicken Fen (r_9 = 0.30, $F_{1,8}$ = 0.78, P = 0.402 for residents, and r_9 = 0.49, $F_{1,8}$ = 2.56, P = 0.148 for transients and residents combined) regardless of correction for autocorrelation in the Sahel rainfall indices (r_9 = 0.12 $F_{1,8}$ = 0.12, P = 0.733 for residents, and r_9 = 0.35, $F_{1,8}$ = 1.09, P = 0.328 for transients and residents combined).

DISCUSSION

Survival of adult Reed Warblers

The estimates of survival rates for adult Reed Warblers at Wicken Fen were similar to those obtained by Peach *et al* (1990) who gave estimates of between 0.44 and 0.64 for the period 1969 to 1983. Previously, Bibby (1971), Green (1975, 1976), and Redfern (1978) obtained estimates of between 0.43 and 0.57, despite older methodology and lack of sophisticated analytical software. For Gosforth Park, Redfern & Davidson (2002) estimated adult survival rates for the period 1998–2003 to be 0.515, which was also comparable to the present study. Although Peach *et al* (1990) reported large time variations in survival rates for Wicken Fen birds, time on its own was not a significant factor in the present analysis, but there was evidence for differential fluctuation in male and female survival rates over time. This suggests that males and females at this site may respond slightly differently to factors either within or outside the breeding season; however, the time period analysed was quite short and more years must be included before major conclusions can be drawn. For the Gosforth Park data there was evidence that year-to-year variations in adult survival rates were greater than might be expected by random effects alone, implying that other factors that have varied in magnitude from year to year over the period analysed may have influenced adult Reed Warbler survival rates.

The term 'survival rate' used in this context actually refers to the 'return rate' because it is a combination of true annual survival rate and the rate of permanent emigration. A lower rate of permanent emigration could explain why resident males at Gosforth Park showed a
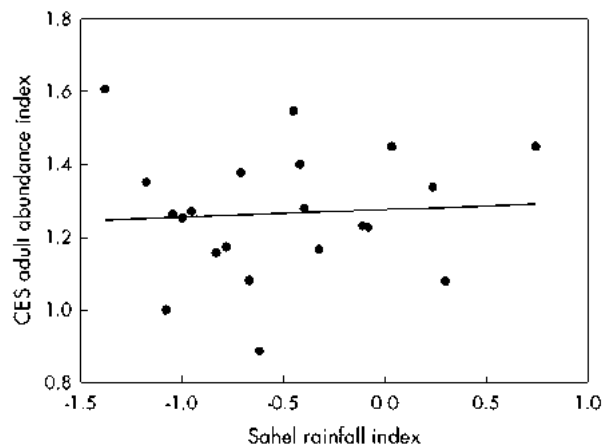

Figure 5. CES abundance population index for Reed Warblers, relative to an arbitrary value of 1 in 2003, plotted against an index of annual wet season (June–October) rainfall in the Sahel region of West Africa.

trend towards a slightly higher overall apparent survival rate (0.603) compared to females (0.549), since females would disperse and not be re-encountered. However, this would not account for the opposite pattern shown at Wicken Fen (males: 0.329, females: 0.520). It is important to note that, at both sites, females had similar apparent survival rates, but for males these were much lower at Wicken Fen than at Gosforth Park. Redfern (1978) also found lower apparent survival rates for males than females at Wicken Fen. Differences in habitat availability and breeding dispersal between sites may be a plausible explanation for the difference in apparent male survival rates between Gosforth Park and Wicken Fen. In the UK there are approximately 5,000 ha of freshwater reedbed, of which 86% (4,310 ha) is in East Anglia (RSPB 2004). Near to Wicken Fen, there are numerous fen and gravel-pit reedbeds, as well as reed vegetation fringing many drainage ditches. The nearest large reedbed sites to Gosforth Park are some distance away; for example, *c*30 km north at Druridge Bay on the east coast of northern England (39 ha), and 125 km southwest at Leighton Moss in Lancashire (93 ha). Also, Gosforth Park has approximately 3.5–4.0 ha of reedbed compared with around 40 ha at Wicken Fen (Cadbury 1997). Therefore, Wicken Fen is adjacent to a much greater extent of continuous and near-continuous habitat, which could facilitate breeding dispersal, than Gosforth Park in northeast England, where habitat is patchier and far less extensive. If Reed Warbler life histories favour preferential dispersal of male birds, then this could account for differences between Gosforth Park and Wicken Fen in the apparent survival rates of males. This difference in extent of adjacent available habitat could also explain the differences in recapture rates between the two sites (Wicken Fen: 0.337, Gosforth Park: 0.722), and the greater effect of transient birds on estimates of population change at Wicken Fen. A resident male bird at Wicken Fen may have greater potential for permanent emigration and breeding dispersal than an equivalent male in Gosforth Park, thus producing a lower apparent survival rate for Wicken Fen birds. In contrast, at a different study site in England, Catchpole (1972) concluded that female Reed Warblers had a lower breeding site fidelity than males. Therefore sex-specific rates of breeding dispersal may vary in relation to the availability of suitable breeding habitat nearby. It would be interesting to carry out multi-site metapopulation analyses in a comparison of north and south regions introducing the added parameter of movement between sites.

