

# Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*

Lucy J. Wright<sup>1\*</sup>, Ron A. Hoblyn<sup>2</sup>, Rhys E. Green<sup>3,4</sup>, Christopher G. R. Bowden<sup>3</sup>, John W. Mallord<sup>5</sup>, William J. Sutherland<sup>4</sup> and Paul M. Dolman<sup>1</sup>

<sup>1</sup>School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK; <sup>2</sup>Forestry Commission, Santon Downham, Brandon, Suffolk IP27 0TJ, UK; <sup>3</sup>Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK; <sup>4</sup>Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK; and <sup>5</sup>School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

## Summary

1. We examined the influence of local weather conditions on reproductive success, timing of breeding and survival in a population of a multi-brooded ground nesting passerine (woodlark *Lullula arborea*) over 35 years.
2. Woodlarks laid larger clutches when rainfall was low and temperature high during the egg-laying and pre-laying period. Nest success increased with higher temperatures during the nesting period. In successful nests, the number of chicks fledged per egg laid was greater when weather was drier during the brood stage.
3. Although woodlarks bred earlier in years with warmer early spring temperatures, with the onset of breeding varying by 25 days, there was no significant advance in the onset of breeding over the 35 years of study, due to considerable inter-annual variability, and no overall trend, in weather.
4. Simulation modelling of annual reproductive output demonstrated that earlier breeding could increase productivity by 23.5% in the warmest compared to the coldest year, due to birds having more nesting attempts. Other effects of weather on productivity affected breeding output to a lesser extent.
5. Effects of weather on productivity were minor compared to an increased rate of nest predation through the period of study, which reduced productivity by 49.8% by 2004 compared to 1971.
6. Turning points analysis identified three distinct demographic periods: from 1971 to 1988 the population grew slowly, during 1988–1999 the population grew rapidly, but after 1999 the population declined. Increased population growth after 1988 was associated with higher first-year survival rates (estimated using a population model). Population decline after 1999 was caused by a combination of reduced productivity (resulting from increased nest failure rates attributed to predation) and lower first-year survival rates, that appear unrelated to winter temperature.
7. Climate change (long-term changes in weather) did not explain the marked changes observed in the population trajectory over 35 years. We suggest that understanding effects of both climate and habitat change on populations is essential in predictive population modelling.

**Key-words:** climate change, nest predation, phenology, population dynamics

## Introduction

Climatic conditions, the prevailing weather patterns in an area over a long period, are a key factor affecting many ecological processes (Stenseth *et al.* 2002; Parmesan & Yohe 2003; Portner & Farrell 2008) and climate change will alter

many species' population dynamics (Root *et al.* 2003; Pounds *et al.* 2006; Hughes *et al.* 2008). Understanding the influences of weather on populations and predicting responses to future climate change is an urgent priority (Sæther, Sutherland & Engen 2004; Sutherland 2006; Sekercioglu *et al.* 2008). However, human activity has many other environmental impacts that may limit species' potential to respond to climate change (Sala *et al.* 2000; Warren *et al.* 2001).

\*Correspondence author. E-mail: lucy.wright@bto.org

Weather variability has well-documented effects on bird populations; changes in survival rates caused by winter temperatures are key drivers of population dynamics in many species (Siriwardena, Baillie & Wilson 1998b; Grosbois *et al.* 2006; Robinson, Baillie & Crick 2007), while during the breeding season, weather affects both phenology (Crick & Sparks 1999; Both & Visser 2001; Reed *et al.* 2006) and breeding success (Møller 2002; Rodriguez & Bustamante 2003; Both *et al.* 2006). However, there is a need for greater understanding of the consequences for species' population dynamics of these responses (Crick 2004; Both *et al.* 2006). For example, although changes in phenology in response to climate change can reduce breeding success by causing a mismatch between peak food demand and peak food availability (Thomas *et al.* 2001; Visser & Both 2005; Both *et al.* 2006), in other cases phenological responses can maintain synchrony (Cresswell & McCleery 2003). Multi-brooded species may be able to increase productivity by having more nesting attempts (Jenni & Kéry 2003), however few studies have tested whether this occurs (Wilson & Arcese 2003; Saino *et al.* 2004; Møller 2007).

We use data from a 35-year study of a ground nesting, multi-brooded passerine to examine effects that changes in patterns of weather and other environmental changes have had on population dynamics. The majority of studies examining effects of climate change on avian phenology and breeding success have focussed on single-brooded species, often in artificial nestboxes; however, responses of multi-brooded species may be very different. We explore the challenges and problems of assessing consequences of changing weather and environment on the productivity and survival of a multi-brooded species with few marked individuals. Our study investigates the following questions: (i) Does weather affect nesting success? (ii) Does early spring temperature affect the timing of breeding? (iii) Does weather affect annual productivity? (iv) How do responses to weather affect demography? (v) Is there evidence that climatic change has affected demography? (vi) What are the relative effects of other environmental changes, such as changes in nest predation rates, on long-term changes in demography?

## Materials and methods

### STUDY SITE AND POPULATION

The woodlark, *Lullula arborea*, is a species of European Conservation Concern due to a widespread decline in population size and range (Burfield & van Bommel 2004). A woodlark population was studied between 1971 and 2004 in Thetford Forest (52°30' N, 0°60' W), which covers 185 km<sup>2</sup> of Breckland, a biogeographic region of eastern England. The Breckland region supports 25–30% of the UK breeding woodlark population (Wotton & Gillings 2000), largely within Thetford Forest. The forest is divided into 16 geographical blocks (mean area 1174 ha, 548 SD), and comprises pine-dominated plantations managed by rotational clear-felling and replanting of even-aged stands, creating a mosaic of growth stages

(Eycott, Watkinson & Dolman 2006). Woodlarks breed in clear-felled and re-planted stands with trees up to 9 years old, but most (98% of all woodlarks across all years) are found on stands less than 6 years old or areas of permanent open space (Wright 2006).

Woodlark territory surveys were conducted annually. Several visits were made to every patch of suitable habitat during March–May and numbers and locations of singing males recorded following Wotton & Gillings (2000). Nests were located by observation of adults. In repeat visits (mean interval 4.6 days  $\pm$  3.1 SD) nest status and numbers of eggs and chicks were recorded (following Crick, Baillie & Leech 2003) as well as notes on fledging, adult behaviour and signs of predation of failed nests. As human scent may provide either a cue or deterrent to mammalian predators, observers did not kneel at nests during monitoring. The methodology and frequency of nest monitoring has remained constant, with most nests monitored by a single individual (RAH). Frequency of nest visits did not affect nest survival rates of woodlarks in Dorset UK, when nests were monitored using the protocols of this study (Mallord *et al.* 2007b). Nests were assumed to be successful if chicks had reached fledging age (10–12 days), the nest was empty but intact with signs of success such as trampled droppings in or next to the nest, adults were alarming or feeding fledged young nearby, or fledged young were seen. If cold eggs or dead chicks were found in or near the nest we assumed the nest had failed due to desertion or chick starvation. We assumed the nest had failed due to predation if there was nest damage or if remains of eggs, young or adult birds were found nearby. Sometimes there were no obvious signs of predation but the clutch or brood disappeared from the nest before chicks had reached fledging age and the usual signs of a successful nest were not present. In these cases, we assumed that predation was the cause of nest failure but the predator had not damaged the nest. For all failed nests, we noted whether the nest lining was torn out or whether the nest cup was empty but intact.

Woodlarks are multi-brooded, making many repeated nesting attempts following nest failure and up to two further broods following successful fledging of an earlier brood (Mallord *et al.* 2008). Analyses here are based on a sample of nests located throughout the breeding season. Successive nesting attempts of known pairs were not monitored, so it was not possible to differentiate between first and later clutches.

From 1986 chicks were ringed with unique colour combinations at 5–8 days old. In each subsequent year, resightings of marked individuals were recorded.

Territory surveys were not completed in 2001, and nest monitoring and resighting of birds were reduced, as an outbreak of foot and mouth disease restricted access.

### DATA ANALYSES

The woodlark population growth curve, measured by observed numbers of territorial males, was smoothed using a thin-plate spline with 11 d.f. in SAS PROC TPSPLINE (SAS Institute, Inc 1999). The second derivatives of the smoothed trend were used to identify turning points in the population trend (following Siriwardena *et al.* 1998a; Fewster *et al.* 2000; Robinson *et al.* 2004).

