5-1-2015

Negative effects of rapid warming and drought on reproductive dynamics and population size of an avian predator in the arid southwest

Kirsten Cruz-McDonnell

Recommended Citation

Cruz-McDonnell, Kirsten. "Negative effects of rapid warming and drought on reproductive dynamics and population size of an avian predator in the arid southwest." (2015). https://digitalrepository.unm.edu/biol_etds/21

Kirsten Cruz-McDonnell
Candidate

Biology
Department

This thesis is approved, and it is acceptable in quality and form for publication:

Approved by the Thesis Committee:

Blair O. Wolf, Chairperson

Christopher C. Witt

David S. Gutzler

NEGATIVE EFFECTS OF RAPID WARMING AND DROUGHT ON REPRODUCTIVE DYNAMICS AND POPULATION SIZE OF AN AVIAN PREDATOR IN THE ARID SOUTHWEST

by

KIRSTEN CRUZ-MCDONNELL

B.S., NATURAL RESOURCES AND ENVIRONMENT,
UNIVERSITY OF MICHIGAN, 1999

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science
Biology

The University of New Mexico
Albuquerque, New Mexico

May, 2015

ACKNOWLEDGEMENTS

I thank my advisor, Dr. Blair Wolf, for providing me this opportunity to earn my Master's degree from the University of New Mexico, and for his guidance in processing the large dataset that became my Master's thesis project. I also thank my committee members, Dr. David Gutzler and Dr. Christopher Witt, for their guidance and helpful comments on this manuscript.

I am grateful to the U.S. Department of Defense and Natural Resource Management of Kirtland Air Force Base, and particularly Carol Finley and Dustin Akins, for their years of funding, logistical support, and concern for declining species. Sincere thanks to my co-workers at Envirological Services, Inc., Octavio Cruz-Carretero, Ken Babcock, Victoria Bailey, and Corrie Borgman, for their endless support. Without their fieldwork assistance, this project and detailed results would not be possible. And many, many thanks to Envirological's director, Marianne Wootten, for allowing me the flexibility to pursue graduate school and for her endless encouragement.

Special thanks to my husband and stress manager, Octavio Cruz-Carretero, for his love, support, and understanding through this degree process, and my dear friend and co-conspirator in graduate school, Corrie Borgman; both of whom I endlessly thank for their humor and friendship. I also extend loving, heartfelt thanks to my parents for their encouragement throughout each of my life endeavors and to my family and friends for their moral support each step of the way.

NEGATIVE EFFECTS OF RAPID WARMING AND DROUGHT ON REPRODUCTIVE DYNAMICS AND POPULATION SIZE OF AN AVIAN PREDATOR IN THE ARID SOUTHWEST

by

Kirsten K. Cruz-McDonnell

B.S., Natural Resources and Environment, University of Michigan, 1999
M.S., Biology, University of New Mexico, 2015

ABSTRACT

Avian communities of arid ecosystems may be particularly vulnerable to global climate change due to the magnitude of model projected change for desert regions and the inherent challenges for species of resource limited ecosystems. How arid zone birds will be affected by rapid increases in air temperature and increased drought frequency and severity is poorly understood. To date, avian responses to climate change have primarily been studied in northern temperate regions in relatively mesic habitats. We studied the effects of increasing air temperature and aridity on a Burrowing Owl (*Athene cunicularia*) population in the southwestern USA from 1998-2013. Over 16 years, the breeding population declined 98.1%, from 52 pairs to 1 pair, and nest success and fledgling output also declined significantly. These trends were strongly associated with the combined effects of decreased precipitation and increased air temperature. Arrival on the breeding grounds, pair formation, nest initiation, and hatch dates all showed significant delays ranging from 9.4 - 25.1 days over 9 years, which have negative effects on reproduction. Adult and juvenile body mass decreased significantly over time, with a loss of 10.9% mass in adult males and 7.9% mass in adult females over 16 years, and a loss of 20.0% mass in nestlings over 8 years. These population and reproductive trends have serious implications for population persistence. The southwestern USA has been identified as a climate change hotspot, with projections of warmer temperatures, less winter precipitation, and an increase in frequency and severity of extreme events including drought and heat waves. An increasingly warm and dry climate may contribute to this species' decline, and may already be a driving force of their apparent decline in the desert southwest.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Introduction

Assessing species vulnerability to climate change is increasingly important for conservation and management, particularly for species already of conservation concern. Climate change models project warming in the USA to exceed 2°C during this century with greater increases of 3°C to 5°C in the summer (Romero-Lankao *et al.*, 2014). Avian populations may respond to increasing temperatures with shifts in phenology and range, and changes in morphology and reproduction. Some of these impacts are already being observed, such as range shifts (Johnson, 1994), earlier arrival to breeding grounds (Butler, 2003), earlier egg laying (Brown *et al.*, 1999; Dunn & Winkler, 1999), and decreasing population density (Anders & Post, 2006) and reproduction (Bolger *et al.*, 2005).