Breeding dispersal may not be the only factor accounting for variations in survival and recapture rates. Predation risk must also be considered, but this may not influence these particular survival rates as both males and females face different predation pressures as a result of sex-differences in behaviour and roles. For example, females may be more conspicuous and susceptible to predation whilst incubating and carrying eggs, but males may be more at risk when singing and defending territories.

Local populations

Although there were differences in population dynamics between the two sites, both showed positive population growth rates over time: Wicken Fen = 1.015, Gosforth Park = 1.055, which was verified by yearly breeding season captures. In terms of habitat, Gosforth Park has seen increases in reedbed area and quality over the last 20 years. This, coupled with national range expansion of Reed Warblers north and west has undoubtedly facilitated the growth of the population at this site. Over the years, scrub has been cut back and water levels controlled enabling reedbeds to expand. Reed Warblers are also known to favour reedbeds cut on a rotation (Bibby & Lunn 1982), which is a management strategy employed at Wicken Fen. This removes the accumulation of dead litter and induces more vigorous reed growth which may provide better food resources and stronger reeds for nesting (Poulin *et al* 2002). At Gosforth Park, population growth may have been more influenced by the survival of adult residents, rather than new recruits from immigration and natal recruitment. Again, this is in agreement with the idea that Gosforth Park represents a small island of suitable habitat with less opportunity for immigration from nearby sites. In contrast to Gosforth Park, new recruits were of greater importance to population growth at Wicken Fen. Birds may immigrate (and emigrate) more readily in the south, which would enhance the contribution of new recruits to population growth. However, this conclusion is speculative since immigration cannot be separated from natal recruitment in this analysis.

Productivity and breeding performance in a season will also influence the recruitment of new adults to resident breeding populations. These factors were not examined here, and could also explain fluctuations in adult abundance locally and nationally. The presence of the Cuckoo *Cuculus canorus* at Wicken Fen may also reduce productivity and recruitment, although the Cuckoo population has recently declined in England (Crick *et al* 2004).

There was a small but statistically significant difference in the mean wing lengths of males, with the mean wing length of male Reed Warblers at Wicken Fen being 0.7 mm greater than the mean for males at Gosforth Park. Conversely, the mean wing length for females was similar at both sites, and this suggests that there may be a real biological explanation for the difference in wing length between males at the two sites. For example, small differences in mean wing length of males between the two

sites could be linked to differences in breeding dispersal, facilitated by the extent of habitat available for dispersal and driven by differences in male quality (perhaps stronger sexual selection pressure), with smaller birds being more likely to disperse to adjacent areas.

