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Published paper

Gullett, P, Evans, K.L, Hatchwell, B.J and Robinson, R.A (2014) Climate change and annual survival in a temperate passerine: Partitioning seasonal effects and predicting future patterns. *Oikos*, 123 (4). 389 - 400. Doi: 10.1111/j.1600-0706.2013.00620.x



Climate change and annual survival in a temperate passerine: partitioning seasonal effects and predicting future patterns

Philippa Gullett, Karl L. Evans, Robert A. Robinson and Ben J. Hatchwell

P. Gullett (p.gullett@sheffield.ac.uk), K. L. Evans and B. J. Hatchwell, Dept of Animal and Plant Sciences, Univ. of Sheffield, Sheffield, S10 2TN, UK. – R. A. Robinson, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK.

Predicting climate change impacts on population size requires detailed understanding of how climate influences key demographic rates, such as survival. This knowledge is frequently unavailable, even in well-studied taxa such as birds. In temperate regions, most research into climatic effects on annual survival in resident passerines has focussed on winter temperature. Few studies have investigated potential precipitation effects and most assume little impact of breeding season weather. We use a 19-year capture–mark–recapture study to provide a rare empirical analysis of how variation in temperature and precipitation throughout the entire year influences adult annual survival in a temperate passerine, the long-tailed tit *Aegithalos caudatus*. We use model averaging to predict longer-term historical survival rates, and future survival until the year 2100. Our model explains 73% of the interannual variation in survival rates. In contrast to current theory, we find a strong precipitation effect and no effect of variation in winter weather on adult annual survival, which is correlated most strongly to breeding season (spring) weather. Warm springs and autumns increase annual survival, but wet springs reduce survival and alter the form of the relationship between spring temperature and annual survival. There is little evidence for density dependence across the observed variation in population size. Using our model to estimate historical survival rates indicates that recent spring warming has led to an upward trend in survival rates, which has probably contributed to the observed long-term increase in the UK long-tailed tit population. Future climate change is predicted to further increase survival, under a broad range of carbon emissions scenarios and probabilistic climate change outcomes, even if precipitation increases substantially. We demonstrate the importance of considering weather over the entire annual cycle, and of considering precipitation and temperature in combination, in order to develop robust predictive models of demographic responses to climate change.

Synthesis

Prediction of climate change impacts demands understanding of how climate influences key demographic rates. In our 19-year mark-recapture study of long-tailed tits *Aegithalos caudatus*, weather explained 73% of the inter-annual variation in adult survival; warm springs and autumns increased survival, wet springs reduced survival, but winter weather had little effect. Robust predictions thus require consideration of the entire annual cycle and should not focus solely on temperature. Unexpectedly, survival appeared not to be strongly density-dependent, so we use historical climate data to infer that recent climate change has enhanced survival over the four decades in which the UK long-tailed tit population has more than doubled. Furthermore, survival rates in this species are predicted to further increase under a wide range of future climate scenarios.

Climate change is expected to become a major driver of species' extinctions in the coming decades, with numerous shifts in the abundance and distribution of animal and plant species already documented across the globe (Walther et al. 2002). Such shifts are driven largely by local changes in population size as a result of altered productivity and survival (Huntley et al. 2007, Leech and Crick 2007). The mechanisms underpinning such demographic changes are not well understood (Seavy et al. 2008, Balbontín et al. 2009, van de Pol et al. 2010), despite increasing evidence that incorporating demographic mechanisms into predictive models of future climate change impacts greatly improves their performance

(Buckley et al. 2010, Bykova et al. 2012). In order to improve predictive capacity it is essential to advance understanding of how variation in climate drives demographic processes, by using historical data to uncover detailed relationships between climate and demography. The resultant models can then be combined with future climate projections to predict demographic shifts (Grosbois et al. 2006, Seavy et al. 2008).

Survival is a key demographic trait. In small-bodied birds in temperate regions, climatic influences on survival are one of the most important demographic processes contributing to annual variation in population size (Newton 1998, Sæther et al. 2004, Leech and Crick 2007).

Following the ideas of Lack (1954), survival is thought to be influenced primarily by weather during the non-breeding season ('tub hypothesis'). Breeding season weather is thought to influence population size via changes in productivity, offspring quality and subsequent recruitment ('tap hypothesis', Sæther et al. 2004). This tub-tap hypothesis is supported by observations that temperate populations of several small-bodied resident species fluctuate according to weather during November to April (Newton 1998, Sæther et al. 2000, 2004), and by correlations between survival rates and winter conditions in many species (Lahti et al. 1998, Peach et al. 1999, Perdeck et al. 2000, Doherty and Grubb 2002, Nilsson et al. 2011). Such correlations are, however, often weak and the majority of interannual variation in survival is frequently unexplained (Lahti et al. 1998, Peach et al. 1999, Perdeck et al. 2000, Doherty and Grubb 2002). Consequently, there is still considerable uncertainty regarding the relative importance of weather at different times of year, and the precise demographic consequences of these weather effects (Sæther et al. 2004, Grosbois et al. 2006, Robinson et al. 2007, Santisteban et al. 2012).

Previous studies have suggested that low temperatures can be detrimental for birds by increasing thermoregulatory costs and reducing food abundance or availability, particularly during winter when thermoregulatory investment is highest and food is most scarce (Clobert et al. 1988, Perdeck et al. 2000, Sæther et al. 2000). Precipitation may also increase energy demand or reduce feeding opportunities (Altwegg et al. 2003), and interactions between temperature and precipitation may be important. Insectivorous birds may, for example, be unable to glean sufficient food from vegetation that is covered in ice following cold and wet conditions (Robinson et al. 2007). Despite this recognition of the potential role of precipitation in determining avian survival rates, empirical assessments have largely focussed on the role of temperature (Clobert et al. 1988, Perdeck et al. 2000, Santisteban et al. 2012). Summer heat stress may also become a more important determinant of survival under future climatic conditions, even in temperate regions (Jiguet et al. 2006, Grosbois et al. 2006, Santisteban et al. 2012), but are rarely considered in models of survival rates.

Here we provide an empirical assessment of how climatic variation influences annual adult survival in a temperate passerine, using a 19-year capture–mark–recapture study of a population of long-tailed tits *Aegithalos caudatus* in the Rivelin Valley, Sheffield. We use a novel approach to simultaneously assess the effects of both temperature and precipitation throughout the entire annual cycle. We also test for potential interactions between temperature and precipitation, and for summer heat stress effects. Furthermore, we use model-averaged parameter estimates to infer historical survival rates and predict future survival until the end of the century under a broad range of probabilistic climates and future emissions scenarios. We consider all three emissions scenarios defined by UK Climate Projections 2009 (UKCP 2009), termed 'low', 'medium' and 'high'. These emissions scenarios are based respectively on the B1, A1B and A1F1 greenhouse gas emissions scenarios developed by the Intergovernmental Panel on

Climate Change (IPCC) Special Report on Emissions Scenarios, which are projected from a wide range of potential future socio-economic scenarios (for full details see Nakicenovic et al. 2000).