Nest success was modelled as the daily nest survival rate using logistic generalized linear models (GLMs) with binomial errors and logit link (Aebischer 1999), constructed using PROC GENMOD in SAS and compared using likelihood ratio tests assuming a chi-squared distribution. Daily nest survival rate did not differ between clutch and brood stages ( $\chi^2_1 = 0.69$ ,  $P = 0.41$ ) which were pooled in subsequent analyses. Nest survival was estimated over the entire nesting period of 28 days, comprising 3 days laying (modal clutch size 4, found in

67% of  $n = 518$  nests, laying one egg per day, with incubation commencing on the last day), 14 days incubation and 11 days to fledging (Cramp & Perrins 1988). First egg dates were observed, or estimated from clutch increments or hatch dates.

To investigate effects of weather during the breeding season on nest success, we tested the effects of mean daily minimum temperatures and total rainfall from 1 March to 30 June of each year. We also investigated the effect of weather during the period specific to each nesting attempt, using the mean of daily minimum temperatures and total rainfall from the date the first egg was laid in the nest to the date the nest either fledged or failed. Daily minimum (rather than maximum) temperatures were used as we assumed that in this location, at the north-western limit of their range, woodlark productivity was likely to be limited by the coldest not the warmest temperatures. Weather variables were measured at Santon Downham, located centrally in the study region (52°46' N, 0°67' W).

Whether the proportion of nests that failed with the lining removed, or failed with the lining left intact, changed through time was tested using GLMs with logit link and binomial error with each nest as a binomial trial.

Clutch size was modelled in relation to weather using GLMs with Poisson error, log link, a scale parameter estimated by the square root of Pearson's chi-square/d.f. ratio to account for under dispersion of the data, and nest-specific weather covariates (means of daily minimum temperatures and rainfall during the egg-laying period and the 4 days prior to laying the first egg). All models controlled for significant effects of lay date by incorporating it as a covariate. The number of fledglings per egg was modelled using GLMs with binomial errors and logit link, in relation to means of daily minimum temperatures and rainfall during a 12-day period from the day prior to hatching (in case of error in estimated hatch date) to fledging.

The relation between timing of breeding and spring temperatures was investigated using linear regression. The start of the breeding season was estimated from the fifth, 10th and 25th percentiles of the distribution of first egg dates, calculated for all years with more than 21 nests found ( $n = 18$  years). Spring temperature for each year was measured as the mean of daily minima between 15 February and 15 March.

#### MODELS OF REPRODUCTIVE OUTPUT

Total annual productivity (the number of fledglings produced in one breeding season by one pair) could not be directly measured, as successive nesting attempts of individual pairs were not monitored throughout the breeding season (most adults are not marked, a new nest is constructed for each repeat attempt, and territories of neighbouring pairs may overlap or shift as the breeding season proceeds). Instead we simulated breeding activity of woodlarks throughout the breeding season to estimate mean annual productivity, using a similar modelling approach to Beintema & Muskens (1987), Bowden & Green (1992), Ratcliffe, Schmitt & Whiffin (2005) and Pearce-Higgins *et al.* (*in press*) (Supporting Information Fig. S1). This allowed estimation of annual breeding output, and assessment of the relative contribution of different components (variation in the timing of breeding, daily nest survival, clutch size and chick survival caused by weather and inter-year variation in daily nest survival caused by predation) to annual variation in total reproductive output.

The dates that woodlarks start and finish breeding, daily nest survival rates and clutch sizes under different conditions were known from our data. We measured the intervals between a nest either fledging or failing, and the start of the next nesting attempt, for a small number of intensively monitored pairs. For each modelled pair (each

of which was considered for 1 year only with no pair-specific values carried over across years), unique values of each parameter were drawn at random from normal distributions based on means and standard deviations derived from empirical data, such that variation in the total productivity between modelled pairs should be representative of variation in total productivity between real pairs of woodlarks in the population. Values and derivation of model parameters are shown in online Supporting Information (Table S1). For each combination of year-specific parameters and each of 34 years (1971–2004), 10 000 breeding pairs were simulated to estimate the mean productivity of, and the variation between, pairs of woodlarks in each year.

The effect of change in nest success on productivity was assessed first without considering weather effects. This model incorporated stochastic variation in the mean first lay date, varying between pairs but not years, with an overall mean first laying date of 28 March. Further models assessed the effect of weather-induced variation between years in the timing of breeding, and effects of weather on nest success and clutch size. Here, the mean first lay date was predicted from spring temperatures in each year. For all models, the first lay date for each pair was drawn from a distribution around the predicted mean first lay date, with SD of 12 days (Supporting Information, Table S1).

The productivity model assumes that the relationship between first laying date and early spring weather derived from 1986 onwards also held for years prior to 1986, and that the mean date at which females stop laying is the same in all years. However, if inter-annual variation in the end of the breeding season covaries with the timing of the start of the season, or differs among periods, this could introduce systematic error into the simulation model results. To test this, we split years into three groups according to turning points in the population growth curve (1971–1987, 1988–1998 and 1999–2004) and between two groups (each of  $n = 17$  years) according to early spring temperature (with mean daily minima between mid-February and mid-March either  $< 0.5$  or  $> 0.5$  °C). Within the observed data, the numbers of nests laid in each week from 1st May onwards were compared among groups using GLMs with Poisson error terms and scale parameters estimated by the square root of the deviance/degrees of freedom ratio, with laying week as a covariate. In each instance, the interaction between week and the temporal group variable was examined to determine whether the timing of the tail of the laying date distribution differed among these *a priori* groups.

#### SURVIVAL MODELS

Survival rates were modelled in two ways. Capture–mark–resighting data were used to model survival from 1986 onwards. This method could not be used to estimate survival for 1971–1986 when there were no marked birds. Therefore, a demographic model was used to provide estimates of survival in all years of the study, from observed changes in population size between years and estimated annual productivity.

In the first method, survival rates were modelled for 1664 colour-ringed birds (of which 1624 were marked as nestlings and 40 as full-grown birds) with 367 resightings between 1986 and 2004, using MARK (White & Burnham 1999) with logit link functions. Thirteen alternative models were considered. First winter and adult survival was modelled separately, except in one model where they covaried. Models with year-specific or constant survival rates, with linear or quadratic trends in survival, or with survival rates varying between three periods with differing rates of population growth defined by turning points analysis (1986–1988, 1988–1999 and 1999–2004) were

compared using Akaike Information Criterion (AICc) (Anderson, Burnham & White 1994). Effects of winter temperature were examined by modelling year-specific survival in relation to the mean of daily minimum temperatures (°C) from 1st December to 28th February at Santon Downham. Further details are given in the Supporting Information. To test whether resighting rates differed between returning juveniles (1 year old when resighted) and older birds, as may occur if there is delayed territorial settlement, we compared the ratio of birds recorded to those not seen in any one year, for all birds known to be alive in that year (i.e. seen in a subsequent year). Likelihood of resighting did not differ between first-years (39% of  $n = 83$  resighted) or older adults (42% of 77 resighted, Fisher exact test,  $P = 0.7489$ ). We therefore modelled resighting as constant across age classes. Resighting rates may differ between males and females, however sex was not confirmed for 49.7% of resighted adults therefore combined resighting rates and pooled survival estimates were used for both sexes. This will reduce precision of survival estimates, but will not create any bias unless mortality rates also differ markedly between sexes.

