Climate change may account for the decline in British ring ouzels *Turdus torquatus*

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Summary

1. Climate change is already affecting biodiversity, but the number of species for which reliable models relate weather and climate to demographic parameters is low.

2. We modelled the effect of temperature and rainfall on the breeding success and territory occupancy of ring ouzels *Turdus torquatus* (L.) in northern Britain, using data from a range of study areas, including one where there was a long-term decline in ring ouzel abundance.

3. Timing of breeding was significantly related to meteorological variables affecting birds in the early spring, though there was no evidence that laying dates had advanced. Breeding success was not significantly related to weather variables; instead, over 90% of annual variation in this parameter could be explained by density dependence.

4. Annual change in territory occupancy was linked to rainfall and temperature the preceding summer, after the main breeding season and to rainfall in the wintering grounds 24 months previously, coincident with the period of juniper *Juniperus* sp. (L.) flowering. High temperature in late summer, intermediate levels of late summer rainfall, and high spring rainfall in Morocco 24 months previously all had negative impacts on territory occupancy the following year.

5. All three weather variables have changed over recent decades, with a significant increase in summer temperature, a significant decrease in summer rainfall, and a non-significant decline in Moroccan spring rainfall. A model based on these trends alone predicted an annual decline in occupancy of 3·6% (compared with an observed decline of 1·2%), and suggested that increased summer temperatures may underlie declines in the British ring ouzel population.

6. Changes in summer temperature after the main breeding period could affect the survival rates of adult and/or juvenile birds. An improved understanding of the post-breeding ecology of ring ouzels is required to elucidate the mechanisms and causes of this relationship. Such knowledge might allow management aimed at buffering the impacts of climate change on ring ouzels.

Key-words: breeding success, density dependence, rainfall, survival, temperature.

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Introduction

Global climate change is arguably the most pressing environmental issue of our time (Root *et al*. 2003), and appears to have already contributed to one global extinction (Pounds, Fogden & Campbell 1999). It is considered that climate change in northern and upland areas in particular may reduce the area of suitable habitat to the extent that many species will be committed to extinction by 2050 (Thomas *et al*. 2004).

Faced with such serious predictions, we need a comprehensive understanding of how climate change will affect animal populations if we are to manage them appropriately (Sæther *et al*. 2000; Rodríguez & Bustamante 2003). Despite widespread concern about the probable sensitivity of northern and upland species, there are surprisingly few studies of the impacts of climate change in the British uplands (Root *et al*. 2003; Thomas *et al*. 2004). Even among the best-known taxonomic groups, evidence for climatic impacts on upland species is scarce (Pearce-Higgins, Yalden & Whittingham 2005).

Among bird species, the likely impacts of climate change are wide-ranging and disparate. There is concern that known climatic impacts on the phenology (timing) of breeding may lead to a mismatch between hatching and peak food availability (Visser *et al*. 1998; Both & Visser 2001; Crick 2004). Extreme weather events may also have detrimental effects on breeding success and survival (Askins & Ewert 1991; Lens & Dhont 1992). Conversely, direct impacts of warming may benefit populations by reducing cold-related mortality, at least in the short term (Peach, du Feu & McMeeking 1995; Insley *et al*. 1997). Such disparate weather impacts make identifying the population consequences of climate change extremely difficult. In this paper, we investigate whether climate could be responsible for the long-term decline in the British ring ouzel *Turdus torquatus* (L.) population, by analysing population trends and breeding ecology at a range of study areas in northern Britain.

The ring ouzel has been declining in Britain since at least the first half of the twentieth century (Baxter & Rintoul 1953; Thom 1986; Gibbons, Avery & Brown 1996). This decline has continued in recent times, with perhaps as much as a 58% decline occurring between 1988–91 and 1999, resulting in only 6000–7500 remaining pairs (Gregory *et al*. 2002; Wotton, Langston & Gregory 2002). Diagnosing the causes of such rapid declines is usually a prerequisite to halting and reversing them (Green 1994). Unfortunately, relatively little has been published on ring ouzel ecology, hampering the effective conservation of the species (Burfield 2002a). To date, the only published study identifying correlates of change in the abundance of ring ouzels indicates that losses in Scotland were greatest at the upper and lower extremes of their altitudinal range and in flatter areas, with some additional land management effects (Buchanan *et al*. 2003). Similarly, altitude and heather cover were positively correlated with the probability of individual territories remaining occupied in southern Scotland (Sim *et al*. unpublished). Such strong topographical effects are consistent with a retraction into the core range with limited evidence for the ultimate mechanisms behind a decline (Burfield 2002a). British nest records show that the species now lays its first clutch approximately 8 days earlier than in 1968 (Baillie *et al*. 2005), suggesting that climate change has already affected this aspect