The long-tailed tit is an ideal species for this analysis, because its small body size makes it particularly sensitive to fluctuations in weather conditions (Newton 1998, Leech and Crick 2007). The UK population has been increasing since the early 1980s, and the suggestion that this increase is a result of improved overwinter survival following recent climate change is currently untested (Baillie et al. 2012). Long-tailed tits are woodland residents that do not use nest boxes, and are subject to very low levels of winter food supplementation within our study site.

Methods

Study system and capture–mark–recapture data

We studied annual survival in a population of long-tailed tits in the temperate climate of the Rivelin Valley, Sheffield (53°38'N 1°56'W; altitude at centre of site = 168 m a.s.l., range = 150–270 m). The study area is approximately 2.5 km², about half of which comprises mixed deciduous woodland that offers suitable breeding habitat for long-tailed tits, whilst the remainder is open pasture and therefore not used by long-tailed tits. The present analysis was restricted to adult survival (i.e. survival from the age of 9 months onwards), due to problems with distinguishing between dispersal and mortality during the first 9 months of life, when the majority of dispersal occurs (Sharp et al. 2008). Adult breeding population size in the study site ranged from 34 to 130 birds (Supplementary material Appendix A1 Table A1), equating to a mean population density of about 70 adults km⁻² of breeding habitat. We used a capture–mark–recapture (CMR) approach (following Lebreton et al. 1992), constructing individual encounter histories for 985 individuals of known sex caught in the breeding seasons of 1994–2012, giving 19 encounter occasions. These 985 individuals comprised birds originally caught as unringed adults (673 individuals) and birds ringed as nestlings and recaptured/resighted as adults at least once (312 individuals). For this latter group, only adult encounters were considered. An additional 14 birds were excluded from the analysis because their sex was unknown. The sex of all other individuals was identified by behavioural observations and confirmed via genetic analysis of blood samples. We defined the capture/resighting period as the breeding season (March–May). This is the period of intensive capture/resighting effort within the site, but the vast majority of captures/resightings occurred during March.

Defining a reference survival model

Encounter histories were analysed using methods that provide robust estimates of survival rates (henceforth ϕ) whilst accounting for potential biases due to variation in recapture probabilities (henceforth p), using a logit link function to constrain estimates of ϕ and p to between 0 and 1 (Lebreton et al. 1992). In lieu of developing an a priori candidate set of

models, we instead used several stages to develop a reference model for subsequent modelling of climatic effects on survival. We first fitted a global structural model, with the individual covariates of sex and ringing age (adult or nestling), which could influence survival and recapture probabilities. ϕ was allowed to vary between years, whereas p was assumed to be constant between years because field recapture/resighting protocols were standard across years (Meade and Hatchwell 2010). The exception was during 2001, when p was fixed to 0.4 to reflect the ~50% reduction in capture/resighting effort following foot-and-mouth disease restrictions in the study site (Supplementary material Appendix A1 Table A1). This reflected the estimated recapture rate in a model that allowed p to differ in 2001 compared to all other years. Our global structural model was thus $\phi(\sim \text{time} \times \text{sex} \times \text{ringingAge})p(\sim \text{sex} \times \text{ringingAge})$, where \times represents the interaction term with main effects included. We tested the goodness of fit of this global model using parametric bootstrap methods, which showed slight under-dispersion ($\hat{c} = 0.853$). We then selected a more parsimonious structural reference model by comparing the global model to each of the reduced models nested within the global model (following Lebreton et al. 1992, Grosbois et al. 2006) and selecting the model with the lowest Akaike's information criterion corrected for small sample size (AICc, Burnham and Anderson 2002). The most parsimonious reduced model was $\phi(\sim \text{time})p(\text{sex})$, which we therefore defined as the reference model (Supplementary material Appendix A1 Table A2). Hence p was modelled separately for males and females in all subsequent climatic models. The probability of recapture was high, at 0.92 ± 0.02 for males and 0.83 ± 0.03 for females (estimate \pm 1SE). All analyses were run in R ver. 2.14.1, using package RMark (Laake and Rextad 2008) for CMR analyses as a wrapper to program MARK (White and Burnham 1999).

Climatic survival models

Daily weather data were obtained from Weston Park Weather Station (Weston Park Weather Station, Museums Sheffield 2012), located approximately 5 km east of the study site ($53^{\circ}38'N$, $1^{\circ}49'W$) and at a similar elevation (131 m) to the study site (mean 168 m). To validate our use of off-site weather data, we compared the weather station temperatures with mean monthly air temperature recorded at twenty points distributed throughout the study site during three years of the study (2010–2012). These data were recorded at 4-h intervals using miniature data loggers mounted in a white solar radiation shield. Temperatures at the study site and weather station were very strongly associated (linear regression: $R^2 = 0.997$, $p < 0.0001$, parameter estimate 0.912 ± 0.009). No equivalent comparison of on- and off-site data was possible for precipitation, but personal observations (PG, KLE, BH) suggest that any variation in rainfall patterns on- and off-site is likely to be minor given the negligible difference in elevations of the study site and weather station. We are therefore confident that the off-site weather station captures on-site monthly and annual climatic variation accurately.

To investigate how annual survival is influenced by interannual variation in weather at certain times of year,

we defined four seasons relevant to the biology of long-tailed tits: 1) March–April–May ('spring': breeding season), 2) June–July–August ('summer': immediately post-breeding, moulting), 3) September–October–November ('autumn'), 4) December–January–February ('winter'). We initially considered climatic indices that described the extent of periods of harsh weather ('extreme indices'), as well as average weather patterns ('average indices'). The extreme indices initially considered were: the total number of days with 1) minimum temperature $< 0^{\circ}C$ (seasons 1, 3, 4) or maximum temperature $> 25^{\circ}C$ (season 2), 2) total precipitation ≥ 10 mm, 3) minimum temperature $< 0^{\circ}C$ and total precipitation > 1 mm. Initial average indices considered were: 1) mean seasonal temperature ($^{\circ}C$), 2) total seasonal precipitation (mm). However, extreme indices were highly correlated ($r > 0.8$) with their corresponding average indices (Supplementary material Appendix A1 Table A3). We therefore considered only average indices in survival analyses, namely mean temperature and total precipitation during each of the four seasons (Supplementary material Appendix A1 Table A4). These variables were not significantly correlated (pairwise comparisons: $r < 0.46$, $p > 0.05$), with the exception of precipitation in spring and autumn ($r = 0.56$, $p = 0.014$). This collinearity was well within the threshold to which information theoretic approaches are robust (variance inflation factor < 2.8 for all variables, Freckleton 2011, Supplementary material Appendix A1 Table A3). All climatic indices (including past and future weather variables) were standardized by subtracting the mean and dividing by the standard deviation of the spring 1994 – winter 2011 time series, as recommended for CMR analyses (White and Burnham 1999).