In the second method, survival rates were estimated using a population model. Numbers of woodlarks in the Breckland region were known for each year up to 1999, and breeding productivity was estimated from the simulation model, allowing annual survival rates for 1971–1999 to be estimated from a demographic model. To extend the analysis beyond 1999 we also calculated survival rates for the forest population only. We assumed an equal sex ratio and that all pairs attempted to breed in each year. We considered a demographic model in which we assumed adult survival,  $A$ , was constant throughout the study period and estimated using mark–resighting analysis for 1986–2004. Yearly survival rates of first-year birds,  $F_t$ , were estimated from:

$$N_{t+1} = 0.5 N_t P_t F_t + N_t A \quad (1)$$

where  $N_t$  is the population in year  $t$ , and  $P_t$  the year-specific breeding productivity per pair. We also produced a second model, in which year-specific adult ( $A_t$ ) and first-year ( $F_t$ ) survival rates covaried. To allow this to be solved for  $F_t$ , we assumed that in any one year the ratio of adult to first-year survival is fixed as the ratio of mean adult ( $A$ ) to mean first-year survival ( $F$ ) estimated by mark–resighting analysis. In this model:

$$F_t = A_t (F/A) \quad (2)$$

$$N_{t+1} = 0.5 N_t P_t F_t + N_t F_t (A/F) \quad (3)$$

These models represent two extremes. In the first, environmental effects on winter survival act solely on vulnerable first-year birds, with adult survival constant. This is likely to over-estimate the amplitude of variability in first-year survival. In the second adult and first-year survival covary; their ratio is fixed so that they have the same inter-annual variance. As adult survival is likely to be less variable than that of first-year birds (Siriwardena *et al.* 1998b), this will underestimate the variability in first-year survival.

Both models assume a closed population; while this may not be strictly true, the Breckland woodlark population was the largest regional population by far throughout the period of study. In 1997, the relative size of nearby populations was: Suffolk Sandlings (~70 km away) 209 territories, North Norfolk (~35 km) 11 territories, Lincolnshire (~145 km) 30 territories, Nottinghamshire (~120 km) 29 territories, compared to at least 420 territories in Breckland (Wotton & Gillings 2000). Between 1986 and 2004, there

were only a small number of resightings of colour-ringed birds demonstrating emigration from Breckland to the Suffolk Sandlings (three individuals), Nottinghamshire (four individuals) and Lincolnshire (six individuals), despite significant resighting effort. Although in 1997, the Suffolk Sandlings held a substantial population of woodlarks, numbers have subsequently declined in this area (Macklin 2004). Immigration and emigration thus likely involved only a small proportion of the population.

To ensure consistency, only records of woodlarks from sites that were continuously monitored throughout the period of study were included in the annual estimates of Breckland population size. These comprised all of Thetford Forest (18 786 ha) and 87% (7032 ha) of all heathland remaining in Breckland (considered as 8119 ha of heathland Sites of Special Scientific Interest). The maximum proportion of total recorded woodlark numbers in any one year that was located on sites outside our continuously monitored area was 6.5% in 1999.

First-year survival rates calculated from the population model were related to winter temperature (mean of daily minima between December and February) using linear regression. Weather variables were taken from Santon Downham, as many woodlarks winter in Breckland (Atkinson 2001; Dunmore 2006). Although locations of wintering sites beyond Breckland are not known, annual variation in winter temperature is broadly correlated across large areas of central and southern England (Jones & Hulme 1997). We also ran GLMs incorporating a categorical variable comparing first-year survival rates before and after a turning point in the population trajectory.

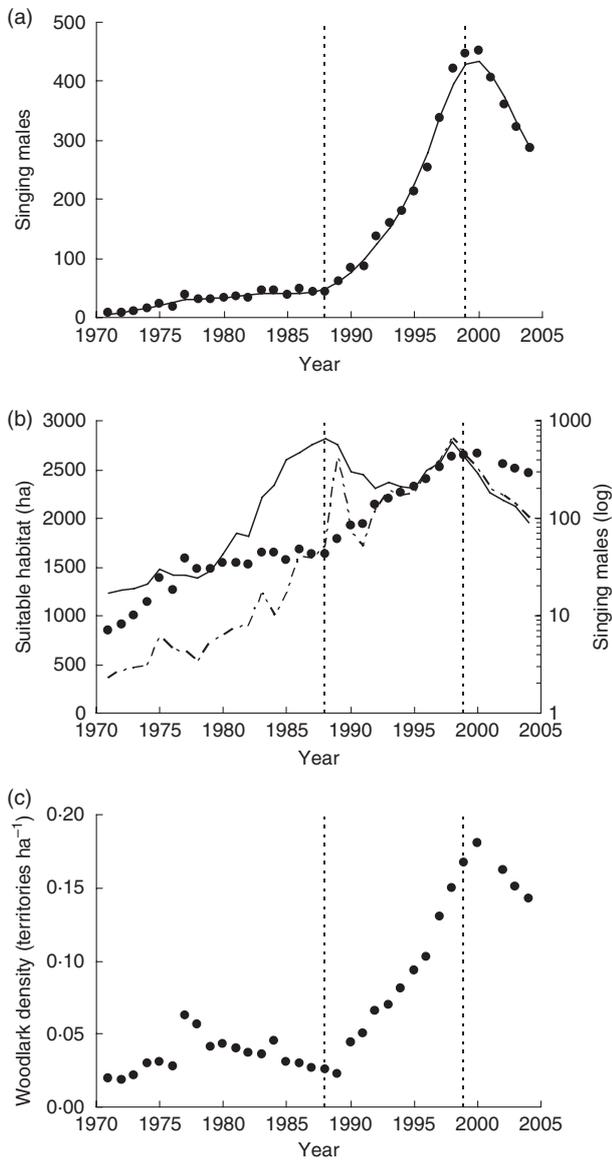
## Results

### POPULATION TRENDS

Woodlark populations increased more than 10-fold during the period of study (Fig. 1). Turning points were identified in 1988, when the rate of population growth accelerated, and 1999, when the rate of growth declined (Fig. 1a). Observed annual population growth rates for the three periods, estimated from the population time series using autoregressive models of order 1, were: 1971–1988,  $\lambda = 1.13$ ; 1988–1999,  $\lambda = 1.22$ ; 1999–2004,  $\lambda = 0.92$ . Habitat availability in the entire forest increased until 1988, fluctuated during 1989–1998, and subsequently declined (Fig. 1b). However, during the 1990s woodlarks expanded their range within the forest, colonizing previously unoccupied blocks, so that the area of habitat available in occupied blocks generally increased throughout the period 1971–1998 (Fig. 1b). Furthermore, there was a fourfold increase in woodlark density after 1988 (Fig. 1c), suggesting the upturn in population growth rate from 1988 cannot be attributed to a release from habitat limitation. Although the availability of habitat decreased after the 1999 turning point, woodlark density also decreased, again suggesting that factors other than habitat extent contributed to the population decline.

### SUCCESS AND PRODUCTIVITY OF NESTING ATTEMPTS

Daily nest survival rate declined significantly through the period of the study (Table 1a), from 0.984 (95% CL 0.976–0.989) in 1975 to 0.949 (0.939–0.959) in 2004. Nest failure



**Fig. 1.** Woodlark population size and the availability of suitable breeding habitat in Thetford Forest with respect to time. (a) The smoothed population trend from a thin plate spline with 11 d.f., with turning points marked by vertical dotted lines. (b) Numbers of singing males (points) and area of suitable breeding habitat (re-stocked stands aged 0–6 years and areas of open space), shown for the entire forest (continuous line) and occupied blocks of forest (broken line). (c) The density of woodlarks, measured as the number of singing males per hectare of suitable habitat in occupied blocks.

over the entire 28-day nest period, from laying the first egg to producing at least one fledgling, increased from 36% (95% CL 26–50%) of nesting attempts in 1975 to 76% (69–83%) in 2004 (Fig. 2a). Few instances of partial brood loss were observed (2.6% of broods) and chick survival was high in surviving nests (95.7% of hatched chicks, in nests that fledged at least one chick, survived to fledging), suggesting starvation was not an important source of chick mortality. Desertion accounted for only 3% of nest failures, with the remaining 97% of failures attributed to predation. The proportion of nesting attempts that failed with the lining torn out, repre-

senting a subset of predation events that may relate to particular predator species, increased through time ( $\chi^2_1 = 16.85$ ,  $n = 864$ ,  $P < 0.0001$ ), from 2% (95% CL 0.7–5%) of all nests in 1975 to 17% (12–22%) in 2004 (Fig. 2b,c). In contrast, the estimated proportion of nesting attempts that failed with the lining left intact did not change ( $\chi^2_1 = 0.94$ ,  $n = 864$ ,  $P = 0.33$ ). Colonization year of the forest block in which the nest was located did not affect nest survival (adding colonization date to the minimum adequate model:  $\chi^2_1 = 0.03$ ,  $P = 0.8681$ ,  $n = 709$  nests), suggesting spatial density dependence is an unlikely mechanism for the change in nest success. Other analyses showed no effect of local population density (per forest block) on nest survival (Wright 2006).