Sahel precipitation and adult survival rates

The population demography of some migrant passerine species has been linked to precipitation patterns on the Sahel where these species overwinter (eg Winstanley et al 1974, Jones 1986, Peach et al 1991). In an analysis of Sedge Warblers in southern England, Peach et al (1991) found a strong correlation between adult survival and abundance and Sahel rainfall. Abrupt alternations of dry and wet seasons can result in seasonal increases of plants and invertebrates, important for migratory species (Morel 1973). Lack of precipitation can also lead to increased competition for a smaller food resource and decreased shelter from predators; therefore overwintering mortality is density-dependent (Peach et al 1991). The Reed Warbler is also a trans-Saharan migrant, but variation in Sahel rainfall was not correlated with variations in adult survival rates at Gosforth Park and Wicken Fen, nor with abundance of adult Reed Warblers in the UK from CES data. Likewise, sex variation in survival rates over time also showed no correlation to Sahel rainfall. Although there were increases in adult survival rates at Wicken Fen in two years when there had been plentiful rainfall in preceding wet seasons, overall the relationship between survival rates and Sahel rainfall was not significant. These results suggest that other factors may be more important in determining Reed Warbler survival and abundance.

The migration pattern of the Reed Warbler differs somewhat to those of other trans-Saharan migrants in that the species uses short migratory stages in contrast to the direct migration route of the Sedge Warbler (Redfern & Alker 2002). Recoveries of British-ringed birds in France and the Iberian Peninsula are thought to represent the use of regular 'stop-over' sites for migratory fattening (Bibby & Green 1983), resulting in slower migration speeds. This could render the Reed Warbler population less susceptible to environmental conditions in the Sahel in the early and late parts of the wintering period. Birds may also winter south of the Sahel in the Guinea Coast area between Guinea and Benin. Although annually this area has seen fluctuations in precipitation over time (Nicholson 2001), the yearly regional total is much higher and big differences exist between regions with regard to August/September rainfall (Nicholson & Palao 1993); thus any populations wintering here are likely to fare much better. However, as the wintering locations of Reed Warblers are not precisely known (Redfern & Alker 2002), this is speculative.

The recent decline in adult Reed Warbler abundance for the UK as measured by CES may reflect productivity and climate variations during the UK breeding season, rather than rainfall fluctuations in the wintering quarters. This decline may be a temporary one caused by poor breeding seasons in 2001 and 2003, in contrast to the good seasons of 1999 and 2002. This study provides indirect evidence linking good habitat management to local abundance and survival of Reed Warblers. Good-quality habitat is important for survival and retention of breeding birds. Differences in habitat availability between the north and south of the UK may lead to increased breeding dispersal in the south and a higher site fidelity of male Reed Warblers in the north, which will both contribute to variations in apparent survival rates between sites. Therefore, increasing the availability of suitable habitat in the north of the UK will allow movement and dispersal of Reed Warblers between sites and assist the recruitment of new individuals to the breeding population.

ACKNOWLEDGEMENTS

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APPENDIX 1

Transient birds

In MARK, the occurrence of transient birds in mist-net samples can be dealt with by altering the model structure [using the Parameter Information Matrix (PIM)]. Each cohort of the PIM can be 'corrected' for the transients occurring alongside residents in the interval between encounter occasions 1 and 2. This can be achieved by numbering the first diagonal of the PIM separately to the 'resident' section of the matrix thus giving delineation of transient and resident parameters. Assuming all birds regarded as transients permanently emigrate, survival rates between encounter occasions 2 and 3 and between subsequent occasions should represent resident birds only. Models constructed with this transient/resident constraint are referred to as 'time-since-marking' (TSM) models, and are referred to separately from 'age' models (Cooch & White 2005). Another approach to dealing with transients is to estimate survival rates for a 'second sample' of birds retrapped at least 10 days after marking (Buckland & Baillie 1987; Peach *et al* 1990). This approach was also tested but gave only a slight improvement in precision with small reductions in the standard error of estimates. Therefore, we have used the first approach to account for transient birds.