of its ecology. As the British population shares its wintering grounds with ring ouzels from other parts of Europe with apparently stable populations (BirdLife International 2004), the causes of decline may be local to Britain (or represent a withdrawal to the core *T. t. torquatus* range in Fennoscandia). However, not all European populations are well monitored. Here, we assess the correlations between meteorological variables likely to affect aspects of ring ouzel ecology throughout the species' annual cycle as the recommended method to assess whether climate change may be a cause of the decline (Rodríguez & Bustamante 2003).

Methods

STUDY SPECIES

As a summer migrant the ring ouzel may be declining due to factors operating during the breeding season in its upland habitats, the post-breeding period in the UK, on migration through Europe, or during the winter in montane areas of southern Spain and north-west Africa. Climate change in any or all of these locations might affect populations either directly (though extreme weather events), or indirectly (through altering the food availability). We focused our analyses on the impacts of meteorological variables on breeding ecology (including laying dates and nest survival) and variation in annual population (assessed as changes in territory occupancy), thus encompassing the whole of the annual cycle. Subheadings in our methods and results sections reflect these separate analyses.

From the literature, we identified several meteorological variables possibly affecting ring ouzels at different times (Table 1). During the breeding season, we first assessed the effects of local rainfall and temperature during March and April (when most ring ouzels return to their British breeding grounds: Burfield 2002a) on determining the timing of breeding. During the breeding season, ring ouzels feed nestlings almost exclusively on invertebrates, particularly earthworms *Lumbricidae* (Burfield 2002a). *Lumbricidae* availability is largely determined by rainfall and temperature (Askew & Yalden 1985). As most ring ouzel broods are raised during May and June (Flegg & Glue 1975), we considered temperature and rainfall during these months as possible determinants of nest survival.

When analysing changes in territory occupancy, it was important to include meteorological variables that operate throughout the year. After breeding and before migration ring ouzels have been reported feeding on rowan *Sorbus aucuparia* (L.) and blaeberry *Vaccinium myrtillus* (L.) (Arthur & White 2001). The annual berry crop of these plants is related to a complex suite of weather variables (Wallenius 1999; Selås 2000). Consequently, we incorporated the most important variables from these studies (June–August temperature and rainfall) as factors possibly affecting change in

Table 1. Meteorological variables considered potentially important in ring ouzel ecology. Different parameters were included in different analyses, as indicated in the first column. Where the reason for including these variables is not obvious, we briefly explain the justification

Analysis	Parameter	Justification
Laying date	March/April precipitation	Time when most birds return to territories
	March/April temperature	As above
Nest success	May/June precipitation	Time when most nests are active
	May/June temperature	As above
Territory occupancy	Spring NAO index during return migration	Values of the North Atlantic Oscillation are known to correlate with many aspects of migrant bird ecology in Europe (Forchhammer, Post & Stenseth 2002; Hüppop & Hüppop 2003)
	Average temperature November–February in Morocco	Direct weather impacts on survival are possible
	Average precipitation November–February in Morocco	Direct weather impacts on survival are possible
	Average June–August precipitation in Britain the preceding summer (and its square)	These variables explain the highest degree of variation in the annual *V. myrtillus* crop (Wallenius 1999; Selås 2000), considered an important food resource during the late summer (Arthur & White 2001). Direct weather impacts on survival are possible
	Average June–August temperature in Britain the preceding summer	As above
	Average rainfall April–June in Morocco the preceding spring	Rainfall during the spring affects alpine fruit availability during the winter in Spanish uplands (Jordano 1993) and plausibly in Morocco
	Average March/April precipitation in Morocco 24 months prior to spring arrival	Rainfall during spring flowering of *Juniperus* sp. is known to reduce fruit abundance when these ripen 18 months later by washing away wind-dispersed pollen (Jordano 1993; Belmonte *et al.* 1999; García *et al.* 2002)
	Year	If significant, including year as a continuous covariate may highlight the continued decline of another, unmeasured parameter

Table 2. Studies used in the current analysis and the types of data recorded. Latitude and longitude are given for approximate centre of study areas, UK Met Office station is the official name of the weather station used. Territory occupancy data indicates whether the study recorded an index of the number of territories occupied within a study area each year