Nest survival was greater when temperatures were higher during the individual nesting period but was not related to rainfall (Table 1c). There was no relationship between annual nest success and either temperature or rainfall during that year's breeding season (Table 1b), probably because of high intra-seasonal variability in weather. Year-specific nest survival rates were not correlated with population growth rate for either the forest ( $r = 0.190$ ,  $P = 0.344$ ) or Breckland ( $r = 0.105$ ,  $P = 0.642$ ) population, indicating that changes in nest survival were not responsible for observed population changes.

Clutch size was significantly related to rainfall (negative) and temperature (positive) during the laying and pre-laying period (Table 2). Although highly significant, the effect of variations in weather on clutch size were relatively small, resulting in a difference in predicted clutch size between the best and worst years of 11% for 28th March and 8% for 2nd May (times of peak nesting activity).

Rainfall during the brood stage had a marginal effect on the number of fledglings per egg (Table 2). Temperature did not affect the number of fledglings per egg (Table 2). The effect of rainfall during the brood stage caused a difference in the predicted number of fledglings per egg between the years with the wettest and driest weather during the brood stage, of 7% for a lay date of 28th March and 11% for 2nd May. Because the effect of rainfall on the number of fledglings per egg was small and only marginally significant, it was not included in simulation models of breeding productivity.

Woodlarks bred earlier in warmer springs (Fig. 3). The timing of the start of the breeding season was strongly negatively related to local temperatures between 15 February and 15 March (fifth percentile of the laydate distribution:  $r^2 = 0.72$ ,  $F_{1,16} = 41.85$ ,  $P < 0.001$ ,  $n = 18$ ; 10th percentile  $r^2 = 0.63$ ,  $F_{1,16} = 26.73$ ,  $P < 0.001$ ,  $n = 18$ ; 25th percentile  $r^2 = 0.51$ ,  $F_{1,16} = 16.60$ ,  $P = 0.001$ ,  $n = 18$ ). The advance in the start of the breeding season per 1 °C increase in temperature was virtually identical whether estimated by the fifth, 10th or 25th percentile (2.6 days  $\pm$  0.4 SE; 2.7 days  $\pm$  0.5 SE; 2.5 days  $\pm$  0.6 SE respectively). As the best-fitting model was obtained for the fifth percentile, we use this for subsequent analyses of spring weather effects on the timing of breeding. Although spring temperature significantly affected the timing of nesting in each year, breeding

**Table 1.** Generalized linear models of nest success for woodlarks breeding in Thetford Forest in relation to a linear trend over years, temperature (mean of daily minimum temperatures, 0.1 °C) and rainfall (daily mean, mm)

	Model details			Likelihood ratio test results					
	Deviance	<i>n</i>	d.f.	Variable estimates	SE of estimate	$\chi^2$	d.f.	<i>P</i>	
(a) Linear trend over years	835.32	717	715	Year	-0.0408	0.0098	19.21	1	< 0.0001
(b) Linear trend over years and March–June weather	833.97	717	714	Year	-0.0447	0.0105	20.40	1	< 0.0001
				Temperature	0.0845	0.0730	1.35	1	0.2446
				Year	-0.0401	0.0108	14.37	1	0.0002
(c) Linear trend over years and nest-specific weather	835.30	717	714	Rainfall	0.0150	0.1059	0.02	1	0.8875
				Year	-0.0510	0.0108	25.62	1	< 0.0001
				Temperature	0.0070	0.0026	7.16	1	0.0075
				Year	-0.0516	0.0109	25.95	1	< 0.0001
	675.61	677	674	Temperature	0.0076	0.0028	7.35	1	0.0067
				Rainfall	-0.0044	0.0075	0.34	1	0.5591

The relationship with weather was tested during the whole breeding season (1 March–30 June) and during the period specific to each nesting attempt (from the date the first egg was laid in the nest to the date the nest either fledged or failed).

did not advance over the study period due to considerable inter-annual variability in weather (Fig. 4:  $r^2 = 0.01$ ,  $F_{1,16} = 0.015$ ,  $P = 0.904$ ,  $n = 18$ ).

#### CHANGES IN ANNUAL REPRODUCTIVE OUTPUT

We used the simulation model to examine the relative effect of weather and changing nest success on annual breeding productivity (the total number of fledglings per pair per year). Running the model with constant daily nest survival rate, and varying one reproductive parameter in turn, demonstrated that effects of weather on clutch size altered productivity by 4.7% between the best and worst years. Effects of temperature on nest survival altered productivity by up to 9.0%, while the change in the timing of breeding due to weather altered productivity by up to 23.5%. The combined effect of all these weather variations (without incorporating change over years in nest failure rates) caused a difference in productivity of 24.3% between the best and worst years. Combined weather effects increased potential reproductive output over the study period, so that reproductive output was somewhat higher after 1988. However, this effect was small, with an increase of just 0.3 chicks per breeding pair (7.9%) in the latter period.

In contrast, increased nest failure rates alone (with other parameters held constant) caused a decline in productivity of 49.8% over the 34 years of the study; from a mean of 5.7 ( $\pm 2.6$  SD) fledglings per pair in 1971 to just 2.9 ( $\pm 2.5$  SD) in 2004 (Fig. 5). Incorporating combined effects of weather on the timing of breeding, nest success and clutch size did not overcome this trend. The full model incorporating increased nest failure (attributed to increased predation) and weather effects, predicted a marked decline in breeding output through time, although inter-year variation in weather caused productivity to fluctuate around this trend (Fig. 5).

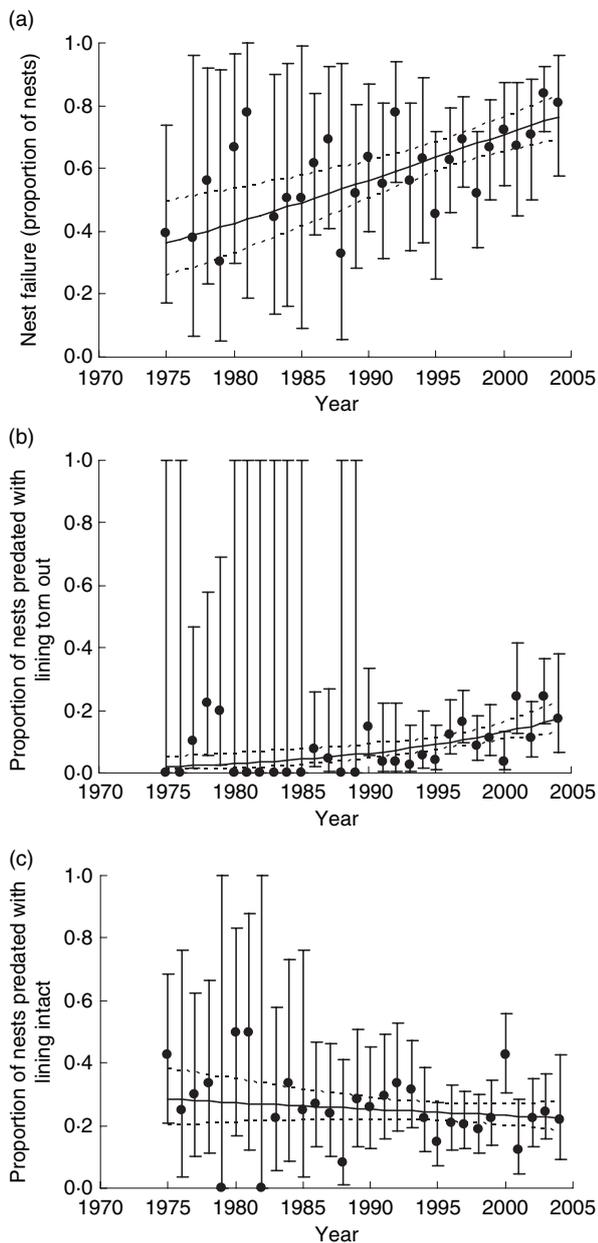
To test the relative importance of different effects on annual productivity, results of the full productivity model were compared with those of models with some effects

excluded, by linear regression. Increased nest failure explained 88.2% of the variation in the full model; the combination of increasing failure rates and the effect of variation in spring temperatures on the timing of breeding improved the  $r^2$  to 0.975; adding the effect of temperature on nest survival further improved the  $r^2$  to 0.996 and the remaining variation was explained by effects of weather on clutch size. The model that included all weather effects but with nest failure rate held constant gave an  $r^2$  of just 0.010 and was not significantly related to the full model ( $P = 0.568$ ).