APPENDIX 2

Methodology of estimating overdispersion

We tested two ways of estimating the overdispersion parameter $\hat{c}$. The first was to use the observed $\hat{c}$ value (model deviance divided by the deviance degrees of freedom) divided by the mean $\hat{c}$ from 500 boot-strapped simulations (Cooch & White 2005). The values obtained for both sites under this approach were Wicken Fen: $\hat{c}_{observed} / \hat{c}_{simulated}$ = 1.336, Gosforth Park: $\hat{c}_{observed} / \hat{c}_{simulated}$ = 1.325. To avoid bias under this particular approach another was also tested using the observed model deviance divided by the mean deviance of 500 bootstrap simulations (Cooch & White 2005). This approach gave lower values than the ones given above so the higher of the two estimates were used for both sites. Since the use of particular $\hat{c}$ values can also cause great changes to model orders, varying values were also tested for both sites. Wicken Fen model orders were modified greatly. Before any adjustment was made, time variant models with group interactions were more parsimonious than others – hence the overdispersion value changed the original order considerably. Model orders, however, remained relatively unchanged for values in the range $1.336 < \hat{c} < 2.00$ at Wicken Fen. In contrast, Gosforth Park models showed little difference in order for the top five models in the range $1.325 < \hat{c} < 3.00$. Below the chosen value of $\hat{c}$, the top two parsimonious models were simply swapped and the third in the list was one specifying time effect on resident recapture, which subsequently became far less important with higher overdispersion values. Reasonable confidence was assumed in $\hat{c}$ values chosen since no values > 2.0 were obtained at either site.

For the analysis of Sahel rainfall (after transient correction), the $\hat{c}_{observed} / \hat{c}_{simulated}$ ratio was given as: 1.211 for Gosforth Park, and 1.372 for Wicken Fen. These were the largest $\hat{c}$ values obtained from all methods tested, with little changes in model orders from $1.00 < \hat{c} < 2.00$. Likewise, the overdispersion adjustment ($\hat{c}_{observed} / \hat{c}_{simulated}$ ratio) for the separate analysis of ringing effort at Wicken Fen was found to be 1.710 under the approach used above, with no change in the most parsimonious model in the range $1.00 < \hat{c} < 2.00$, and only minor changes to model orders favouring models with fewer parameters.

Note that recent advances in the overdispersion parameter have now shown the chosen estimation of $\hat{c}$ may be biased for CJS methods and must therefore be treated with caution; however, since a range of $\hat{c}$ values were also tested, at the time of writing reasonable confidence may be assumed in parsimony of models.

APPENDIX 3

Results from Program MARK

Table i. Set of competing models of annual apparent survival (φ), and recapture probability (p) for Reed Warblers ringed and captured at Gosforth Park Nature Reserve, Newcastle upon Tyne, UK (1988–2004). Models were allowed to vary by sex (s), time (t), and both sex and time (s*t), with some models examining survival of birds in the first year after marking (including residents and transients) ($\varphi1$) and survival of birds during the intervals after the second year following marking (representing residents only) ($\varphi2$). QAIC$_c$ values were used to indicate model parsimony, adjusted for overdispersion ($\hat{c}$). The weight of the respective model is calculated from the difference between the QAIC$_c$ of a given model and the next in the list (ΔQAIC$_c$). Section 1 indicates the top 10 models obtained from all combinations, section 2 indicates those extra models used in likelihood ratio tests, and section 3 indicates the full model from which overdispersion ($\hat{c}$) was obtained.

	Model	QAIC$_c$	Δ QAIC$_c$	QAIC$_c$ weight	Model likelihood	No. of parameters	Deviance
1	$\varphi1_s\ \varphi2\ p$	415.92	0.00	0.30	1.00	4	143.37
	$\varphi1_s\ \varphi2_s\ p$	416.70	0.78	0.20	0.68	5	142.08
	$\varphi1_s\ \varphi2\ p_s$	417.68	1.76	0.12	0.41	5	143.07
	$\varphi1_s\ \varphi2\ p_s$	417.95	2.03	0.11	0.36	5	143.33
	$\varphi_s\ p_s$	418.81	2.89	0.07	0.24	4	146.26
	$\varphi1\ \varphi2\ p_s$	420.31	4.39	0.03	0.11	4	147.76
	$\varphi1\ \varphi2\ p$	420.46	4.54	0.03	0.10	3	149.96
	$\varphi1_s\ \varphi2_s\ p_s$	420.51	4.59	0.03	0.10	5	145.90
	$\varphi1\ \varphi2_s\ p_s$	420.51	4.59	0.03	0.10	5	145.90
	$\varphi1\ \varphi2_s\ p$	420.60	4.68	0.03	0.10	4	148.05
2	$\varphi1_s\ \varphi2_t\ p$	422.18	6.26	0.01	0.04	15	126.20
	$\varphi1_s\ \varphi2_{s*t}\ p$	431.03	15.11	0.00	0.00	22	119.24
	$\varphi1_s\ \varphi2\ p_t$	433.72	17.80	0.00	0.00	17	133.30
	$\varphi1_t\ \varphi2\ p$	439.50	23.58	0.00	0.00	18	136.83
3	$\varphi1_{s*t}\ \varphi2_{s*t}\ p_{s*t}$	482.0	66.13	0.00	0.00	56	81.72