Area	Reference	Latitude/longitude	UK Met Office station	Study period	Territory occupancy	Nest records (mean no./year)
Yorkshire Dales	Appleyard (1994)	54°07′N 01°49′W	Scar House Reservoir	1979–1995		7
Glen Clunie	Rebecca (2001)	56°76′N 03°24′W	Braemar	1998–2004	X	51
Glen Esk	Arthur & White (2001)	56°54′N 02°58′W	Whitehillocks	1998–2000	X	44
Moorfoot Hills (1)	Brotherston *et al.* unpublished	55°42′N 03°04′W	Glentress	1952–1985	X	
Moorfoot Hills (2)	Burfield (2002a)	55°42′N 03°04′W	Glentress	1998–2000	X	36

territory occupancy the following year. As rainfall showed a quadratic relationship with berry crop, we included the quadratic term for this variable. Ringing recoveries of British breeding ring ouzels indicate that most of the population winters in the Moroccan High Atlas, with smaller numbers in southern Spain (Burfield 2002b). During the winter, ring ouzels feed mainly on *Juniperus* sp. (L.) berries (Jordano 1993; Arthur *et al.* 2000), a crop that shows high annual variability (García *et al.* 2002). The abundance of *Juniperus* berries is related to rainfall during pollination because heavy rain prevents effective pollination (Belmonte *et al.* 1999). Hence, we included March/April rainfall 24 months before the spring of interest as a candidate variable (ripening takes 18 months: Jordano 1993; García *et al.* 2002). More directly, we considered the spring (March–May) index of the North Atlantic Oscillation (NAO) and winter (November–February) temperature and rainfall in Morocco. The NAO is a large-scale climatic process that influences wind speeds and directions, rainfall and temperature over most of northern Europe and impacts a wide range of biological processes (Hüppop & Hüppop 2003). Finally, we included rainfall in Morocco during the preceding spring (April–June) as a candidate variable, because rain at this time affects alpine fruit availability during the following winter in other Mediterranean uplands (Jordano 1993).

RING OUZEL DATA

Data on ring ouzel ecology were gathered over a number of years by a variety of individuals working at study areas throughout northern Britain (Table 2).

From the data available, we determined that analyses of the factors affecting laying dates, nest survival and territory occupancy (an index of population) would be feasible. Data quality, quantity and type varied between studies and years, but the variation in these factors was known and the limitations of each data set were reflected in the subsequent analysis. This approach allowed us to maximize the data available for each analysis while minimizing unknown biases. In most studies, data were recorded from every nest found, and multiple visits were made to each breeding site. Differences in survey intensity between years were known and could be accounted for in analyses by using the Mayfield method to estimate nest survival (nests were deemed successful if they fledged at least one chick; Mayfield 1975).

STATISTICAL ANALYSIS

All statistical analysis was carried out in R v 2.0.1 (R Development Core Team 2004) following Crawley (2002). For all analyses where data from more than one study were combined, we included study as a nuisance variable in a Generalized Linear Model (GLM). In all cases, minimum adequate models were selected using a standard backward stepwise procedure and appropriate error structures were specified. We tested goodness-of-fit (where relevant) using a Chi-squared test on the saturated model: as all models were acceptable, we did not further adjust estimates.

CLIMATE DATA

British climate data were provided by the UK Meteorological Office and the University of East Anglia's Climate Research Unit (data set CRU TS 2·0: New, Hulme & Jones 1999, 2000). The latter data set also provided data for non-UK variables. For analyses of breeding season data, meteorological records from the recording station nearest to each study area were used (always within 30 km: Table 2). For analyses of change in annual territory occupancy, we used national averages for Britain and Morocco, as the precise location of individual birds outside the breeding season was unknown. In all analyses, averaging weather data by calendar month is in some way artificial, which may hide subtle short-lasting effects and does not allow precise identification of critical time-periods (Hallet *et al*. 2004). Our analyses are therefore conservative. For each climatic variable identified as a significant correlate, we used a one-tailed test to estimate whether trends consistent with recent climate change were apparent during the study period.