The start and end dates of the breeding season are the least robust parameters in the simulation model of breeding productivity. These values were determined by comparing the model generated lay date distribution to the pattern of observed lay dates at the start and end of the season and the model successfully replicated the 'tails' at each end of the season. We tested the sensitivity of the model to start and end dates by shortening the breeding season by 10 days at each end. However, this made virtually no difference to estimates of the effect of predicted climate change.

The date when birds stop breeding is also likely to depend on the fate of their previous nesting attempt, with birds that have successfully fledged young stopping earlier (Bowden & Green 1992; Mallord *et al.* 2008). We were unable to incorporate this effect into our model as we did not have sufficient data for pairs followed throughout the breeding season.

We tested the validity of assuming that the mean date females stop laying is the same in all years by comparing whether the rate of decline in observed numbers of first egg dates in the latter part of the season differs among groups of years categorized by turning points in the population trend (1971–1987, 1988–1998 and 1999–2004). The interaction between laying week and year group was nonsignificant ( $F_{2,24} = 0.05$ ,  $P = 0.948$ ) suggesting no difference in the timing of the end of the breeding season among these time periods. Similarly, the timing of the end of the breeding season did not differ significantly between years with colder vs. milder early spring temperatures ( $F_{1,16} = 1.54$ ,  $P = 0.233$ ).



**Fig. 2.** (a) Annual mean nest failure of Thetford Forest woodlarks from 1974 to 2004. (b) The proportion of all nesting attempts where the lining was torn out. (c) The proportion of all nesting attempts that failed with the nest left intact. Error bars show 95% confidence intervals; continuous and dotted lines show fitted models and their 95% confidence limits respectively.

#### SURVIVAL RATES (MARK-RESIGHTING ANALYSIS)

The mark-resighting model estimate of mean first-year survival across 1986–2004, was 0.22 (95% CL 0.16–0.28), while estimated mean adult survival rate was 0.60 (95% CL 0.54–0.66). The most parsimonious model (lowest AICc) had year-specific first-winter and constant adult survival estimates. A model with a linear trend in first-winter survival and constant adult survival had an AICc only 0.02 higher and suggested survival declined between 1986 and 2004 [analysis of deviance (Grosbois *et al.* 2008):  $F = 17.65$ ,  $P = 0.0003$ ]. Models

that incorporated winter temperature had higher AICc values and nonsignificant analyses of deviance, suggesting temperature at Santon Downham did not significantly affect survival. Further details are given online (Supporting Information, Table S2).

#### SURVIVAL RATES (DEMOGRAPHIC MODEL)

First-year survival rates increased with winter temperatures (Fig. 6, GLM with identity link and normal errors,  $r^2 = 0.148$ ,  $B = 0.028 \pm 0.013$  SE,  $F_{1,26} = 4.53$ ,  $P = 0.043$ ,  $n = 28$ ). Incorporating a categorical variable contrasting the periods before and after 1988, while controlling for temperature, improved model fit ( $r^2 = 0.307$ : change in residual variance,  $F_{1,25} = 4.88$ ,  $P < 0.05$ ) with higher survival rates in the latter period ( $B = 0.083 \pm 0.035$  SE,  $F_{1,25} = 5.708$ ,  $P = 0.025$ ). However, the effect of temperature was no longer significant ( $F_{1,25} = 2.416$ ,  $P = 0.133$ ), suggesting a factor other than temperature caused higher survival rates in the latter period. The temperature effect likely relates to just three particularly cold winters during the earlier time-period with mean temperatures around  $-2$  °C; no years after 1988 were this cold. This may explain why no winter temperature effect was found in capture-mark-resighting models of survival that did not include earlier years. Despite these three early cold winters there was no overall trend in winter temperature between 1971 and 2004 ( $F_{1,31} = 1.757$ ,  $P = 0.195$ ).

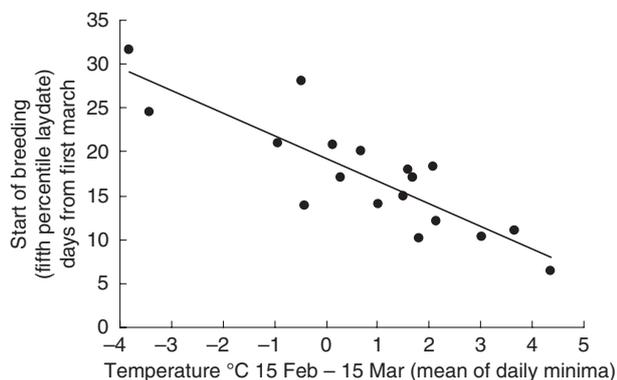
Examining first-year survival rates for the forest population only, still assuming constant adult survival (Fig. 6c,d), showed that forest survival rates were very similar to the overall Breckland survival rates during the period when both populations were monitored (up to 1999). First-year survival rates differed significantly among time-periods defined by the turning points (Kruskal-Wallis test,  $\chi^2 = 8.59$ ;  $P = 0.014$ ), with first-year survival rates after the 1999 turning point in the population trend considerably lower than during earlier periods (Table 3).

These results must be interpreted with caution as the derived survival estimates have no measure of uncertainty so that models relating these to other variables may be subject to type 1 error. However, the difference between the latter two time periods is consistent with survival estimates from capture-mark-resighting models. Survival estimates in the first time-period cannot be compared to capture-mark-resighting models as colour ringing did not begin until the end of this period. The geometric mean of first-year survival derived from the population model between 1986 and 2004 was 0.23, compared to an estimate of 0.22 from the capture-mark-resighting model for the same period. Annual survival estimates using the two methods were reasonably well matched, but for some years the demographic model predicted lower first-year survival (Supporting Information, Fig. S2). The close agreement between these two independent estimates of survival suggests both models are reasonably accurate.

**Table 2.** Generalized linear models of clutch size and number of fledglings per egg for woodlarks breeding in Thetford Forest

	Model details			Variable estimates			Likelihood ratio test results		
	Deviance	<i>n</i>	d.f.			SE of estimate	<i>F</i>	d.f.	<i>P</i>
(a) Clutch size	48.97	532	527	Lay date	0.0039	0.0011	13.37	1	0.0003
				Lay date <sup>2</sup>	$-2.17 \times 10^5$	$9.03 \times 10^{-6}$	5.82	1	0.0162
				Temperature	0.0007	0.0003	5.94	1	0.0152
				Rainfall	-0.0018	0.0005	15.08	1	0.0001
(b) Fledglings per egg (brood stage weather)	414.42	330	326	Lay date	-0.0077	0.0054	2.04	1	0.1529
				Temperature	0.0048	0.0043	1.26	1	0.2608
				Rainfall	-0.0125	0.0057	4.44	1	0.0351
(c) Fledglings per egg (breeding season weather)	414.46	330	328	Rainfall	-0.0111	0.0056	3.71	1	0.0541
				Lay date	-0.0032	0.0034	0.86	1	0.3547
				Temperature	0.0071	0.0095	0.58	1	0.4479
				Rainfall	-0.0139	0.0157	0.79	1	0.3753

(a) GLM of clutch size; temperature (mean of daily minimum temperatures, 0.1 °C) and rainfall (daily mean, mm) refer to the period from four days before to four days after the date the first egg was laid (lay date). (b) GLM of number of fledglings per egg (in successful nests), related to weather during the 12 days prior to fledging. (c) GLM of number of fledglings per egg in relation to April–June weather.



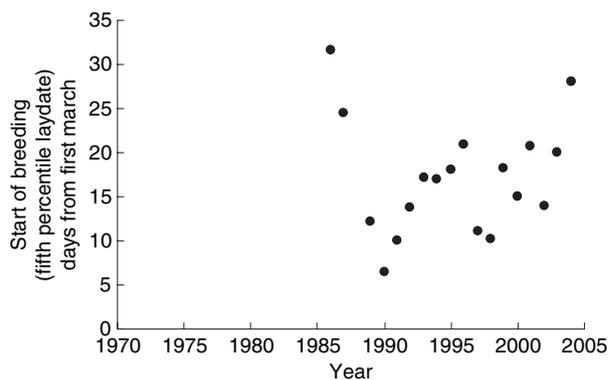
**Fig. 3.** Timing of the start of the woodlark breeding season, estimated from the fifth percentile of the lay date distribution, related to early spring temperatures.