Table ii. Set of competing models of annual apparent survival (φ), and recapture probability (p) for Reed Warblers ringed and captured at Wicken Fen Nature Reserve, Cambridgeshire, UK (1995–2004). Models were allowed to vary by sex (s), time (t), and both sex and time (s*t), with some models examining survival of birds in the first year after marking (including residents and transients) ($\varphi1$) and survival of birds during the intervals after the second year following marking (representing residents only) ($\varphi2$) separately. QAIC$_c$ values were used to indicate model parsimony, adjusted for overdispersion ($\hat{c}$). The weight of the respective model is calculated from the difference between the QAIC$_c$ of a given model and the next in the list (ΔQAIC$_c$). Section 1 indicates the top 10 models obtained from all combinations, section 2 indicates those extra models used in likelihood ratio tests, and section 3 indicates the full model from which overdispersion ($\hat{c}$) was obtained.

	Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Model likelihood	No. of parameters	Deviance
1	$\varphi1_s\ \varphi2_s\ p$	286.19	0.00	0.17	1.00	5	50.53
	$\varphi1\ \varphi2_s\ p_s$	286.30	0.12	0.16	0.94	5	50.64
	$\varphi1\ \varphi2\ p_s$	287.30	1.12	0.10	0.57	4	53.68
	$\varphi1_s\ \varphi2\ p$	287.76	1.58	0.08	0.45	4	54.14
	$\varphi1_s\ \varphi2_s\ p_s$	287.80	1.62	0.08	0.45	6	50.10
	$\varphi1_s\ \varphi2_{s*t}\ p_s$	288.41	2.23	0.06	0.33	11	40.41
	$\varphi1\ \varphi2_s\ p$	288.68	2.49	0.05	0.29	4	55.05
	$\varphi1_s\ \varphi2_{s*t}\ p$	288.69	2.50	0.05	0.29	11	40.68
	$\varphi1_s\ \varphi2\ p_s$	289.26	3.08	0.04	0.21	5	53.61
	$\varphi_s\ p_s$	289.47	3.28	0.03	0.19	4	55.84
2	$\varphi1\ \varphi2\ p$	290.05	3.86	0.02	0.15	4	56.42
	$\varphi1_t\ \varphi2_s\ p_s$	292.17	5.98	0.01	0.05	13	39.99
	$\varphi1\ \varphi2_t\ p$	292.45	6.26	0.01	0.04	8	50.65
	$\varphi1_s\ \varphi2_s\ p_t$	294.30	8.11	0.00	0.02	13	42.13
3	$\varphi1_{s*t}\ \varphi2_{s*t}\ p_{s*t}$	297.89	11.71	0.00	0.00	28	13.53

Table iii. Competing models of annual resident survival (φ), and recapture probability (p) for Reed Warblers at (a) Wicken Fen (1995–2004) and (b) Gosforth Park (1988–2004), previously corrected for transients by removing the first occasion. Models were first allowed to vary by sex (s) and time (t), with interaction (s*t) and additive (s+t) effects. A Sahel rainfall covariate (r) was then added which replaced the time effect: hence there was interaction with sex only (s*r, s+r). QAIC$_c$ values were used to indicate model parsimony, adjusted for overdispersion ($\hat{c}$). The weights of respective models are calculated from the difference between the QAIC$_c$ of a given model and the next in the list (ΔQAIC$_c$). Sections 1 and 2 indicates the top 10 models obtained from all combinations, '2' indicates the model used to test the rainfall effect, and section 3 indicates the full model from which overdispersion ($\hat{c}$) was obtained.