To determine broad patterns between weather variables and survival, we first used a univariate approach to compare linear and quadratic models for all eight of these weather variables (x), thus constructing models of type $\phi(-x)p(\text{sex})$ and $\phi(\sim x + x^2)p(\text{sex})$. Given that we suspected within-season interactions between temperature (t) and precipitation (p) may be important, we then compared single-season models with interactive ($t \times p$) versus additive ($t + p$) effects within each season. We ran these models both with and without quadratic terms for the main effects. Neither univariate nor single-season models showed evidence of a relationship between survival and weather during seasons 2 and 4, with AICc scores similar to or exceeding that of the null model, but they did show evidence of weather effects during seasons 1 and 3, with potential within-season interactions and quadratic main effects (AICc < 10 compared to the best climatic model, Table 1, 2, Burnham and Anderson 2002). We therefore included in our 'full climatic model' the linear and quadratic effects of temperature and precipitation during spring and autumn, and their linear within-season interactions. Due to limited degrees of freedom, we did not consider interactions of climatic parameters between different seasons as such interactions were assumed to be of low potential importance.

Model selection and model averaging

Our full climatic model comprised 10 climatic parameters. We compared all models that comprised three or more of

Table 1. Univariate climatic models of adult long-tailed tit survival in the Rivelin population, 1994–2012. Survival ϕ is modelled as a linear ($\sim x$) response to year (the reference model, 20 parameters, first row) and as a linear ($\sim x$) and quadratic ($\sim x + x^2$) response to each weather variable, where t indicates mean seasonal temperature, p total seasonal precipitation and the numerals 1–4 seasons as defined in the text. The null model (last row) contains no explanatory terms, only an intercept. In all models, recapture is modelled separately for males and females and is fixed to 0.4 in 2001. $\Delta AICc$ is the change in AICc relative to the temporal reference model; R^2 is % temporal variation explained (deviance of temporal model = 451.21; deviance of null model = 523.68).

x	Linear $\Delta AICc$	R^2	Slope \pm 1SE	Quadratic $\Delta AICc$	R^2	Slope \pm 1SE (linear term)	Slope \pm 1SE (quadratic term)
Year	0	100	–	–	–	–	–
t1	22.9	23.6	+0.24 \pm 0.06	16.0	35.8	+0.31 \pm 0.06	+0.15 \pm 0.05
t2	39.0	1.3	+0.05 \pm 0.06	40.9	1.5	+0.06 \pm 0.06	–0.01 \pm 0.05
t3	35.3	6.4	+0.12 \pm 0.05	30.0	16.5	+0.23 \pm 0.07	–0.14 \pm 0.05
t4	38.5	2.0	–0.07 \pm 0.06	38.8	4.4	–0.04 \pm 0.06	+0.07 \pm 0.05
p1	22.5	24.1	–0.23 \pm 0.06	20.3	29.9	–0.26 \pm 0.06	–0.12 \pm 0.06
p2	40.0	0.0	+0.00 \pm 0.06	30.2	16.3	–0.13 \pm 0.07	+0.17 \pm 0.05
p3	15.1	34.3	–0.30 \pm 0.06	16.6	35.0	–0.29 \pm 0.06	–0.03 \pm 0.05
p4	39.8	0.2	–0.02 \pm 0.06	40.3	2.3	–0.01 \pm 0.06	–0.06 \pm 0.05
Null	37.9	–	–	–	–	–	–

these climatic parameters. From this candidate set, we identified the climatic survival model with the lowest AICc, and calculated the $\Delta AICc$ compared to this model for all other climatic models, henceforth termed ' $\Delta AICc_{climatic}$ '. All models with $\Delta AICc_{climatic} < 2$ were considered as having approximately equal support (Burnham and Anderson 2002). We termed these the ' $\Delta AICc < 2$ top subset' of models. For all models, we calculated the percentage of temporal variation explained by weather variables, which is commonly used as a measure of effect size in CMR analyses. We used the formula $R^2_{Dev} = [dev(n) - dev(c)/dev(n) - dev(t)] \times 100$, where $dev(n/c/t)$ represent the deviance of the null, covariate, and time-dependent models respectively (Grosbois et al. 2008). For simplicity, R^2_{Dev} is henceforth referred to as R^2 .

We averaged the estimates of all 11 models in the $\Delta AICc < 2$ top subset of models (following Grosbois et al. 2006, Martins et al. 2011). We calculated the partial R^2 of each climatic parameter in each of these 11 models, using the formula $partial\ R^2(x_i) = \%var(c) - \%var(c_{x_i})$, where $\%var(c)$ and $\%var(c_{x_i})$ represent the percentage of temporal variation explained by weather variables in models with and without climatic parameter x_i , respectively (Burnham and Anderson 2002). We then calculated model-averaged partial R^2 s and parameter estimates by first multiplying the re-scaled Akaike weight of a model with the partial R^2 and parameter estimate of each climatic parameter in that model, and then summing these model-specific estimates across all 11 models in the set (Burnham and Anderson 2002).

Density dependence

We calculated an index of population density, which was the total number of adults plus fledglings at the end of the breeding season (season 1). We were unable to estimate population sizes separately for the other seasons, but these are highly likely to reflect population size at the end of the breeding season. Adult plus fledgling population size ranged from 73 to 336 (mean \pm 1 SD = 181 \pm 61). This 'popSize' index showed little or no relationship with survival in univariate comparison, with the model $\phi(\sim popSize)p(sex)$ having the same AICc as the null model $\phi(\sim 1)p(sex)$. To test for density dependence of weather effects, we re-ran the top climatic model with population density as a main effect and as an interactive effect with each individual weather variable, and compared their results with those of the corresponding models lacking density dependent effects.

Prediction of past and future survival

We investigated whether the recent increase in the UK population of long-tailed tits (Baillie et al. 2012) may be linked to recent weather patterns, by using the Rivelin model-averaged parameter estimates to predict past survival in the Rivelin population during 1966–2011 (corresponding to the period of national population monitoring by the British Trust for Ornithology; Baillie et al. 2012). Historical climate data were obtained from Weston Park Weather Station and were thus directly comparable to the data used

Table 2. Single-season climatic models of adult long-tailed tit survival in the Rivelin population, 1994–2012. Survival is modelled in response to temperature and precipitation within each of four seasons (S1–S4); these main effects are fitted as both linear and quadratic terms in all models; within-season combined temperature/precipitation effects are fitted as both additive ($t + p$) and interactive ($t \times p$) linear effects. For each model, $\Delta AICc_{time}$ indicates $\Delta AICc$ compared to the temporal reference model $\phi(time)p(sex)$; R^2 indicates % temporal variation explained (deviance of temporal model = 451.2; deviance of null model = 523.7). 'Linear' and 'Quadratic' indicate models in which main effects were fitted as linear and quadratic terms respectively; interaction effects were fitted only as linear terms. The temporal reference model (20 parameters, first row) and null model (1 parameter, last row) are shown for reference purposes.