The southwestern USA has been identified as a climate change hotspot, with projections of increasing air temperature, aridity, and inter-annual variability (Diffenbaugh *et al.*, 2008; Seager & Vecchi, 2010; Gutzler & Robbins, 2011). Along with higher air temperatures, winter precipitation is projected to decrease and extreme events including drought and heat waves will occur more frequently, show increased severity and be of longer duration (Meehl & Tebaldi, 2004; Seager *et al.*, 2007; Sheffield & Wood, 2008; Weiss *et al.*, 2009; Cayan *et al.*, 2010). The recent climate record of the southwest United States typifies these projections (Andreadis & Lettenmaier, 2006; Seager *et al.*, 2007; Barnett *et al.*, 2008; Gutzler, 2013). In New Mexico, for example, current air temperatures have been trending upward since the 1900s, with sharper increases since the 1960s. Recent drought events are equally challenging and June 2013 ranked as the driest month for drought severity out of the 119 years in the instrumental record (NOAA, 2013). As a region characterized by low and highly variable precipitation, high air temperatures and high solar heat loads, increasingly extreme conditions may make avian species more vulnerable to extirpation by disrupting reproductive cycles or through direct mortality of adults (McKechnie & Wolf, 2010). Interestingly, how these climatic changes will affect bird populations and communities in arid regions is poorly understood.

Increased heat and water stress can impact bird communities directly through extreme events such as heat waves and droughts that produce mortality, and indirectly through influences on habitat quality or prey availability. The quantity and seasonal timing of precipitation strongly influences primary productivity in arid and semiarid ecosystems (Sala *et al.*, 1988; Muldavin *et al.*, 2008), and vegetative growth and seed production importantly influences population growth of consumers. High air temperatures and heat stress elicit behavioral and physiological responses in desert birds, with potential impacts on survival (Wolf, 2000; du Plessis *et al.*, 2012). Increasing temperatures have also been associated with decreases in survival and abundance in vertebrate and invertebrate prey species (Bale *et al.*, 2002; Pearce-Higgins *et al.*, 2010), including in arid zone rodents (Moses *et al.*, 2012) and lizards (Sinervo *et al.*, 2010), which may lead to demographic consequences for avian predators.

Western Burrowing Owls (*Athene cunicularia hypugaea*) are a small (~150g), ground-dwelling species that inhabits North American deserts and grasslands. They are unique among owls as they are active both night and day, and nest in underground burrows created by burrowing mammals. Throughout their range they are listed to varying degrees as a species of concern due to their declining populations. Recent estimates from the North American Breeding Bird Survey indicate that Burrowing Owl populations have declined at a rate of 1.1% per year from 1966 to 2012 (Sauer *et al.*, 2014). These range-wide declines have broadly been attributed to habitat loss resulting from land conversion for urban and agricultural growth and loss of nest sites due to the decline of prairie dogs and other burrowing mammals (Poulin *et al.*, 2011).