LAYING DATE

Wherever possible, the date at which the first egg of a clutch was laid was estimated from nest records (following Burfield 2002a). If the nest was found during laying, the first egg date was calculated assuming one new egg per day. Otherwise, we back-calculated laying date from hatching date or estimated chick age where these were available. We assumed that incubation took an average of 13 days and began on the day the penultimate egg was laid. To analyse changes in laying date, we used first clutches only and judged that all nesting attempts initiated after 15 May were either replacements or second clutches (Arthur & White 2001). For all study areas where laying dates were calculated, 15 May fell midway between the two main peaks of laying, confirming that this date was appropriate throughout. We calculated the mean first egg laying date of first clutches for each year of each study, and assumed annual estimates to be independent. We began our analysis of mean laying date of first clutches by assessing simple annual trends, independent of weather variables but equivalent to earlier analyses (Baillie *et al*. 2005). Our analysis continued by assessing the climatic correlates of annual variation in laying date. The maximal model (with identity link and Gaussian errors) included study area, year, average March/April precipitation and temperature on the breeding grounds. We expected laying date to vary according to climatic cues (spring temperature and precipitation), as found in other species (McCleery & Perrins 1998; Crick & Sparks 1999).

NEST SUCCESS

First, we attempted to assess the impacts of laying date on nest success using individual nests from the study area with the most detailed nest monitoring data (Glen Clunie). We modelled daily survival probability as a GLM with logit link and binomial errors (following Aebischer 1999) predicting the proportion of failures, including year and attempt (early, up to 15 May, or late, after 15 May) as factors and laying date as a continuous covariate, together with its interaction with the two factors.

Next, we investigated the annual difference in Mayfield estimates of nest survival using data from Glen Clunie, Glen Esk and the second study in the Moorfoot Hills, where minimum population estimates were made each year. This enabled us to assess both the climatic impacts on annual nest survival and any density-dependent effects. The minimum population estimates were total counts of the number of occupied territories (singing males present on at least two consecutive visits) in core study areas during the early nesting season. This method must be considered an index of the actual population as some territories apparently unoccupied in the early season were subsequently occupied later. To standardize the measurement of annual variation in minimum population between the different studies, we calculated an annual index for each study as the actual annual population divided by the highest minimum population recorded at that study area. Thus, the peak population in any study

was one, and different years varied below this. We used an arcsine square-root transformation of this proportion in analyses.

TERRITORY OCCUPANCY

Territory occupancy was measured in the Moorfoot Hills. Here, a variable number (20–65) of known ring ouzel territories were visited two to four times per month during April–July between 1952 and 1981 (by the late W. Brotherston) and 1998–2000 (by IJB), but only two to four times during April–July in 1983–85, and a simple presence/absence score was recorded annually. For the last period (1998–2000), tape playback was used to identify occupied territories, possibly increasing the number of territories recorded as occupied, though observations ended in mid-May in 2000 (Burfield 2002a). For species such as the ring ouzel where territories are limited to traditional nesting sites, territory occupancy is an effective index of population size, which was not measured directly during most of the Moorfoot Hills study. To model the temporal change in territory occupancy, we fitted a GLM with logit link and binomial error to the proportion of territories occupied each year. To ensure that this analysis was not biased by occasional inclusion of territories outside the core study, we repeated this analysis using only territories visited in 10 or more years. Additionally, we repeated the analysis using only those territories surveyed at least once during the first 10 years of the study, to ensure that changes in territories surveyed during later years of the survey did not bias the results.

To assess changes in populations from territory occupancy data, we calculated two indices from the Moorfoot's data set. The first was simply the log change in proportion occupancy from one year to the next. This gave a change index that was independent of population size and made maximum use of the available data. We also calculated an index of change for each year by identifying only those territories that were surveyed in successive years and calculating the average net change between years. We used this estimate of mean change to calculate a new occupancy index (standardized to 100% occupancy in year 1) and again calculated the log change in the proportion of territories occupied from one year to the next. This ensured that the index reflected changes in actual territory occupancy rather than random changes in survey areas, but it was data inefficient as we could only use territories surveyed in successive years. Both indexes were strongly correlated ($R^2 = 0.74$), but to ensure that our results were consistent irrespective of index, we conducted all analyses using both indexes. In our assessment of annual change in territory occupancy, we considered a number of variables that could affect ring ouzel survival (Table 1). For statistical analysis, we used the log number of territories surveyed each year as a weighting factor, Gaussian errors and an identity link.