	Additive linear		Additive quadratic		Interactive linear		Interactive quadratic	
	$\Delta AICc_{time}$	R^2	$\Delta AICc_{time}$	R^2	$\Delta AICc_{time}$	R^2	$\Delta AICc_{time}$	R^2
Reference	0	100	–	–	–	–	–	–
S1: spring	14.6	37.8	7.0	53.9	8.0	49.6	6.1	57.9
S2: summer	40.9	1.5	29.5	22.7	42.5	2.0	26.5	29.7
S3: autumn	16.8	34.8	14.9	42.9	17.4	36.7	16.7	43.2
S4: winter	40.4	2.1	41.0	6.8	41.7	3.1	42.0	8.4
Null	37.9	–	–	–	–	–	–	–

to construct the survival models. To test for a general trend in estimated historical survival, we ran a linear and a quadratic regression through the annual survival probabilities for the period 1966–2011.

We investigated how climate change may influence long-tailed tit survival in the future by estimating survival under a range of future climatic scenarios, for each of three non-overlapping time periods encompassing the remainder of this century (2010–2039, 2040–2069, 2070–2099). Data on historical (1994–2011) and projected future (2010–2100) absolute climatic variables were extracted from UKCP 2009 for the 25 × 25 km grid square including the Rivelin Valley close to its centre, and used to calculate a percentage change factor for each of the four climate variables appearing in the survival model average (i.e. mean temperature and total precipitation in spring and autumn). We then applied these projected percentage change estimates to the observed weather station data used in this study (i.e. mean seasonal values for the period 1994–2011 at the Weston Park Weather Station), to estimate future weather conditions for this study site.

Future weather variables were projected for each of the three emissions scenarios defined by UKCP 2009 (low, medium and high). These scenarios are based respectively on the B1, A1B and A1F1 greenhouse gas emissions scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (Nakicenovic et al. 2000), and encompass a wide range of future potential emissions levels (UKCP 2009). A key feature of these data is that they provide probabilistic projections, i.e. they take uncertainty into account by calculating the likelihood of the estimated level of change. As recommended by UKCP (2009), we used the 50% cumulative distribution function (CDF) level as the 'likely' estimate of moderate change, the 10% CDF as the low-end estimate of change (which is 'highly likely' to be lower than the observed change), and the 90% CDF as the high-end estimate (which is 'highly likely' to be higher than the observed change, UKCP 2009).

We then used the model-averaged parameter estimates from the Rivelin survival model to predict future survival for each of the three future time periods. For each period and under each emissions scenario, we produced three future survival scenarios that reflected our results that warmer temperatures increased survival and high precipitation decreased survival: 'moderate', based on the moderate (50% CDF) estimates for both temperature and precipitation; 'best case', based on the high-end (90% CDF) estimate for temperature and the low-end (10% CDF) estimate for precipitation; 'worst case', based on the low-end estimate for temperature and the high-end estimate for precipitation.

Results

Climatic effects on survival

Univariate and multivariate comparisons showed the most important periods to be spring and autumn, with low temperatures and high precipitation reducing annual survival

(Table 1, Fig. 1). In contrast, interannual variations in summer and winter weather showed no relationship with annual survival (Table 1, Supplementary material Appendix A1 Fig. A1). Quadratic models were generally slightly more parsimonious than linear models (Table 1), and there was some evidence of a temperature-precipitation interaction in spring and in autumn (Table 2). The 'full' climatic model therefore comprised the linear and quadratic terms of temperature and precipitation in spring and autumn, and the within-season linear interactions of temperature and precipitation (indicated by ':'), thus $\phi(\sim t1 + p1 + t3 + p3 + t1^2 + p1^2 + t3^2 + p3^2 + t1 : p1 + t3 : p3)p(\text{sex})$.

Eleven models were retained in the $\Delta\text{AICc} < 2$ top subset, all of which included the linear effects of spring temperature and precipitation and their interaction (Supplementary material Appendix A1 Table A5). Weather explained a very large proportion (73%) of the interannual variation in survival rates (model averaged $R^2 = 73\%$; Fig. 2), showing a decrease in survival with increasing spring precipitation (partial $R^2 = 16.0\%$, parameter est. = -0.21) and with decreasing spring and autumn temperature (partial $R^2 = 17.9\%$ and 16.7% respectively, parameter est. = $+0.25$ for both; Table 3). Importantly, the strong interaction between temperature and precipitation in spring indicated that the negative effects of low temperatures were greatly exacerbated by high precipitation (Fig. 3). In contrast, the strong univariate relationship between annual survival and autumn precipitation was no longer apparent in multivariate models (partial $R^2 = 1.0\%$, parameter est. = -0.05 ; Table 3). Density dependence was only weakly apparent; high population density seemed to slightly reduce annual survival (Table 4), but parameter estimates of the best model changed little regardless of whether population size was included as a main effect (Fig. 4) and there was little evidence of an interaction between population size and weather (Table 4).

Prediction of past and future survival

Predictions of historical annual survival rates in the Rivelin long-tailed tit population indicated substantial between-year variation over the period 1966–2011, but a general rising trend (linear regression: $F_{1,44} = 15.34$, $R^2 = 26.0\%$, $p < 0.001$, Fig. 5a). By contrast, there was no apparent trend in annual survival over the 1994–2012 period of the local study ($F_{1,16} = 0.35$, $R^2 = 2.0\%$, $p = 0.56$).

Future projections of climatic change for the 25 × 25 km grid square including the Rivelin study site showed that mean spring and autumn temperature is expected to increase over the remainder of the century under all three emissions scenarios, even according to low-end estimates (Supplementary material Appendix A1 Table A6). Total seasonal precipitation in spring and autumn is also expected to increase slightly under all emissions scenarios, according to the mid-likelihood estimates, but there is greater uncertainty around these estimates, and precipitation may actually decrease according to low-end estimates (Supplementary material Appendix A1 Table A6). Despite this uncertainty, the overriding positive effects of increasing spring and autumn temperatures mean that future annual survival is expected to increase even under the worst-case scenario of