How an increasingly warm and dry climate may affect Burrowing Owl populations is an open question. Decreased precipitation coupled with increasing temperatures may impact Burrowing Owls by reducing their food availability and altering their behavior or phenology. Burrowing Owls are opportunistic foragers, feeding primarily on arthropods and small mammals, but also on lizards, snakes, and small birds. As insects and small mammals are the main prey sources, Burrowing Owl dynamics may fluctuate in relation to insect and mammal abundance and thus climate dynamics. As generalist feeders, Burrowing Owls show both a numerical and functional response to an abundance of prey (Silva *et al.*, 1995; Jaksic *et al.*, 1997; Poulin *et al.*, 2001), therefore their response to climate variability may be immediate or delayed, and may vary according to climate extremes. Given these increasing stressors on owl populations, we examined the effects of rising air temperatures and drought on a Burrowing Owl population in central New Mexico over a 16-year study period. Owls were intensively monitored and reproductive activity quantified from 1998-2013. We examined the relationships between owl population and reproductive trends, and temperature, precipitation, and drought. We also assessed trends in arthropod prey abundance related to climate variables, and examined the relationships between prey availability and Burrowing Owl reproduction. We asked the following questions: 1) has reproductive phenology, including timing of arrival on the breeding grounds, pair formation, nest initiation, and hatch dates, changed over time? 2) do temporal trends in phenology affect reproductive potential? 3) has the local population size declined during periods of increased air temperature and drought? 4) does reproductive output vary with climate variation? 5) have there been changes in functional traits such as body condition that may have affected reproductive activity and success? 6) have changes in fledgling condition been observed?

Materials and methods

Study area

The study site was located southeast of Albuquerque, New Mexico on Kirtland Air Force Base (KAFB). KAFB covers 20,348 ha with an elevation range of 1573 m to 2433 m. Developed urban and suburban areas of business and residential infrastructure are concentrated in the northwest corner, while the remaining majority is designated semi-improved and unimproved grounds for military uses and widely spaced research and administrative developments. Burrowing Owls are found in both urban and undeveloped areas of the grassland vegetation community. Primary grass species include *Muhlenbergia* spp., *Aristida* spp., *Sporobolus cryptandrus* (Torr.) A. Gray, and *Pleuraphis jamesii* Torr. The dominant shrubs include *Gutierrezia sarothrae* (Pursh) Britton & Rusby, *Cylindropuntia imbricate* (Haw.) F.M. Knuth, *Yucca* spp., *Opuntia* spp., *Atriplex canescens*, *Salsola kali*, and *Krascheninnikovia lanata* (Pursh) Meeuse & Smits. Burrowing Owls on KAFB nest in Gunnison’s prairie dog (*Cynomys gunnisonii*) burrows.

Climate of the region is characterized by wide annual and diurnal temperature ranges, clear skies and high solar radiation, frequent drying winds, low relative humidity, and low annual precipitation. Using recent 1983-2013 climatology, average temperature ranges from -3.6°C in January to 33.1°C in July; annual mean temperature is 14.2°C. Mean annual precipitation is 23.6 cm and ranges from 12.0 cm to 33.3 cm annually. Approximately half of this precipitation is received between July and September from the North American monsoon, and the remainder falls during the winter and spring, typically in low amounts.

In central New Mexico Burrowing Owls are migratory, and the nesting period typically runs from March through June. Owls arrive on the breeding grounds in late February through early April, lay and incubate eggs mid-April through May, and emergence of young above ground occurs late May through mid-June. Departure from the breeding grounds begins in July and August although some owls may remain through October. Burrowing Owls are thought to winter in the southwestern U.S. and throughout Mexico (Holroyd *et al.*, 2010, Poulin *et al.*, 2011), although wintering grounds of New Mexican breeders are currently unknown.

Data collection

Intensive annual surveys of population and reproductive dynamics of Burrowing Owls were conducted from 1998-2013 on Kirtland Air Force Base. Recurring surveys were conducted throughout suitable grassland habitat to locate all non-breeding and breeding birds in the survey area. Standardized surveys conducted from mid-February through August according to established protocols (Conway & Simon, 2003; NMBOWG,

2005) ensured complete coverage of the survey area. Nest sites were considered active once the pair was observed at the nest burrow for more than two weeks and were monitored every 1-3 days until all adults and fledglings left the base. Breeding pairs were monitored to determine nest success and productivity. Both adults and nestlings were trapped and color banded. Color banding allowed us to identify adult movements and to gather accurate counts of juvenile owls. Nestlings were counted on every visit and totals per pair were determined after repeated counts at dawn and dusk when young were most active. We estimated the age of young on each visit using plumage characteristics and behavior (Zarn, 1974; Priest, 1997). We defined successful nests as those that fledged at least one young to 44 days old (Landry, 1979). Apparent nest success was used to estimate proportion of success as intensive survey efforts provided high detection probability and allowed detection of owls upon arrival to the breeding grounds. Nest sites were approached on foot after multiple visits with no owls observed in order to investigate failure and possible causes. Arrival, pair formation, nest initiation, and hatch dates were recorded from 2005-2013.