First-year survival rates predicted by the second model (eqns 2, 3), that assumes adult and first-year survival covary with a fixed ratio ( $A/F = 2.73$ ), had a similar mean (Breckland population: 0.23 compared to 0.24 for the first model) but were less variable (coefficient of variation = 0.20 compared to 0.41 for the first model). However, relationships between first-year survival and winter temperature were similar to those obtained using the first demographic model.

## Discussion

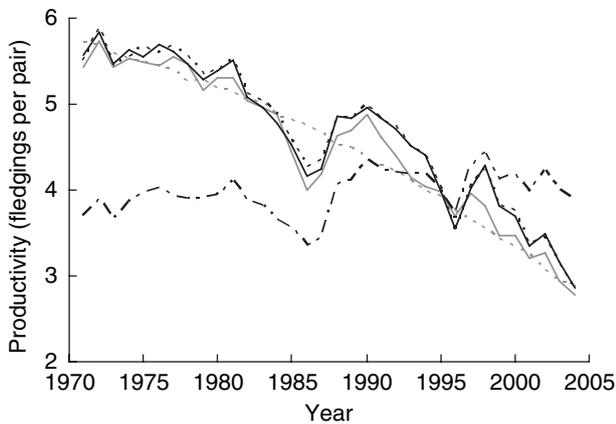
### EFFECTS OF CLIMATE CHANGE VERSUS ENVIRONMENTAL CHANGE

Although variation in weather among and within years affected breeding output, we could find no long-term signature of climate change on the productivity of this woodlark population. Woodlarks nested earlier in years with warmer spring temperatures, as do numerous other species (Crick &



**Fig. 4.** Timing of the start of the breeding season, estimated from the fifth percentile of the lay date distribution, shown for all years where more than 21 nests were found.

Sparks 1999; Dunn & Winkler 1999; Both & Visser 2001; Cresswell & McCleery 2003; Both *et al.* 2004; Reed *et al.* 2006). The difference in early spring temperature between the warmest and coldest years of 8.2 °C was sufficient to cause a 25 day advance in breeding, potentially increasing annual productivity by 0.90 chicks per pair (23%). However, across the years of this study (1986–2004) we found no significant trend in laying date due to considerable inter-annual variability, with no overall trend, in local early spring temperature during this period ( $F_{1,17} = 1.26$ ,  $P = 0.278$ ). Although many other studies have found recent advances in egg laying (Crick *et al.* 1997; Winkler, Dunn & McCulloch 2002; Both *et al.* 2004), Crick & Sparks (1999) only found significant long-term trends for 53% of the 36 species they studied, while Beale *et al.* (2006) found no evidence that laying dates of ring ouzels *Turdus torquatus* had advanced despite a significant relationship between spring weather and timing of breeding. When considering nest-specific weather (rather than that for the annual breeding season) nesting success was greater when temperatures were higher, and clutch size was slightly larger

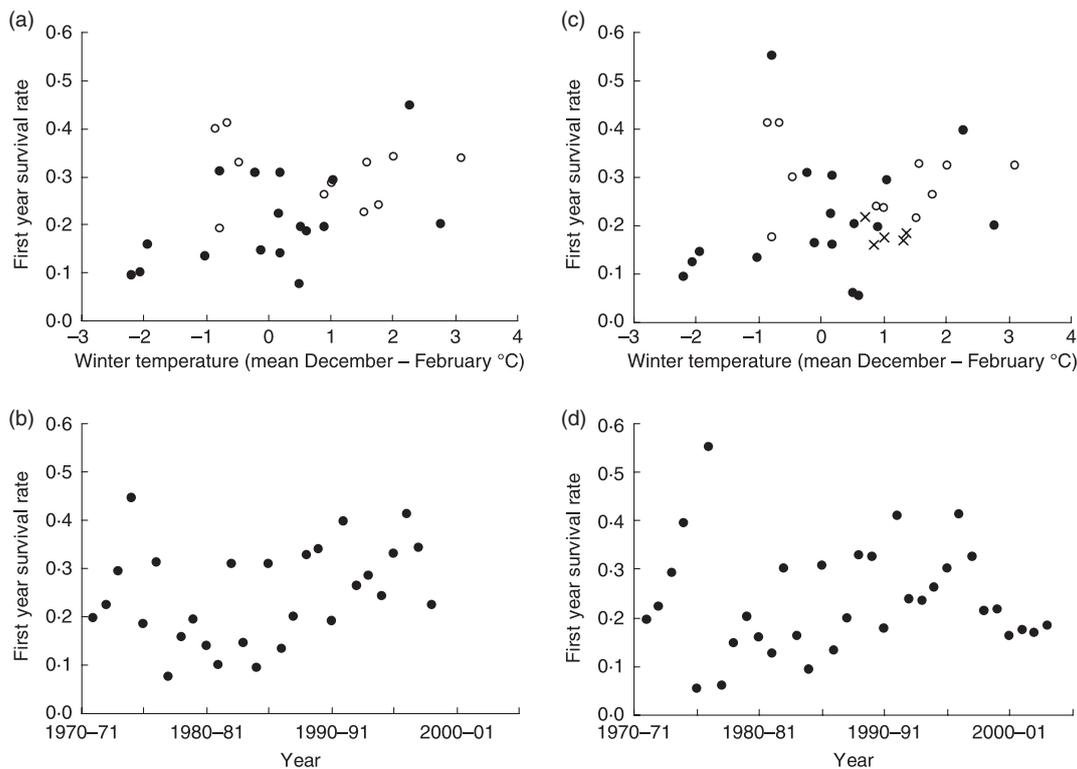


**Fig. 5.** Predicted mean number of fledglings produced per pair in each year from 1971 to 2004, estimated by iterative simulation modelling ( $n = 10\,000$  pairs per year). The dotted grey line shows only the effect of increased nest predation rates; the solid grey line shows combined effects of changes in nest predation and timing of breeding; the dotted black line includes these factors, plus effects of temperature on nest success; and the solid black line shows the full model that includes all previous factors plus additional effects of temperature and rainfall on clutch size. The double-dotted black line shows the model output with all three weather effects, but with nest predation rate held constant.

when weather was drier and warmer, but these relationships had minor consequences, increasing annual productivity by less than 10% after 1988 compared to the earlier period.

Late winter and early spring temperatures in eastern England are predicted to rise by 1–2 °C on average over the next 50 years (Hulme *et al.* 2002). This would result in an advance in woodlark laying dates of 2.6–5.2 days, increasing annual productivity by 0.1–0.3 fledglings per pair, just 2–7% compared to the 30-year mean of 4.1 fledglings per pair. Climate is also predicted to become more variable, with an increased frequency of ‘extremely warm days’ (Hulme *et al.* 2002); the effects of this are unknown.

In marked contrast to the weak signature of climate change, an increase in the rate of nest failure (97% of which was attributed to predation) resulted in a substantial decline in annual productivity of 2.8 chicks per pair, or 50%, between 1975 and 2004. Nest failure rates were not related to woodlark territory density, either in Thetford Forest (this study) or in Dorset (Mallord *et al.* 2007c) and did not differ with lay date, plantation age, nest concealment, vegetation, soil type or distance to forest edge (Wright 2006). Thus increased nest failure is most likely due to changes in predator abundance (Dion, Hobson & Larivière 2000; Luginbuhl, Marzluff & Bradley 2001) not settlement of suboptimal territories at higher density. The proportion of nests predated with the lining torn out increased significantly between 1975 and 2004, while the proportion of nests predated but left intact did not change (Fig. 2), suggesting increased activity of a particular class of nest predator.



**Fig. 6.** (a) First-year survival rates (calculated from a demographic model that assumes constant adult survival) in the Breckland region in relation to winter temperatures for 1971/1972–1987/1988 (closed circles) and 1988/1989–1999/2000 (open circles). (b, d) First-year survival rates against year for Breckland and Thetford Forest respectively. (c) First-year survival rates in Thetford Forest in relation to winter temperatures, as (a) but also showing first-year survival rates in 1999/2000–2003/2004 (crosses).