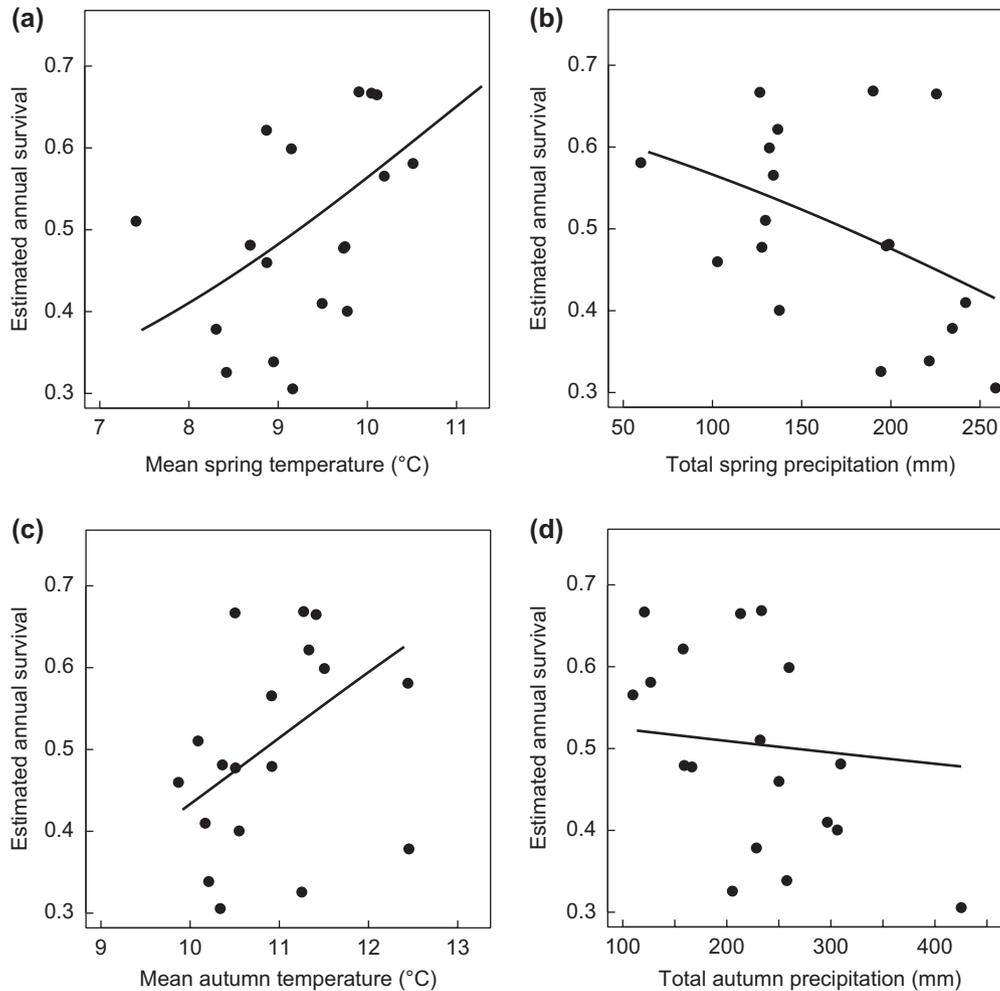


Figure 1. Relationships between adult long-tailed tit survival estimates (●) from the reference model $\phi(\sim \text{time})p(\text{sex})$ and four weather variables, for the Rivelin population in the years 1994–2012. Solid lines indicate survival estimated from model-averaged parameter estimates for each weather variable, calculated over the range in weather experienced during the study. Only weather variables showing a univariate relationship with survival are displayed here: (a) mean spring temperature, model-averaged partial $R^2 = 18.5\%$, (b) total spring precipitation, model-averaged partial $R^2 = 15.5\%$, (c) mean autumn temperature, model-averaged partial $R^2 = 16.3\%$, (d) total autumn precipitation, model-averaged partial $R^2 = 1.0\%$; for relationships between survival and summer/winter weather, see Supplementary material Appendix A1 Fig. A1.

a small temperature increase in spring/autumn and large precipitation increase in spring (Fig. 5).

Discussion

Climatic effects on survival

Adult long-tailed tit survival in our study population was strongly linked to interannual variability in weather, with the model average explaining 73% of the variation in annual survival. Weather during the spring breeding season exerted the strongest effects, with cool and wet conditions reducing annual survival, particularly when such conditions occurred simultaneously. Cold autumn temperatures also reduced survival on average. There was no evidence of an effect of interannual variability in winter weather on survival. This contrasts with previous suggestions that interannual variation in passerine survival is primarily determined by

winter weather (Lack 1954, Cawthorne and Marchant 1980, Peach et al. 1999, Sæther et al. 2004). There was no evidence for adverse effects of high temperatures on survival rates, even though daily maximum temperatures exceeded 30°C in six of the 19 years of study, and regularly exceeded 25°C ; this is of interest as summer heat stress events have been associated with population declines in some temperate passerines (Jiguet et al. 2006).

The strong reduction in adult survival observed in the Rivelin population following cold and wet breeding seasons does not support the tub-tap hypothesis (Sæther et al. 2004), which states that interannual variation in breeding season weather influences demography by altering fecundity rather than survival. Breeding season weather has long been considered of relatively low importance in determining survival rates in small-bodied temperate passerines (Lack 1954, Sæther et al. 2004, Moreno and Møller 2011), despite very few rigorous tests of this suggestion (but see Grosbois et al. 2006, Glenn et al. 2010). We show the

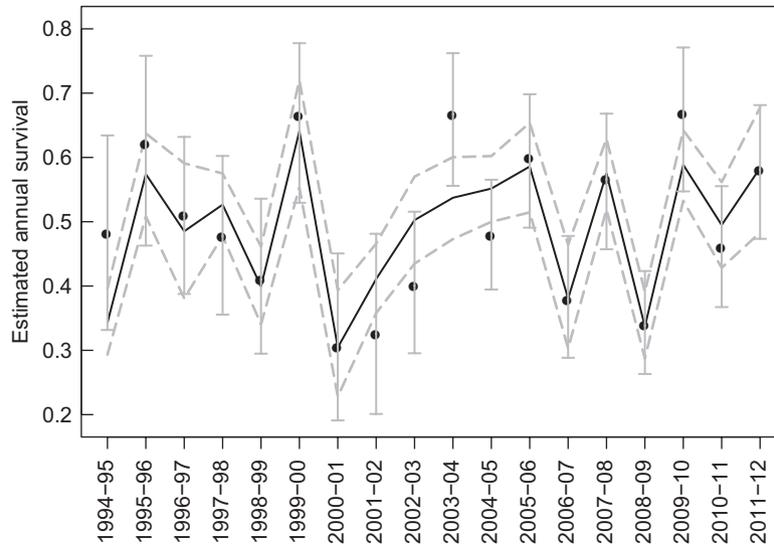


Figure 2. Adult long-tailed tit survival estimates obtained from the reference model $\phi(\sim \text{time})p(\text{sex})$ compared to the final climatic model average $\phi(\sim t1 + p1 + t3 + p3 + t1^2 + p1^2 + p3^2 + t1 : p1 + t3 : p3)p(\text{sex})$, for the Rivelin population in the years 1994–2012. Closed circles (●) with grey error bars represent survival estimates from the reference model with 95% CI; solid line with dashed grey lines represents survival estimates from the climatic model average with 95% CI.

value of a multivariate approach to assessments of weather effects on survival, which has revealed previously unrecognised climatic and seasonal drivers of annual survival.