To analyze prey abundance and distribution, two trapping methods were utilized to assess the surface-active arthropod population. Pitfall trap arrays were installed in three sites used by breeding Burrowing Owls, and sampling occurred monthly April-August. From 2008-2013, we used trapping methods modified from Smith and Conway (2007). At each site, two traps 1m apart were installed in two locations and were opened for a 7 day period, producing 12 arthropod samples each month. To increase arthropod capture, a second method was added from 2010-2013 using methods modified from Crawford (1988). At each site, 20 traps were installed 10m apart in a 4x5 grid and were opened for a 48 hour period, producing 60 samples per month. Samples from each method were dried, weighed, identified (order, family, or genus), and total biomass calculated. Trends were analyzed for each method separately, and we found monthly biomass from each method was strongly correlated. We used biomass from the first method in statistical analyses due to the longer collection period.

Climate data from 1931-2013 were obtained from the NOAA National Climatic Data Center (NOAA, 2013) for the Albuquerque International Sunport (35.042° N, 106.616° W), which lies adjacent to the study area. Climate variables used for analysis included temperature (monthly mean maximum), precipitation (monthly total), and the Palmer Modified Drought Index (PMDI). PMDI uses precipitation, temperature, and regional soil conditions in a water balance model to reflect long-term drought and was used to examine the combined effects of precipitation and temperature. PMDI values ≤ -4 indicate extreme drought and ≥ 4 indicate extreme wet.

Statistical analyses

Linear regression was used to test the effects of climate variability on Burrowing Owl population and reproductive dynamics and on arthropod prey abundance, and to examine the change over time in breeding pairs, nest success, productivity, body mass, and breeding phenology. Model fit was assessed using plot diagnostics. To investigate shifts in phenology we examined trends using all records (for the seasonal distribution), subset of first quartile (as index of start of breeding), and subset of interquartile range (to remove early and late breeders) for individual owls and first nesting attempts only. Poisson models were used to analyze individual counts of number of fledglings from each successful pair. Robust standard errors were calculated for the parameter estimates and model fit was tested with goodness-of-fit chi-squared tests of residual deviance. Logistic regression was used to model the probability of nest success as a function of precipitation, temperature, and PMDI and to test whether phenological variables affect nest success. Model fit was tested with likelihood ratio tests. Akaike's Information Criterion corrected for small sample size (AICc) was used to compare alternative models and to evaluate how well each model fit the data. Explanatory variables were evaluated for pairwise collinearity using Pearson correlation and were used in multiple regressions if correlation was relatively low ($|r| < 0.5$). Statistical analyses were performed using R (R Core Team, 2013).

Climate data from 1983-2013 were used to examine local climate trends, and linear trend models were used to calculate trend estimates and 95% confidence intervals. Residual diagnostic plots were used to check the adequacy of the fitted models and to test residual series for first order autocorrelation. Results are reported as trend ± 95% confidence interval.

We examined relationships between climate variables and owl parameters including population size (number of breeding pairs and yearly percentage change), productivity (mean fledglings per breeding pair and fledgling counts per successful pair), nest success (proportion of breeding pairs fledging at least one young and probability of success), and body mass. We tested relationships with weather variables on timescales pertinent for owl physiology and the ecology of arid systems. Insect herbivore abundance can respond rapidly to seasonal precipitation inputs (Polis *et al.*, 1997; Masters *et al.*, 1998; Jones *et al.*, 2003), while rodents and other taxa may respond after a lag period

(Ernest *et al.*, 2000; Lima *et al.*, 2008; Thibault *et al.*, 2010). In desert birds, the physiological costs of high air temperatures and heat stress may affect survival (Wolf, 2000), body condition (du Plessis *et al.*, 2012; Cunningham *et al.*, 2013), reproduction (Bolger *et al.*, 2005; Guthery *et al.*, 2005), and prey resources (Sinervo *et al.*, 2010; Moses *et al.*, 2012) leading to delayed demographic responses (Anders & Post, 2006; Both *et al.*, 2010; Flesch, 2014). To test for the lag effect of climate variability on population change, we tested population size as a function of annual precipitation and drought from the two previous years and owl breeding season (March-June) mean maximum temperature from the previous year. Reproductive rates may show an immediate or delayed response, so we tested various seasonal and inter-annual timescales prior to and during the breeding season that may impact prey availability and owl dynamics. We tested effects of precipitation and drought during the monsoon season (July-September), the non-monsoon season (November-June), the cold season (November-March), and the owl breeding season, and tested the effects of mean maximum temperature during the breeding season.