Results

LAYING DATES

There was no evidence of a linear trend in mean laying dates of the first eggs of first clutches ($F_{1,17} = 1.738$, $P = 0.205$). Only average March/April precipitation was retained in the minimum adequate model predicting the mean laying date of first clutches ($F_{1,17} = 7.08$, $P = 0.016$). For each extra millimetre of average March/April precipitation, the mean laying date of first clutches is delayed by 0·366 (± 0.014) days. Study area did not significantly affecting laying date itself ($F_{3,17} = 1.61$, $P = 0.225$), but was retained in the model as a nuisance variable. During the study periods, March/April precipitation at each study area showed no significant change ($F_{1,18} = 0.643$, $P = 0.434$).

NEST SUCCESS

The number of chicks fledged per nest was strongly bimodal, due to the relatively high level of total nest failure (25% of nests raised no chicks) compared with the low likelihood of partial failure (< 10% of nests). Consequently, nest survival (whether or not a nest fledged at least one chick) was an appropriate unit for analysing breeding success. At Glen Clunie, none of the candidate variables (year, nesting attempt, laying date and their interactions) were significantly associated with apparent nest success (date–attempt interaction: $F_{1,308} = 0.028$; date–year interaction: $F_{6,302} = 0.029$; year: $F_{6,315} = 0.038$; attempt: $F_{1,316} = 1.118$; date: $F_{1,317} = 0.014$; all $P > 0.05$).

In the wider analysis involving more studies, 91% of the annual variation in Mayfield nest survival was explained by the minimum population index and study ($F_{1,8} = 22.341$, $P = 0.005$, Fig. 1). Nest survival was thus highly density-dependent, with higher survival when population density was low. To maximize the power to detect weather impacts on the remaining variation, we built a GLM with identity link and Gaussian errors to predict the residual variation in nest survival from average May/June temperature and precipitation, but neither variable was retained in the minimal model ($F_{1,9} = 0.011$; $F_{1,10} = 0.161$; $P > 0.05$ in both cases).

TERRITORY OCCUPANCY

Data from the Moorfoot studies showed a significant decline in territory occupancy over the period 1952–2000 for all data sets analysed (all data: $F_{1,36} = 101.2$, $P < 0.0001$; territories visited more than 10 times: $F_{1,36} = 90.19$, $P < 0.0001$; territories surveyed during first 10 years of study only: $F_{1,36} = 4.644$, $P = 0.031$). During the period of study, the decline in the proportion of potential territories occupied averaged 1·2% ($\pm$ SE 0·08) per year when all data were used, or 1·4% ($\pm$ SE 0·1) per year if only territories surveyed more
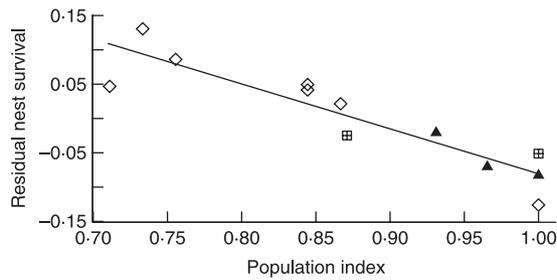
Fig. 1. Density dependence in Ring Ouzel nest survival. Residual annual nest success (after removing differences between study areas) is plotted against the population index. Filled triangles represent Glen Esk; open diamonds represent Glen Clunie, and crossed squares represent Moorfoot Hills studies.

than 10 times were considered. The minimum adequate model for both change indices included four variables: average British June–August rainfall (and its square) in the preceding year, average British June–August temperature in the preceding year and average March/April precipitation in Morocco 24 months previously (Table 3). As both change indices identified the same significant parameters, we continued our analyses of these data using the index calculated from the entire data set only.

There was no significant temporal autocorrelation among the residuals ($F_{1,33}$ = 2·66, P = 0·113). These parameters explained 59·3% of the deviance in the log population change index (Fig. 2) and suggest that the population increases following cool (Fig. 3a) and either very wet or very dry summers (Fig. 3b), and low rainfall during March/April in Morocco 24 months previously (coincident with the period of *Juniperus* flowering) is low (Fig. 3c). As the quadratic relationship between summer rainfall and population change appeared difficult to interpret, we investigated this relationship further by calculating the degree to which it was determined by extreme observations. Thus, those observations with the most influence on the relationship (based on the statistical leverage) were removed

sequentially and the model was refitted until the quadratic term became nonsignificant. After removing the three data points with greatest leverage [in order of influence, years: 1957 (wet), 1977 (dry) and 1985 (dry)] both the quadratic term and linear terms became nonsignificant ($F_{1,26}$ = 1·02, P = 0·32; $F_{1,27}$ = 2·09, P = 0·16, respectively). This left only the negative effects of average British June–August temperature in the preceding summer ($F_{1,28}$ = 6·55, P = 0·016) and spring rainfall in Morocco 24 months previously ($F_{1,28}$ = 6·93, P = 0·014). Replacing June–August rainfall with May/June rainfall did not reveal significant quadratic ($F_{1,30}$ = 3·10, P = 0·090) or linear effects ($F_{1,31}$ = 1·41, P = 0·244). However, replacing June–August rainfall with only July/August rainfall revealed the same quadratic relationship with a similarly high significance ($F_{1,30}$ = 7·94, P = 0·009).