The observed relationship between annual survival and spring conditions is unlikely to be a direct effect of weather on mortality at that time of year because adult long-tailed tits disappear from the study site very rarely during the breeding season (Russell 1999). Instead, the relationship between survival and spring conditions probably reflects an increased energetic investment under adverse conditions, which reduces parental body condition and increases subsequent mortality. Previous studies in various passerine species have shown that adverse weather conditions can increase reproductive investment through higher thermoregulatory and foraging costs (Newton 1998, Bradbury et al. 2003); long-tailed tits also invest more in nest-building during adverse weather (McGowan et al. 2004). In short-lived *r*-selected species like the long-tailed

tit, parents are expected to trade off reduced personal survival against increased productivity, given that they may not have another opportunity to reproduce before they die (Williams 1966, Pianka 1970, Ghalambor and Martin 2001). Increased parental effort, as measured by higher provisioning rates during chick-rearing, is associated with reduced survival of adult long-tailed tits to the subsequent breeding season (Meade et al. 2010). Furthermore, the decision of failed breeders to become helpers or not is partly dependent on their quality or condition, with higher quality individuals being more likely to help (Meade and Hatchwell 2010). Effects of variation in reproductive investment on subsequent survival have been widely reported in other short-lived species (Askenmo 1979, Nur 1984, Reid 1987), as well as in some long-lived species (Deschamps et al. 2009). However, few studies have shown an effect of variation in climate on this productivity versus survival tradeoff (Thomas et al. 2001, Václav and Sánchez

Table 3. Effects of weather on the survival of adult long-tailed tits in the Rivelin population, 1994–2012. Shown here are partial R^2 and parameter estimates from the climatic model average (constructed from the $\Delta\text{AICc}_{\text{climatic}} < 2$ top subset of 11 models; Supplementary material Appendix A1 Table A4) and from the best climatic model, $\phi(\sim t1 + p1 + t3 + p3 + t1 : p1)p(\sim \text{sex})$ (Supplementary material Appendix A1 Table A4). The overall model R^2 for the model average and best model were 72.9% and 73.3% respectively.

Parameter	Model average		Best model		95% CI
	partial R^2	parameter est.	partial R^2	parameter est.	
Intercept	–	+ 0.02	–	0.02	–0.09 to 0.13
Spring temp	18.5	+ 0.25	13.7	0.22	0.08 to 0.35
Autumn temp	16.3	+ 0.25	14.7	0.24	0.09 to 0.38
Spring prec	15.5	– 0.21	11.2	– 0.19	– 0.32 to – 0.06
Autumn prec	1.0	– 0.05	3.1	– 0.12	– 0.29 to 0.04
Spring temp ²	0.6	+ 0.01	–	–	–
Autumn temp ²	0.0	0.00	–	–	–
Spring prec ²	0.2	– 0.01	–	–	–
Autumn prec ²	< 0.001	< 0.001	–	–	–
Spring temp × prec	22.0	+ 0.32	27.5	0.34	0.19 to 0.49
Autumn temp × prec	0.9	0.03	–	–	–

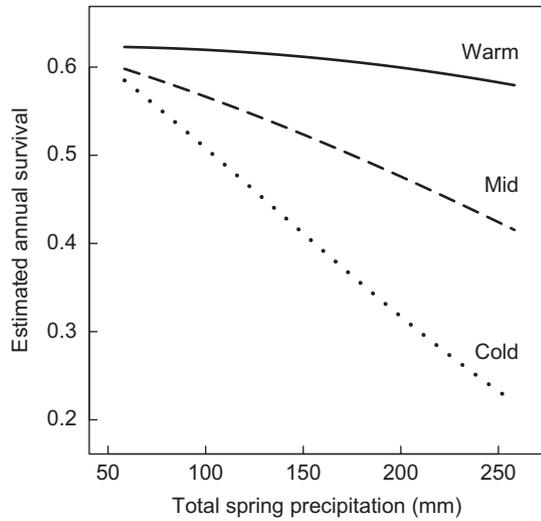


Figure 3. The interaction between temperature and precipitation during spring, showing the model-averaged relationship between adult long-tailed tit survival and precipitation for three levels of temperature: warm, mid and cold correspond respectively to the warmest (10.5°C), mean average (9.3°C), and coldest (7.4°C) mean spring temperatures observed in the Rivelin study in the years 1994–2012.

2008, Moreno and Møller 2011), and the underlying mechanisms remain poorly understood (Harshman and Zera 2007, Deschamps et al. 2009).

The lack of an effect of variation in winter temperatures on adult survival is somewhat surprising given the small body size and high thermoregulatory burden of the long-tailed tit. The observed strong negative effect of cold autumn temperatures suggests that individuals in poorer condition are susceptible to mortality as soon as weather becomes cooler, in autumn. Mean autumn temperature in the study site showed a similar range to that in spring (spring range = 7.4–10.5°C, mean = 9.3°C, autumn

Table 4. Density-dependence of adult long-tailed tit survival in the Rivelin population, 1994–2012. Population size at the end of season 1 is included as a covariate in the best climatic model of survival $\phi(\sim t1 + p1 + t3 + p3 + t1 : p1)p(\sim \text{sex})$, either a linear main effect, or as an interactive effect with a single weather variable; all interaction models also included the linear main effect. For each model, $\Delta\text{AICc}_{\text{climatic}}$ indicates ΔAICc compared to the best climatic model lacking density dependence; R^2 indicates % temporal variation explained (deviance of temporal model = 451.21; deviance of null model = 523.68); slope(main) and slope(interaction) indicate the parameter estimates for the main effect of population size, and for its interaction with the relevant weather variable, respectively.

Type of density dependent effect included	$\Delta\text{AICc}_{\text{climatic}}$	R^2	Slope (main) ± 1 SE	Slope (interaction) ± 1 SE
Interaction with spring temp	-0.43	79.5	-0.134 \pm 0.066	0.006 \pm 0.086
Interaction with autumn temp	-0.69	79.9	-0.127 \pm 0.063	0.054 \pm 0.105
Interaction with spring prec	-0.62	79.8	-0.114 \pm 0.075	0.053 \pm 0.121
Interaction with autumn prec	-0.53	79.6	-0.139 \pm 0.066	0.020 \pm 0.061
Main effect only	-2.45	79.5	-0.133 \pm 0.063	-
No density dependence	0	73.3	-	-

range = 9.9–12.5°C, mean = 10.9°C; Supplementary material Appendix A1 Table A4), with sub-zero temperatures occurring in autumn in most years (15 of the 19 years of study; unpubl.). As such, autumn may act as a filter by which individuals in poorer condition are removed from the population before winter arrives. This finding is not incompatible with previous observations of population crashes after harsh winters in small-bodied species in other geographical regions, where autumns may be relatively clement