Results

Breeding trends

From 1998-2013, 440 breeding Burrowing Owl pairs were recorded on the study site. The annual population size ranged from 52 pairs in 1998 to 1 pair in 2013. Although there was annual variation, the population declined 98.1% over 16 years. The downward trend was significant ($P = 0.0340$), and the observed decline was much more pronounced and linear since 2008, declining from 49 pairs to 1 pair over 6 years.

In addition to the population decline, there was a decline in reproductive rates. During this study, 1175 fledglings were produced, with the annual total ranging from 157 fledglings in 2007 to 1 fledgling in 2013. Annual mean fledglings per breeding pair ranged from 4.6 to 0.8 ($\bar{x} = 2.5$). Productivity significantly declined since 1998 ($P = 0.0398$), with a sharper declining trend since 2007. Annual mean fledglings per successful pair ranged from 5.6 to 1.0 ($\bar{x} = 3.9$) and exhibited no trend over time ($P = 0.71$). To examine nest success trends, we removed 2013 where the 100% success rate was misleading as it resulted from only one pair. From 1998-2012 nest success significantly decreased ($P = 0.0016$), with a stronger decline since 2007.

Effects of precipitation on population and reproductive trends

Examining study site climate data, 30-year trends show precipitation outside of the monsoon season significantly declined, decreasing -61.7 ± 55.9 mm in November-June rainfall since 1983 (Fig. 1b). Monsoon precipitation exhibited no trend and showed large annual variability, ranging from 35.8 mm to 213.2 mm ($\bar{x} = 106.3$ mm). The Burrowing Owl population varied in relation to variation in annual precipitation, with population size following precipitation trends with a one to two year lag. Both previous year precipitation ($R^2 = 0.53$, $P = 0.0013$) and two years previous precipitation ($R^2 = 0.69$, $P = 0.0001$) were significant predictors of the number of breeding pairs. The strength of support of the model improved when both rainfall timescales were included (ΔAICc > 6.3), and the additive effect of rainfall during the two previous years explained 78.9% of the variation in population ($P < 0.0001$) (Fig. 2a, Table 1). We also modelled yearly percentage population change in an effort to explain population fluctuations, as this approach accounted for non-independence of population size among years. The direction and amount of annual change was also positively correlated with precipitation variability from the two previous years ($P < 0.0226$) (Table 1).

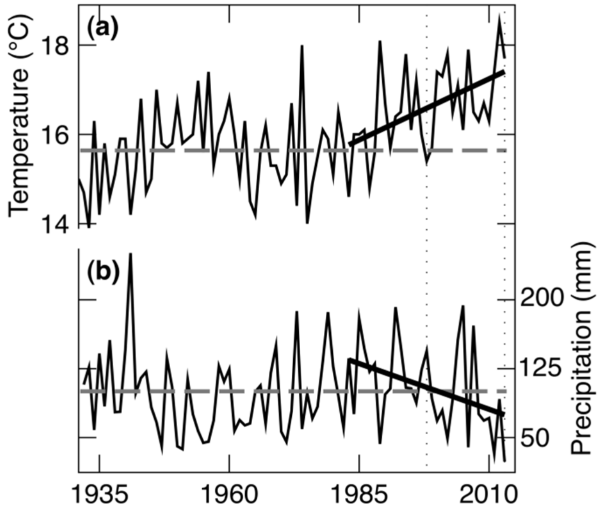

Fig. 1 Climatic trends for the central New Mexico study site from 1931-2013 of variables important for Burrowing Owl reproduction: annual breeding season (Mar-Jun) mean temperature (a) and winter through breeding season (Nov-Jun) precipitation (b) relative to the observed 1961-1990 climatology (dashed grey), with significant 1983-2013 trends (solid black) and vertical dotted lines outlining the 1998-2013 study period. Mean temperature during the Burrowing Owl breeding season has shown a fairly steady increase over time, increasing 1.7 ± 1.1°C since 1983, while precipitation falling outside of the monsoon season has decreased -61.7 ± 55.9 mm since 1983 (trend estimates ± 95% confidence intervals).