Both June–August temperature and rainfall in Britain showed weak but expected patterns of climatic change during the study period (increases in temperature: $F_{1,49}$ = 3·117, P = 0·042; decrease in rainfall: $F_{1,49}$ = 2·983, P = 0·046). Moroccan rainfall showed a non-significant decline during the same period ($F_{1,49}$ = 1·746, P = 0·096). We used these trends to predict changes in the proportion of occupied territories by replacing actual annual temperatures and rainfall with estimates of these from the simple linear trends. Assuming the starting occupancy in 1952 to be 83% (the observed mean occupancy at the start of the survey) of surveyed territories, our model predicted a mean decline in the ring ouzel population equivalent to 3·6% (± SE 1·3) per year during the study period, due to the negative effect of warmer summers.

Discussion

As expected, data from the Moorfoot Hills showed a consistent decline in territory occupancy (Burfield 2002a). However, some confounding factors should be discussed before comparing these results with national population trends. First, recent surveys were carried out using tape playback, a method that can increase

Table 3. Summary of the models describing variation in ring ouzel territory occupancy in the Moorfoot Hills. Variables are listed in reverse chronological order, so factors temporally closest to the spring arrival (and calculation of the change index) come first

| Change index	Parameter	Estimate	Standard error	$F_{1,29}$	P
Log change in proportion of territories occupied	Intercept	2·022	0·418		
	June–August rainfall	−0·0238	0·0051	22·13	<0·001
	(June–August rainfall)^2	0·00013	0·00003	17·62	<0·001
	June–August temperature	−0·0617	0·021	8·827	0·006
	March/April rainfall, Morocco 24 months previously	−0·0024	0·0006	16·78	<0·001
Mean change in occupancy for territories surveyed in successive years	Intercept	2·49	0·761		
	June–August rainfall	−0·026	0·0092	7·936	0·008
	(June–August rainfall)^2	0·00014	0·00006	6·129	0·019
	June–August temperature	−0·086	0·037	5·196	0·030
	March/April rainfall, Morocco 24 months previously	−0·0031	0·0011	8·594	0·007
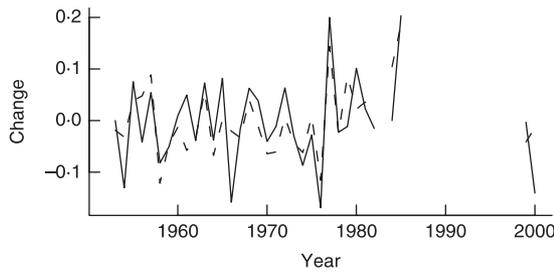
Fig. 2. Actual (solid lines) and modelled (dashed lines) change (the log of the proportion territories occupied in year *t* + 1/proportion occupied in year *t*) in ring ouzel population in the Moorfoot Hills, using data from all areas in all years.

measures of territory occupancy (Burfield 2002a). This effect may cause our results to underestimate the scale of the decline in the Moorfoot Hills study area. Similarly, it is possible that in a study where the territories surveyed are not selected at random, those territories that become vacant are less likely to be surveyed in the future, further reducing the scale of any measured decline. In contrast, a decline could be an artefact of the methodology if birds shift from old territories to entirely new ones that are found and added to the survey while the old territories continue to be surveyed. As territories are by definition only added to the survey if they are occupied at least once, shifts in the birds' distribution alone could bias the results. We attempted to eliminate such bias by additionally analysing data from only those territories identified during the first 10 years of the study, which demonstrated a similarly significant decline in territory occupancy. We therefore conclude that our results do indeed show a decline in ring ouzel territory occupancy in the Moorfoot Hills. At an average of 1·2% per year, this rate of decline is lower than the putative rate of decline in the national population, but it has been recognized that the rates of decline in ring ouzel populations vary spatially (Buchanan *et al.* 2003). Hence, this need not suggest that our data underestimate the true rate of decline in the Moorfoot Hills.