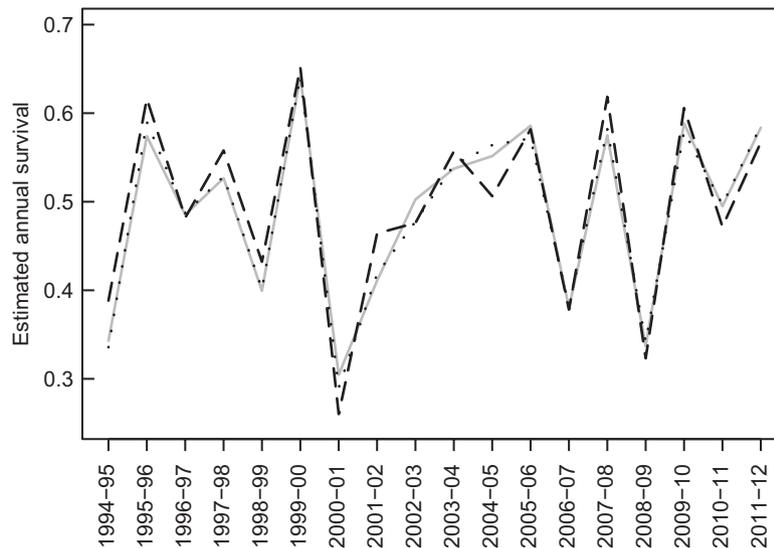


Figure 4. Adult long-tailed tit survival estimates obtained from the final climatic model average (solid grey line), compared to estimates from the best model both with (dashed line) and without (dotted line) population size as a main effect, for the Rivelin population in the years 1994–2012.

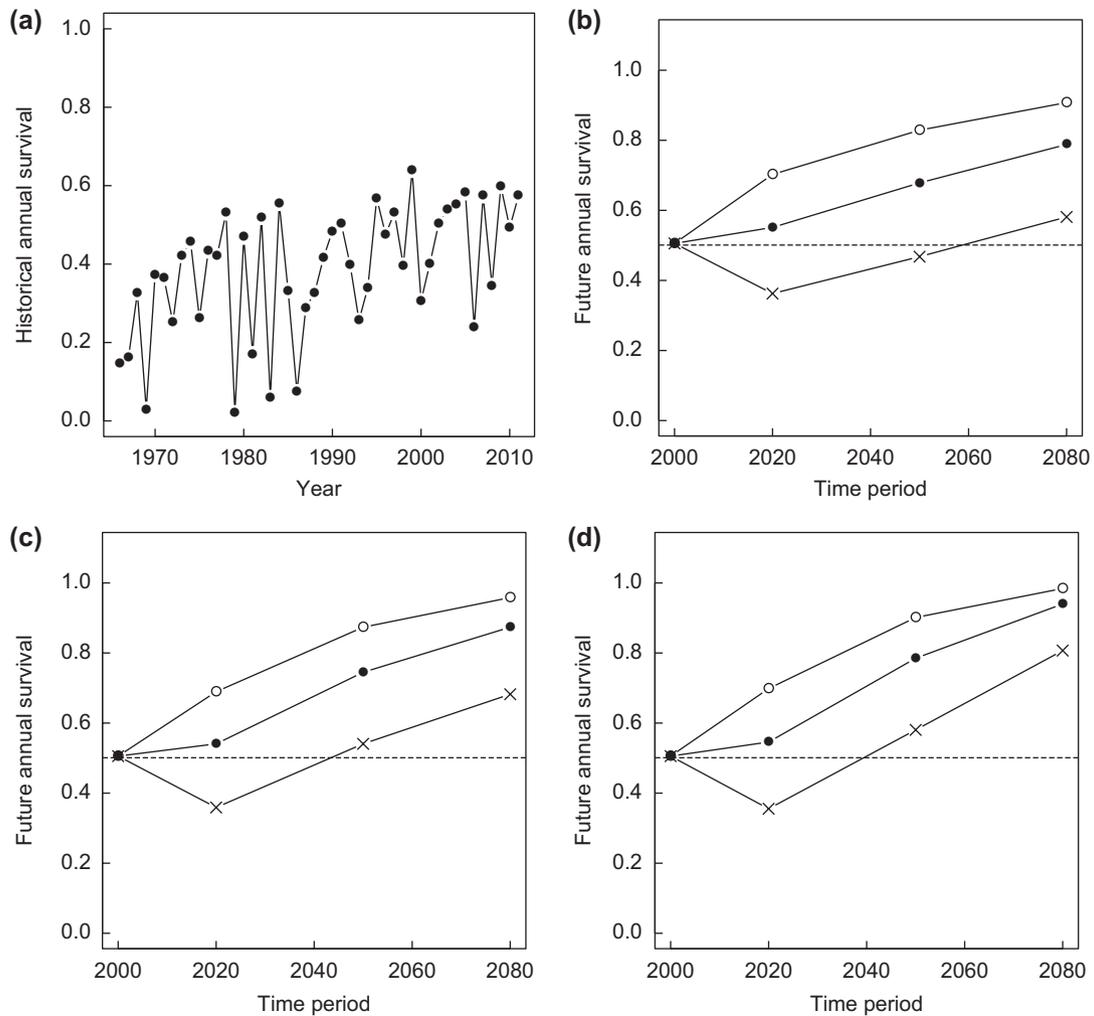


Figure 5. Estimates of (a) past and (b–d) future adult long-tailed tit survival in the Rivelin population, based on model-averaged parameter estimates. Past survival: (a) Historical survival was predicted for the period 1966–2011, using historical climate data. Future survival: (b) Low, (c) medium, and (d) high emissions scenarios of future climate were used to predict future survival for three non-overlapping time periods (2010–2039, 2040–2069, 2070–2099); predictions were made for three potential climate change scenarios, where (○) indicates ‘best case’ climate projections (great temperature change, little precipitation change); (●) indicates ‘mid scenario’ projections (moderate temperature change, moderate precipitation change); × indicates ‘worst case’ projections (little temperature change, great precipitation change); the recent historical (1994–2012) average survival in the Rivelin population is shown for reference purposes (dashed line).

and winters relatively harsh (e.g. woodland species in Illinois, Graber and Graber 1979). However, the present study suggests that such findings cannot be generalised across temperate regions with contrasting climatic regimes, under which climate may exert critical effects during different time periods. Similarly, the present study does not contradict the observed negative effects of exceptionally harsh winters on avian survival (Cawthorne and Marchant 1980), given that no exceptionally harsh winters occurred during our study period (winter temperature range = 2.4–6.5°C, mean = 4.7°C; Supplementary material Appendix A1 Table A4). However our study does suggest that winter weather is not the primary driver of population change in years with more usual weather conditions. Our results therefore bring into question the reliability of some previous assessments of avian survival that consider only winter temperature, as weather variables at other times of year may also be important. Given that different months are likely to

exhibit divergent climatic trends over the coming decades (Houghton et al. 2001), it is crucial to identify the critical temporal periods of climatic influence on survival rates.