(a)	Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Model likelihood	No. of parameters	Deviance
1	$\varphi_s\,p_s$	108.81	0.00	0.29	1.00	2	44.17
	$\varphi_.\,p_s$	109.74	0.93	0.18	0.63	3	42.96
	$\varphi_.\,p_.$	110.89	2.08	0.10	0.35	4	41.92
	$\varphi_s\,p_.$	110.90	2.09	0.10	0.35	3	44.12
	$\varphi_r\,p$	110.93	2.12	0.10	0.35	3	44.15
	$\varphi_r\,p_s$	111.90	3.08	0.06	0.21	4	42.93
	$\varphi_{s*r}\,p_.$	112.67	3.85	0.04	0.15	5	41.47
2	$\varphi_{s+r}\,p_s$	112.99	4.18	0.04	0.12	5	41.79
	$\varphi_{s+r}\,p_.$	113.07	4.26	0.03	0.12	4	44.10
	$\varphi_{s*r}\,p_s$	113.26	4.45	0.03	0.11	6	39.77
3	$\varphi_{s*t}\,p_{s*t}$	138.42	29.60	0.00	0.00	20	26.24

(b)	Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Model likelihood	No. of parameters	Deviance
1	$\varphi_s\,p_.$	268.95	0.00	0.30	1.00	3	122.45
	$\varphi_s\,p_s$	270.56	1.61	0.13	0.45	4	121.97
2	$\varphi_{s+r}\,p_.$	270.69	1.74	0.12	0.42	4	122.10
	$\varphi_.\,p_s$	270.96	2.01	0.11	0.37	3	124.45
	$\varphi_.\,p_.$	271.29	2.34	0.09	0.31	2	126.86
	$\varphi_{s*r}\,p_.$	272.31	3.36	0.06	0.19	5	121.59
	$\varphi_{s+r}\,p_s$	272.32	3.37	0.05	0.19	5	121.61
	$\varphi_{s*r}\,p_s$	272.77	3.82	0.04	0.15	6	119.92
	$\varphi_r\,p_.$	272.86	3.91	0.04	0.14	3	126.36
	$\varphi_{s+r}\,p_{s*t}$	273.11	4.16	0.04	0.12	17	95.01
3	$\varphi_{s*t}\,p_{s*t}$	293.32	24.37	0.00	0.00	31	77.73

Table iv. Set of competing models of annual survival (φ) and recapture probability (p) for Reed Warblers ringed and captured at Wicken Fen (1995–2004). Models were first allowed to vary by sex (s) and time (t), with interaction (s*t) and additive (s+t) effects. The covariate of ringing effort (e) was then included in the data set for recapture rates, which replaced the time effect hence there was interaction with sex only (s*e, s+e). $QAIC_c$ values were used to indicate model parsimony, adjusted for overdispersion ($\hat{c}$). The weights of respective models are calculated from the difference between the $QAIC_c$ of a given model and the next in the list ($\Delta QAIC_c$). Section 1 and 2 indicate the top 10 models obtained from all combinations, '2' indicates the model used to test the effort effect, and section 3 indicates the full model from which overdispersion ($\hat{c}$) was obtained.

	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Model likelihood	No. of parameters	Deviance
1	$\varphi_. \, p_e$	157.75	0.00	0.32	1.00	3	42.56
	$\varphi_. \, p_{s+e}$	159.19	1.44	0.16	0.49	4	41.96
	$\varphi_s \, p_e$	159.78	2.03	0.12	0.36	4	42.55
2	$\varphi_. \, p_.$	159.85	2.10	0.11	0.35	2	46.69
	$\varphi_s \, p_{s+e}$	160.09	2.34	0.10	0.31	5	40.82
	$\varphi_. \, p_{s*e}$	161.23	3.49	0.06	0.18	5	41.96
	$\varphi_. \, p_s$	161.62	3.87	0.05	0.14	3	46.43
	$\varphi_s \, p_.$	161.88	4.13	0.04	0.13	3	46.69
	$\varphi_s \, p_{s*e}$	162.00	4.25	0.04	0.12	6	40.67
	$\varphi_t \, p_.$	169.08	11.33	0.00	0.00	11	37.32
3	$\varphi_{s*t} \, p_{s*t}$	176.82	19.07	0.00	0.00	20	25.66