Our analysis of breeding season data suggested that density dependence is the most important factor predicting annual variation in ring ouzel nest survival. With over 90% of variation in this factor explained by relative density within a study area and smaller differences between studies, very little variation remains to be explained. Consequently, climate cannot explain a significant amount of variance in nest survival. Despite the relationship between laying date of first eggs in first clutches and March/April precipitation, no significant impact of weather-related variables on nest survival was detected. This suggests that while climate change may eventually affect the timing of nesting, it currently has no strong effect on breeding success. This is supported by the lack of significant relationships between nest survival at Glen Clunie and any parameter involving laying date. Thus, while climate-driven changes in laying date are associated with declines in productivity for some bird species (Visser *et al.* 1998; Both & Visser
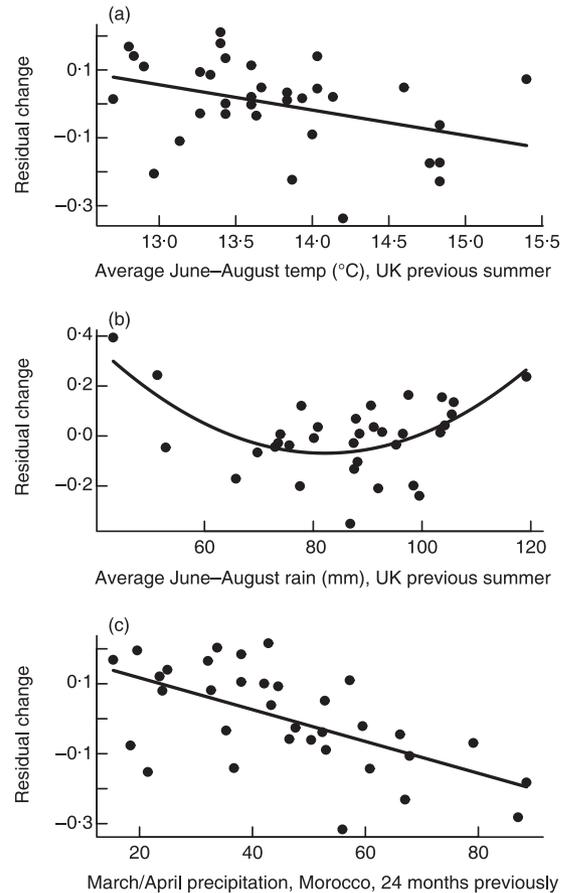
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Ecological Society,
*Journal of Animal
Ecology*, **75**,
826–835

Fig. 3. Residual log change in ring ouzel territory occupancy (all data) and climatic variables measured in the current study: (a) average June–August temperature in Britain during the preceding summer; (b) average June–August rainfall in Britain during the preceding summer; (c) average March/April rainfall in Morocco 24 months previously.

2001), our results suggest that British ring ouzels have so far successfully adjusted their breeding phenology to recent changes in climate, though we note that this does not rule out further changes having stronger impacts (cf. Winkler, Dunn & McCulloch 2002).

The lack of importance of breeding biology in causing the declines in ring ouzel abundance in the study areas considered here supports the findings of previous studies in which no differences in breeding parameters could be detected between the declining population in the Moorfoot Hills and the stable population in Glen Esk (Burfield 2002a). However, detailed data on the true extent of double brooding in these two study areas, and the factors that affect this variable have not been investigated (although the length of the breeding season did not differ between the study areas: Burfield 2002a). Further research in this area may give a more complete picture of climatic impacts on the ring ouzel and highlight other important demographic processes.

Density dependence in nest survival is a relatively common feature of breeding ecology in birds (Both 1998; Paradis *et al.* 2002). As British ring ouzels nest at relatively low densities (< 6 pairs km⁻²; Burfield 2002a),

we speculate that density dependence in ring ouzel nesting success is most likely to be a consequence of additional pairs being forced to nest in more marginal territories where predation risk (the most common cause of failure: Appleyard 1994; Burfield 2002a) is higher. This is also consistent with the observed tendencies for rates of decline to be habitat specific (Buchanan *et al*. 2003; Sim *et al*. unpublished). Although our data do not allow quantitative population modelling, such density-dependent breeding success may to some extent buffer populations experiencing decreased survival, perhaps explaining why observed population declines were of lower magnitude than the modelled decline.