**Table 3.** Demographic rates in periods with differing rates of population increase, as identified by turning points analysis

Period	Predicted lay date of first nest	Annual productivity (per pair)	Clutch size	Nest success rate (per attempt)	Predicted lay date of last nest	Population model first-year survival (Breckland)	Population model first-year survival (forest)	CMR model first-year survival	CMR model adult survival	Population growth rate ( $\lambda$ )
1971–1988	30.18 ± 1.13	5.22 ± 0.12	4.05 ± 0.06	0.52 (0.40–0.63)	93.78 ± 0.20	0.21 ± 0.024	0.21 ± 0.030	0.33 (0.21–0.48)	0.76 (0.20–0.98)	1.15
1988–1999	24.06 ± 1.32	4.45 ± 0.14	4.01 ± 0.04	0.40 (0.33–0.47)	93.68 ± 0.24	0.30 ± 0.021	0.29 ± 0.023	0.20 (0.14–0.26)	0.60 (0.53–0.68)	1.25
1999–2004	27.66 ± 1.09	3.40 ± 0.14	3.87 ± 0.04	0.26 (0.19–0.33)	92.70 ± 0.33	No data	0.18 ± 0.010	0.09 (0.05–0.17)	0.46 (0.34–0.60)	0.90

Values shown are mean ± SE, except nest success and CMR-modelled survival which show the mean and 95% confidence limits. Values for clutch size are based on observed data, nest success rates are derived from a GLM of daily nest survival rates in each period, other breeding parameters are values from a simulation model of annual breeding output, and first-year survival rates are derived from population models based on either the entire Breckland population or the Thetford Forest population that assume constant adult and varying first-year survival. Dates are given as days from 1st March = day 1. CMR-modelled survival rates during the first time-period only cover 1986–1987 for first-year birds and 1987 for adults, and thus are not representative of the entire period from 1971–1988. The population growth rate is estimated using eqn 1, with annual productivity estimated from the simulation model of breeding (incorporating all weather and nest-survival effects) and first-year survival values estimated from the forest population model shown in this table.

Despite the consistent increase in nest failure rates through the period of the study, the population dynamics showed three markedly different phases. A period of slow population increase during 1971–1988 was followed by faster population growth from 1988 to 1999, after which woodlark numbers declined.

#### PHASE OF RAPID POPULATION INCREASE 1988–1999

The observed increase in population growth rate after 1988 cannot be explained by changes in productivity, which declined throughout the study, thus winter survival rates were likely to be responsible. As winter temperature did not explain higher survival rates after 1988, other changes may have contributed to improved survival. Introduction of arable set-aside schemes, trialled in 1989/1990 with full uptake from 1992, and consequent increased availability of overwintered stubbles that are important for seed-eating farmland birds (Donald *et al.* 2001; Moorcroft *et al.* 2002; Gillings *et al.* 2005), may have benefitted woodlarks. Flocks of up to 95 have been observed on stubble fields in our study area in recent winters (Atkinson 2001; Dunmore 2006).

#### PHASE OF POPULATION DECLINE AFTER 1999

Reduced productivity, resulting from increased rates of nest predation, is likely to have contributed to the population decline after the second turning point in 1999. Assuming the mean values of first-year and adult survival rates estimated using mark–resighting, productivity must be at least 3.6 fledglings per pair per year for the population to remain stable. According to our simulation model, annual breeding output was close to this level (3.7 fledglings per pair) in 2000, but fell below it from 2001 onwards, providing strong support for the importance of increased nest failure rates to the decline. However, first-year survival rates were also lower after 1999, explaining the overall linear decline in survival between 1986 and 2004 apparent in capture–mark–resighting models. During 1999–2004, the population multiplication rate (PMR,  $\lambda$ ) was 0.90 (i.e. the population declines by 10% per year). Substituting the productivity value from the preceding period of growth (1988–1999), but keeping the survival rate from 1999 to 2004 gives a PMR of 0.99 (1% decline per year), while using the first-year survival rate from 1988 to 1999 but keeping the productivity value from 1999 to 2004 produces a PMR of 1.01 (1% increase per year). Thus reduced productivity and lower survival contributed similarly to the observed population decline in the latter period.

Reduced survival rates during 1999–2004 cannot be explained by either winter weather, or the amount of set-aside land or spring sown barley in Breckland, which was similar to that in the mid-1990s. Caution must be exercised in assuming that rates of recruitment predicted from the population model relate directly to survival, although survival rates independently estimated from capture–mark–resighting data were also lower after 1999, supporting the conclusions drawn from these independent methods. During this period

of population decline, woodlark density decreased within open and young growth forest habitats, which supports the conclusion that the population decline post-1999 must be driven by extrinsic demographic factors. However, although our measure of habitat extent is applied consistently across years, it does not capture habitat quality (c.f. Mallord *et al.* 2007a), thus if the suitability of young plantations for woodlarks has reduced then habitat-mediated reduction in settlement could have contributed to observed declines.

## Conclusion

This study has demonstrated the importance of considering other factors in addition to climate change in predictive population modelling. In contrast to clear effects of climate on timing of breeding and productivity in single-brooded species, effects on multi-brooded species are more complex. While many recent studies have focused on incorporating density-dependent effects into predictive models (Stillman *et al.* 2001; Sutherland & Norris 2002; Sutherland 2006; Mallord *et al.* 2007a) or the effects of changes in predation, landscape (Jackson & Green 2000; Evans 2004; Tyler & Green 2004) or climate (Asbjørnsen *et al.* 2005; Pearce-Higgins *et al.* in press), few have incorporated all of these effects (although see Wildhaber & Lamberson 2004; Vucetich, Smith & Stahler 2005). A thorough understanding of such effects is required if accurate predictive modelling is to be possible.

## Acknowledgements

We are extremely grateful to the numerous observers who helped with woodlark population monitoring. We wish to thank the Forestry Commission, Ministry of Defence, Elveden Estate and other landowners for permitting access to land owned or managed by them. The Forestry Commission and the Royal Society for the Protection of Birds funded some of the data collection. We thank the Meteorological Office for providing the climate data through the British Atmospheric Data Centre (<http://www.badc.nerc.ac.uk>), and Phil Atkinson and Rob Robinson for valuable comments on earlier versions of this paper. LJW was funded by a NERC award (NER/S/A/2001/06141).

## References

Aebischer, N.J. (1999) Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study*, **46**, S22–S31.

Anderson, D.R., Burnham, K.P. & White, G.C. (1994) AIC model selection in overdispersed capture-recapture data. *Ecology*, **75**, 1780–1793.

Asbjørnsen, E.J., Sæther, B.E., Linnell, J.D.C., Engen, S., Andersen, R. & Bretten, T. (2005) Predicting the growth of a small introduced muskox population using population prediction intervals. *Journal of Animal Ecology*, **74**, 612–618.

Atkinson, P. (2001) Woodlarks' winter harbour. *BTO News*, **234**, 5.

Beale, C.M., Burfield, I.J., Sim, I.M.W., Rebecca, G.W., Pearce-Higgins, J.W. & Grant, M.C. (2006) Climate change may account for the decline of British ring ouzels *Turdus torquatus*. *Journal of Animal Ecology*, **75**, 826–835.

Beintema, A.J. & Muskens, G.J.D.M. (1987) Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology*, **24**, 743–758.

Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.

Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E.V., Jarvinen, A., Metcalfe, N.B.,

Nyholm, N.E.I., Potti, J., Ravussin, P.A., Sanz, J.J., Silverin, B., Slater, F.M., Sokolov, L.V., Torok, J., Winkel, W., Wright, J., Zang, H. & Visser, M.E. (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London Series B*, **271**, 1657–1662.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.

Bowden, C.G.R. & Green, R.E. (1992) *The Ecology and Management of Woodlarks in Pine Plantations in the Thetford and Sandlings Forests*. RSPB, Sandy.

Burfield, I. & van Bommel, F. (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. Birdlife International, Cambridge.

Cramp, S. & Perrins, C.M. (1988) *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic*. Oxford University Press, Oxford.

Cresswell, W. & McCleery, R. (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, **72**, 356–366.