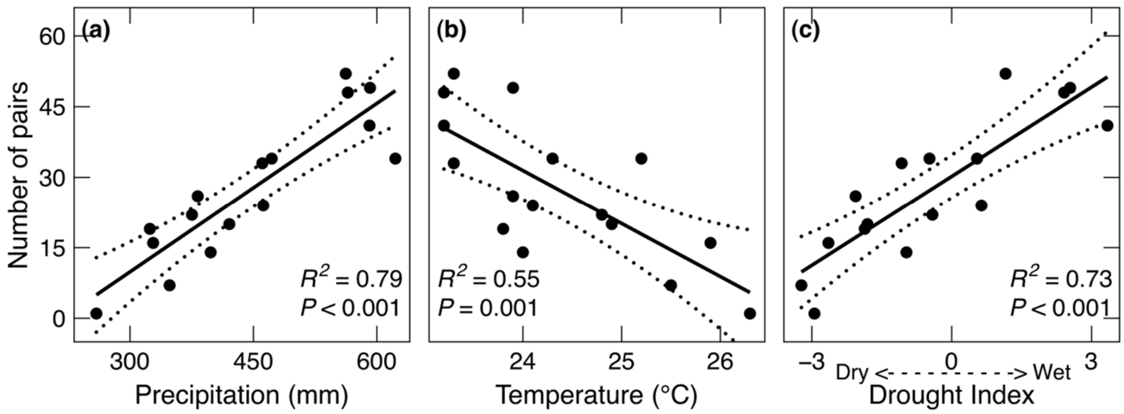

Fig. 2 Annual variation in the Burrowing Owl population as a function of significant precipitation, temperature, and drought variables: population size in relation to (a) annual precipitation during the previous two years, (b) previous breeding season (Mar-Jun) mean maximum temperature, and (c) previous year mean Palmer Modified Drought Index. The combined precipitation and temperature model accounts for 86.5% of the variation in population size.

Although population size showed a delayed response to precipitation, reproductive parameters reacted to precipitation variability from concurrent timescales (Table 1,2). Examining the candidate set of explanatory models for each reproductive parameter, reproductive rates were positively associated with breeding season (Mar-Jun) precipitation and with cold season (Nov-Mar) precipitation; however previous monsoon rainfall (Jul–Sep) was not associated with reproduction (Table 2). To include both significant predictors and remove their temporal overlap, reproductive rates were also correlated with the broader timescale of winter through breeding season (Nov-Jun) precipitation. Winter through breeding season rainfall was included in competitive models (ΔAICc ≤ 3.2) predicting each tested metric of reproduction. The linear relationships between winter through breeding season precipitation and mean fledglings per pair ($R^2 = 0.48$, $P = 0.0028$) and nest success ($R^2 = 0.28$, $P = 0.0406$) predict productivity to increase by 0.2 and success to increase by 2.1% for each 10 mm increase in November-June precipitation (Fig. 3a,d). Modelling success or failure from each of the 440 total nest attempts showed a significant positive effect of increased precipitation on the probability of nest success. For every 10 mm increase in November-June rainfall, the log-odds of success increased by a factor of 0.10 ($P = 0.0001$). Examining fledgling counts from each successful pair (n=306), an increase in fledgling output was expected with increased precipitation ($P < 0.0001$).

Table 1. Linear regression summaries and AICc ranking for tested models examining effects of selected climate variables on Burrowing Owl population size (number of breeding pairs) and population change (percentage change per year) on Kirtland Air Force Base, Albuquerque, NM, from 1998-2013. Change in AICc (ΔAICc) indicates difference from the most parsimonious model. Significant models ($P < 0.05$) were ranked based on ΔAICc and are shown with estimated coefficient (β), coefficient of determination (R^2) and P-values for model variables.