The precise nature of temperature and precipitation effects cannot be identified with certainty from the present study because measures of average monthly conditions (mean temperature and total precipitation) were highly correlated with measures of extreme conditions (number of cold or wet days), and we were therefore unable to distinguish between the effects of average versus extreme conditions. This suggests that average monthly weather conditions offer a valuable and readily available basis for the prediction of future responses to climate change.

Density dependence

Density dependence in the Rivelin population appeared to be low, regardless of whether climatic effects were taken into

account. This contrasts with some previous studies in ecologically similar species such as the great tit *Parus major* (Clobert et al. 1988), perhaps indicating that the Rivelin population is well below the carrying capacity of the site. With an area of approximately 1.25 km² of breeding habitat, the Rivelin site has an average adult population density of about 70 adults km⁻² during spring (range = 35 to 114 adults km⁻²), which is low compared to equivalent densities of ecologically similar species such as the blue tit *Cyanistes caeruleus* (400 adults km⁻² in spring) and great tit (240 adults km⁻² in spring, Gibb 1954). Moreover, unlike cavity-nesting blue and great tits, long-tailed tits do not seem to be limited by nest site availability in the Rivelin site because they nest in a wide variety of locations (Hatchwell et al. 1999) and do not defend breeding territories. For instance, pairs may raise chicks in nests located as little as 10 m apart and many previous nesting locations are vacant each year despite being used again in subsequent years (PG and BJH unpubl.). The present study does not exclude the possibility that density dependence may be important in other long-tailed tit populations, where population densities may exceed the range assessed here (58 to 269 birds km⁻² of breeding habitat, at the end of the breeding season). However, we currently find no evidence for strong density dependent effects on annual survival. This suggests that any beneficial impacts of climate change on population size are, at least initially, unlikely to be counteracted by density-related declines in survival rates.

Prediction of past and future survival

The range of climates assessed over the course of this study was similar to the range in expected future climates in the study site (Supplementary material Appendix A1 Table A5, A6) and therefore enables prediction of the direction of future changes in average annual survival under various projected climatic scenarios. In so doing our objective is to predict the future general trend, rather than making precise predictions for specific years that take stochastic variation in the general climatic trends into account. We encompass the full range of probabilistic estimates and emissions scenarios (Fig. 5b–d). This has rarely been attempted previously (but see Martins et al. 2011, Jenouvrier et al. 2012) and, to our knowledge, offers the first such example in a temperate passerine. The extent and direction of future climatic change is far from certain, yet our projections indicate that survival will have increased by the end of the century under all emissions scenarios, even if the most extreme probabilistic climatic projections occur. This is because the expected increases in spring and autumn temperatures (UKCP 2009) override the negative effects of any increase in precipitation. It is important to note that these projections do not incorporate potential alterations in interspecific relationships under future global change scenarios. Previously, it has been suggested that warmer winters may benefit some species under future climates (Catchpole et al. 1999, Peach et al. 1999, Nilsson et al. 2011), and recent increases in the UK population size of some passerines have been attributed to recent winter warming (Baillie et al. 2012). However, many such studies assess the effects of winter weather in isolation, and our

study thus brings to light the possibility that winter effects are overridden by weather effects at other times of year. Furthermore, previous studies fail to assess the interaction between temperature and precipitation, thus drastically limiting their capacity to inform future survival projections. This is particularly important as we find that the magnitude of precipitation alters the form of the relationship between temperature and annual survival, and that there is substantial potential for precipitation to increase in the future (UKCP 2009).

The UK long-tailed tit population has gradually increased over the past four decades, more than doubling between 1966 and 2010 (Baillie et al. 2012). Spring and autumn temperatures have been increasing nationally over this same time period (Parker et al. 1992), suggesting that climate change-induced increases in survival rates may have contributed to this population increase. A more complete test of this hypothesis requires population modelling that takes both survival and productivity into account. It is notable, however, that back-casting of survival probabilities in the Rivelin over this historical time period suggests that survival rates have increased over the period of national population increase (Fig. 5a). Moreover, past years with very low predicted survival in the Rivelin population (1979, 1981, 1983, 1986, Fig. 5a) coincide with a period of low UK population size (1979–1987, Baillie et al. 2012); such low survival may be an underestimate, but probably reflects the general trend in survival rates. Although we did not model juvenile survival rates (due to difficulty in distinguishing between dispersal and mortality in the first year of life, Sharp et al. 2008), juvenile mortality appears to be highest in the period shortly after fledging in this species (C. Napper pers. comm.) and many other passerines (Naef-Daenzer et al. 2001, Yackel-Adams et al. 2006). It therefore seems likely that juvenile and adult survival rates follow a similar pattern in long-tailed tits, as shown in willow tits *Parus montanus* (Lahti et al. 1998) and red-backed shrikes *Lanius collurio* (Schaub et al. 2011). The apparent covariation of adult survival and population size over the past four decades is therefore highly suggestive that climate-driven changes in survival, due to warmer springs and autumns, could have contributed to the recent increases in long-tailed tit population size, although other factors are also likely to have contributed.

Conclusion

We provide evidence that contradicts two common perceptions regarding climatic impacts on the annual survival of temperate passerines. First, in contrast to the tub-tap hypothesis, we show that interannual variation in weather during the breeding season has the strongest influence on avian annual survival rates, whilst variation in winter temperature had no discernible effect over the range of temperatures encountered by our study population over a 19-year period. Second, whilst precipitation is often ignored in models of avian survival rates we show a strong effect of breeding season precipitation on adult survival, which alters the form of the relationship between temperature and annual survival. Our local climatic model explains 73% of the variation in annual survival rates. Assuming

this model can be applied to historical climatic data to infer annual survival rates in long-tailed tits suggests that survival rates have increased significantly over recent decades in response to warmer spring and autumn conditions. This upward trend in survival rates is predicted to continue over the coming century under even the most extreme climatic projections, although such trends could be influenced by future novel alterations in ecological interactions that are not incorporated into our projections. Recent increases in survival seem likely to have contributed to the recent population growth of this species across the UK, suggesting that future changes in survival may influence population size in a range of species. Crucially, we show that future research into the effects of climate on avian survival must assess responses to both temperature and precipitation, and their interaction, over the entire annual cycle, in order to develop predictive models of demographic responses to climate change.

Acknowledgements – This research was funded by a Natural Environment Research Council (NERC) studentship to PG, with CASE funding from the British Trust for Ornithology. The long-term study of long-tailed tits in the Rivelin Valley has been funded principally by NERC grants to BJH. We thank all those researchers who have contributed to the Rivelin study, the landowners who have allowed us access to their land, and to C. Napper for useful discussion.

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Supplementary material (available as Appendix oik-00620 at <www.oikosoffice.lu.se/appendix>). Appendix A1.