Crick, H.Q.P. (2004) The impact of climate change on birds. *Ibis*, **146** (Suppl. 1), S48–S56.

Crick, H.Q.P. & Sparks, T.H. (1999) Climate change related to egg-laying trends. *Nature*, **399**, 423.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526.

Crick, H.Q.P., Baillie, S.R. & Leech, D.I. (2003) The UK Nest Record Scheme: its value for science and conservation. *Bird Study*, **50**, 254–270.

Dion, N., Hobson, K.A. & Larivière, S. (2000) Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. *Condor*, **102**, 629–634.

Donald, P.F., Buckingham, D.L., Moorcroft, D., Muirhead, L.B., Evans, A.D. & Kirby, W.B. (2001) Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in southern Britain. *Journal of Applied Ecology*, **38**, 536–547.

Dunmore, G. (2006) Systematic list: woodlark. *Transactions of the Norfolk and Norwich Naturalists' Society*, **39**, 208.

Dunn, P.O. & Winkler, D.W. (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London Series B*, **266**, 2487–2490.

Evans, K.L. (2004) The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis*, **146**, 1–13.

Eycott, A.E., Watkinson, A.R. & Dolman, P.M. (2006) Plant diversity in clear-fell forest: ecological patterns and management effects. *Journal of Applied Ecology*, **43**, 1160–1171.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology*, **81**, 1970–1984.

Gillings, S., Newson, S.E., Noble, D.G. & Vickery, J.A. (2005) Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. *Proceedings of the Royal Society of London Series B*, **272**, 733–739.

Grosbois, V., Henry, P.Y., Blondel, J., Perret, P., Lebreton, J.D., Thomas, D.W. & Lambrechts, M.M. (2006) Climate impacts on Mediterranean blue tit survival: an investigation across seasons and at spatial scales. *Global Change Biology*, **12**, 2235–2249.

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.

Hughes, G.O., Thuiller, W., Midgley, G.F. & Collins, K. (2008) Environmental changes hastens the demise of the critically endangered riverine rabbit (*Bunolagus monticularis*). *Biological Conservation*, **141**, 23–24.

Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G., Lowe, J., Murphy, J.M., Hassell, D., Boorman, P., McDonald, R. & Hill, S. (2002) *Climate Change Scenarios for the United Kingdom: The UK-CIPO2 Scientific Report*. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK.

Jackson, D.B. & Green, R.E. (2000) The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. *Biological Conservation*, **93**, 333–348.

Jenni, L. & Kéry, M. (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London Series B*, **270**, 1467–1471.

Jones, P. & Hulme, M. (1997) The changing temperature of 'Central England'. *Climates of the British Isles* (eds M. Hulme & E. Barrow), pp. 173–196. Routledge, London.

- Luginbuhl, J.M., Marzluff, J.M. & Bradley, J.E. (2001) Corvid survey techniques and the relationship between corvid abundance and nest predation. *Journal of Field Ornithology*, **72**, 556–572.
- Macklin, R. (2004) Wood larks on the Suffolk coast 1998 to 2004. *Staffolk Birds*, **54**, 27–30.
- Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007a) Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, **44**, 185–195.
- Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. (2007b) Nest site characteristics of woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study*, **54**, 307–314.
- Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. (2007c) Quantifying density dependence in a bird population using human disturbance. *Oecologia*, **153**, 49–56.
- Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. (2008) Early nesting does not result in greater productivity in the multi-brooded Wood-lark *Lullula arborea*. *Bird Study*, **55**, 145–151.
- Møller, A.P. (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology*, **71**, 201–210.
- Møller, A.P. (2007) Interval between clutches, fitness, and climate change. *Behavioral Ecology*, **18**, 62–70.
- Moorcroft, D., Whittingham, M.J., Bradbury, R.B. & Wilson, J.D. (2002) The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *Journal of Applied Ecology*, **39**, 535–547.
- Parnesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearce-Higgins, J.W., Dennis, P., Whittingham, M.J. & Yalden, D.W. (in press) Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology*. DOI: 10.1111/j.1365-2486.2009.01883.x
- Portner, H.O. & Farrell, A.P. (2008) Ecology, physiology and climate change. *Science*, **322**, 690–692.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161–167.
- Ratcliffe, N., Schmitt, S. & Whiffin, M. (2005) Sink or swim? Viability of a black-tailed godwit population in relation to flooding. *Journal of Applied Ecology*, **42**, 834–843.
- Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B. & Cunningham, E.J.A. (2006) Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proceedings of the Royal Society of London Series B*, **273**, 2713–2719.
- Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J. & Thomson, D.L. (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology*, **73**, 670–682.
- Robinson, R.A., Baillie, S.R. & Crick, H.Q.P. (2007) Weather-dependent survival: implications of climate change for passerine population processes. *Ibis*, **149**, 357–364.
- Rodriguez, C. & Bustamante, J. (2003) The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? *Journal of Animal Ecology*, **72**, 793–810.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Sæther, B.-E., Sutherland, W.J. & Engen, S. (2004) Climate influences on avian population dynamics. *Advances in Ecological Research*, **35**, 185–209.
- Saino, N., Szép, T., Romano, M., Rubolini, D., Spina, F. & Møller, A.P. (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters*, **7**, 21–25.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, J., Huber-Sanwald, E., Huennike, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. *Science*, **287**, 1770–1774.
- SAS Institute, Inc. (1999) *Onlinedoc*, Version 8.0. SAS Institute, Inc., Cary, NC.
- Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008) Climate change, elevational range shifts and bird extinctions. *Conservation Biology*, **22**, 140–150.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R., Marchant, J.H. & Wilson, J.D. (1998a) Trends in abundance of farmland birds: a quantitative comparison of smoothed common bird census indices. *Journal of Applied Ecology*, **35**, 24–33.
- Siriwardena, G., Baillie, S.R. & Wilson, A. (1998b) Variation in survival rates of some British passerines. *Bird Study*, **45**, 276–292.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., Durell, S., McGrorty, S., Caldwell, R.W.G., Norris, K.J., Johnstone, I.G., Ens, B.J., Van der Meer, J. & Triplet, P. (2001) Predicting shorebird mortality and population size under different regimes of shellfishery management. *Journal of Applied Ecology*, **38**, 857–868.
- Sutherland, W.J. (2006) Predicting the ecological consequences of environmental change: a review of the methods. *Journal of Applied Ecology*, **43**, 599–616.
- Sutherland, W.J. & Norris, K. (2002) Behavioural models of population growth rates: implications for conservation and prediction. *Philosophical Transactions of the Royal Society of London Series B*, **357**, 1273–1284.
- Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M. & Speakman, J.R. (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, **291**, 2598–2600.
- Tyler, G.A. & Green, R.E. (2004) Effects of weather on the survival and growth of Corncrake *Crex crex* chicks. *Ibis*, **146**, 69–76.
- Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London Series B*, **272**, 2561–2569.
- Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos*, **111**, 259–270.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120–S139.
- Wildhaber, M.L. & Lamberson, P.J. (2004) Importance of the habitat choice behavior assumed when modeling the effects of food and temperature on fish populations. *Ecological Modelling*, **175**, 395–409.
- Wilson, S. & Arcese, P. (2003) El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). *Proceedings of the National Academy of Sciences USA*, **100**, 11139–11142.
- Winkler, D.W., Dunn, P.O. & McCulloch, C.E. (2002) Predicting the effects of climate change on avian life-history traits. *Proceedings of the National Academy of Sciences USA*, **99**, 13595–13599.
- Wotton, S.R. & Gillings, S. (2000) The status of breeding woodlarks *Lullula arborea* in Britain in 1997. *Bird Study*, **47**, 212–224.
- Wright, L.J. (2006) *Demography and productivity of woodlarks Lullula arborea in Breckland*. PhD thesis, University of East Anglia, Norwich.

Received 13 August 2007; accepted 28 May 2009

Handling Editor: Jean Clobert

## Supporting Information

Additional supporting information may be found in the online version of this article:

**Fig. S1.** Flow-chart illustrating the modelling approach used in the simulation model of total breeding output.

**Fig. S2.** Scatterplot showing estimates of first-year survival derived from a mark–resighting model against those derived from a population model.

**Table S1.** Parameters of the simulation models of total breeding output per pair.

**Table S2.** Structure and results of survival models using capture–mark–resighting data from 1986 to 2004.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.