	Population Size (*n*=16 years)					**Population Change** (*n*=15 years)				
Environmental metric	**ΔAICc**	**Rank**	β	R^2	P	**ΔAICc**	**Rank**	β	R^2	P
Precipitation										
Previous year annual	16.22	6	1.67	0.53	0.0014	8.24	5	3.49	0.29	0.0368
Two years previous annual	9.81	4	2.01	0.69	<0.0001	9.50				0.07
Combined two previous years annual	3.48	2	1.19	0.79	<0.0001	7.24	3	2.11	0.34	0.0226
Temperature										
Previous breeding season mean maximum (Mar-Jun)	15.74	5	-11.30	0.55	0.0011	6.62	2	-25.04	0.37	0.0169
Palmer Modified Drought Index										
Previous year annual	7.37	3	6.32	0.73	<0.0001	0	1	15.09	0.59	0.0008
Precipitation + Temperature										
Combined two previous years annual + Previous breeding season mean maximum (Mar-Jun)	0	1	0.93, -5.16	0.86	<0.0001	8.11	4	1.31, -16.9	0.46	0.0255

Table 2. Generalized linear model summaries and AICc ranking for tested models examining effects of selected climate variables on Burrowing Owl reproductive parameters, including probability of nest success, fledgling counts from each successful pair, annual nest success, and mean fledglings per breeding pair on Kirtland Air Force Base, Albuquerque, NM, from 1998-2013. Change in AICc (ΔAICc) indicates difference from the most parsimonious model. Significant models ($P < 0.05$) were ranked based on ΔAICc and are shown with estimated coefficient (β), coefficient of determination (R^2) and P-values for model variables. For each reproductive parameter, models including both precipitation and temperature improved fit to the data (i.e. AICc decreased), however explanatory variables were correlated ($r = -0.6$ – -0.7), and either temperature, precipitation, or both variables were no longer significant conditional on the other being included in the model.

	Probability of Success (*n*=440 total pairs)				**Fledgling Output** (*n*=306 successful pairs)				**Annual Nest Success** (*n*=15 years)					**Mean Fledglings per Breeding Pair** (*n*=16 years)				
Environmental metric	**ΔAICc**	**Rank**	**β**	**P**	**ΔAICc**	**Rank**	**β**	**P**	**ΔAICc**	**Rank**	**β**	**R^2**	**P**	**ΔAICc**	**Rank**	**β**	**R^2**	**P**
Precipitation																		
Breeding season (Mar-Jun)	0	1	0.16	<0.0001	9.31	5	0.03	0.0066	0.17	2	0.04	0.35	0.0193	5.19	5	0.22	0.40	0.0084
Cold season (Nov-Mar)	4.82	6	0.11	0.0005	13.59			0.08	3.20				0.09	6.81	6	0.17	0.34	0.0183
Winter, breeding season (Nov-Jun)	1.85	3	0.10	0.0001	3.32	4	0.02	0.0002	1.70	5	0.02	0.28	0.0406	2.86	4	0.15	0.48	0.0028
Previous monsoon (Jul-Sep)	17.25			0.31	16.63			0.90	6.71				0.92	12.74				0.46
Temperature																		
Breeding season mean maximum (Mar-Jun)	1.82	2	-0.50	<0.0001	16.19			0.50	0	1	-0.12	0.36	0.0178	8.84	7	-0.57	0.25	0.0498
Palmer Modified Drought Index																		
June	2.27	4	0.16	0.0001	1.69	3	0.04	<0.0001	0.95	3	0.04	0.32	0.0282	0.83	2	0.28	0.54	0.0011
Cold season (Nov-Mar)	6.55	7	0.22	0.0010	0	1	0.07	<0.0001	3.02		0.05		0.08	2.44	3	0.41	0.50	0.0023
Winter, breeding season (Nov-Jun)	3.20	5	0.21	0.0002	0.74	2	0.05	<0.0001	1.48	4	0.05	0.29	0.0365	0	1	0.38	0.57	0.0008