Whereas breeding success is currently not strongly affected by any weather variable, we did find significant climatic correlates of annual change in territory occupancy. A combination of the average British June–August temperature and rainfall during the previous summer, and rainfall during March/April in Morocco 2 years previously, explained 59% of the annual variation in territory occupancy. The strong negative relationship between March/April rainfall in Morocco and territory occupancy was expected from the known effect of spring rainfall on *Juniperus* berry crops, through decreasing the rate of successful pollination (Jordano 1993; García *et al*. 2002). Although rainfall in Britain during the period June–August has no apparent effect on breeding success, it does alter availability of ripe fruit during the late summer and early autumn (Wallenius 1999; Selås 2000). It could therefore affect late summer food availability, in addition to any direct effects. There may be mechanisms by which either high or low summer rainfall could increase survival rates of ring ouzels (e.g. by increasing berry crops/*Lumbricidae* availability and reducing direct mortality effects, respectively). However, the relationship detected should be treated with caution, as it was dependent upon just three data points. If real, the fact that replacing June–August rainfall with May/June rainfall produced no significant relationship (while July/August was significant) provides further evidence that rainfall effects are not a consequence of effects on nestling mortality, but rather operate on the survival of either adult and/or juvenile birds later in the season. We note again, however, that our use of averaged weather variables limits our power to detect precise time periods of interest and it is possible that mortality is concentrated into only a short section within the longer period.

The negative relationship between warm summers and change in territory occupancy the following year remains significant whether or not summer rainfall is included in the analysis. The biological mechanisms that underlie this relationship remain unclear, but it is plausible that some interaction with *Lumbricidae* availability is responsible. It is also possible that climate change interacts with the habitat changes associated with decline discussed earlier (e.g. declines in heather cover). In the closely related song thrush *T. philomelos*, population declines have been related to reduced first-year survival (and fewer late-season breeding attempts) associated with the reduced *Lumbricidae* availability caused by local changes in climate and land management (Peach, du Feu & McMeeking 2004; Robinson *et al*. 2004). A similar process may thus affect ring ouzel populations. Once the trend in climatic variables is taken into account, our model suggests that ring ouzel territory occupancy would decline by an average of 3·6% per year, as a direct consequence of the recent trend towards warmer summers. That a model incorporating only trends in climatic variables predicts that ring ouzel populations will decline at a rate with confidence intervals that overlap the observed rate (1·2% per year) provides further evidence to suggest that changes in the summer climate have contributed to ring ouzel declines in Britain. Additionally, climate during this period of the summer is changing faster in Britain than in other northern European countries with breeding ring ouzels (Watson, Zinyowera & Moss 1997). This may explain the apparent differences in observed population trends between Britain and elsewhere over recent decades (BirdLife International 2004).

Understanding the causes of decreased territory occupancy following warm summers may be critical to identifying management regimes that can buffer populations against the adverse effects of climate change in Britain. It is likely that improving the quality of habitats important at this time of the year may ameliorate the impacts of climate change. As our study does not explicitly address additional impacts of other changes that may impact ring ouzel populations (e.g. reductions in overall habitat quality and area or changes acting during migration periods), such habitat management may have additional benefits to ring ouzel populations. The first priority must be to improve our understanding of the basic ecology of ring ouzels during the post-breeding period, as was undertaken for the song thrush (Peach *et al*. 2004a,b; Robinson *et al*. 2004). Through research focused on determining the factors affecting post-fledging and pre-migratory survival, it may be possible to identify ways to improve survival and hence halt the decline of the British ring ouzel population, despite continued summer warming. At the same time, our results suggest that annual survival is partly mediated by the availability of *Juniperus* berries in the Moroccan wintering areas. Consequently, action in Morocco to ameliorate the threats from increased firewood collection and grazing (Arthur *et al*. 2000; Olson *et al*. 2001) may benefit ring ouzel populations throughout their European range.

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Ecology*, **75**,
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studies, particularly D. Arthur at Glen Esk and to the various landowners and managers at each study area who co-operated with access. We are particularly indebted to the late W. Brotherston and the late I. Appleyard, without whom the main analyses would not have been possible, and to the Scottish Ornithologists' Club for archiving much of the historical data analysed here and their funding of the Glen Clunie study. This analysis was funded by the RSPB and SNH. Fieldwork by IJB was funded through a NERC CASE studentship with RSPB co-supervised by M.C.G. and M. de L. Brooke. J. Wilson, R. Thomas, D. Gibbons, D. Thompson, S. Baillie and an anonymous referee provided valuable comments on earlier drafts of the manuscript.

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