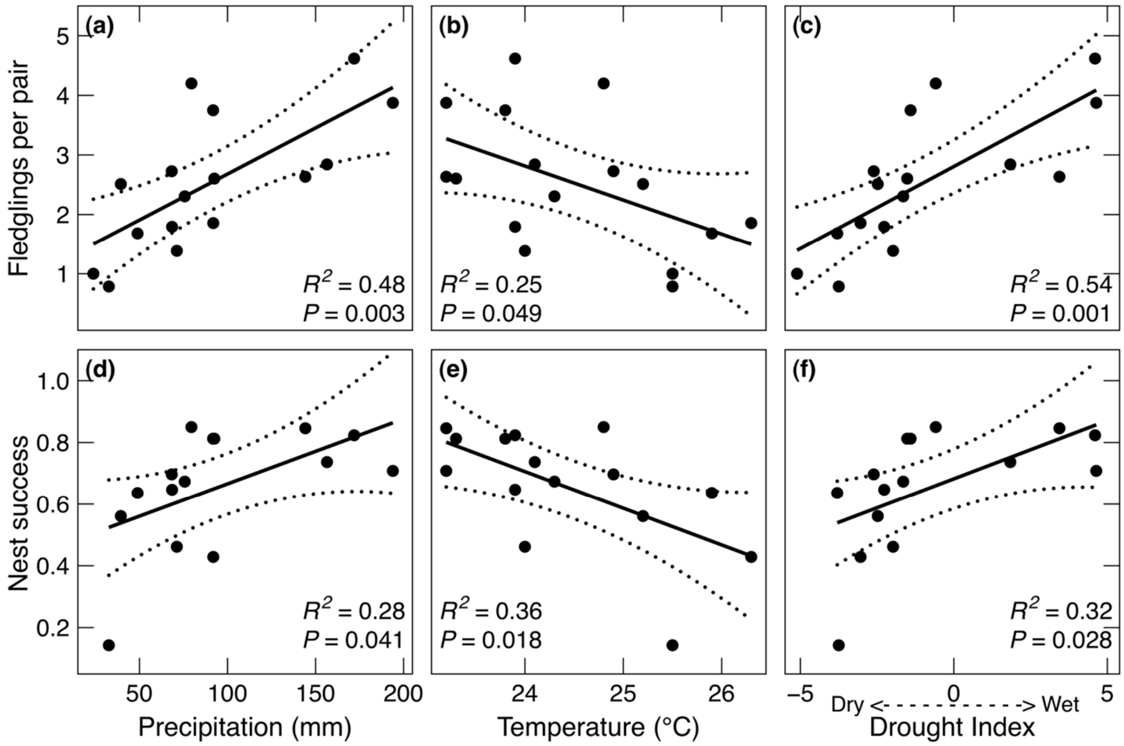

Fig. 3 Annual variation in mean fledglings per breeding pair (a,b,c) and nest success (d,e,f) as a function of winter through breeding season (Nov-Jun) precipitation, breeding season (Mar-Jun) mean maximum temperature, and June Palmer Modified Drought Index.

Effects of air temperature on population and reproductive trends

Study site air temperature has trended upward, with mean annual temperature increasing 1.3 ± 0.6°C since 1983. Mean temperature during the Burrowing Owl breeding season showed a fairly steady increase over time, with a 1.7 ± 1.1°C increase in mean March-June temperature since 1983 (Fig. 1a). June mean temperature showed an even greater increase of 2.5 ± 1.5°C since 1983. During the 16-year study period, June mean temperature showed a significant upward trend, increasing 2.4 ± 2.0°C since 1998. Temperature variability was negatively correlated with the owl population and reproduction fluctuations. The linear relationship between number of breeding pairs and previous breeding season (Mar-Jun) mean maximum temperature showed a decrease in population size following an increase in temperature ($R^2 = 0.55$, $P = 0.0011$) (Fig. 2b). For each 1°C increase in temperature, the breeding population was predicted to decrease by 11.3 pairs in the following year, or to decrease by 25.0% per year when modelling yearly population change ($R^2 = 0.37$, $P = 0.0169$). Fitting a multiple regression model with the important predictors of population size of previous two years of precipitation and previous breeding season mean maximum temperature, both predictors were significant and together explained significantly more of the variability than either simple regression model ($P < 0.0001$). Adding temperature to the precipitation model improved fit to the data (ΔAICc = 3.5). Precipitation in combination with temperature predicted unique variance in population size, and the combined effect explained 86.5% of the variation in population (Table 1).

To account for the potential confounding effect of the decline in owl population and increase in temperature over time, the year effect was added as a covariate in the temperature model. However when temperature and year were both included, the year effect was no longer significant. The annual variation in population size was explained sufficiently by temperature variability, and the relationship explained 31.2% more of the population variation than the simple trend model. The year effect also was no longer significant when added to the model with temperature and precipitation, indicating the population decline over 16 years was largely explained by climate variability. The climate model described 60.9% more of the variation in population size then the trend model.

Analyses of Burrowing Owl reproduction as a function of temperature indicate reproductive rates decreased as breeding season temperature increased. There was a negative linear relationship between mean maximum March-June temperature and mean fledglings per pair ($R^2 = 0.25$, $P = 0.0498$) and annual nest success ($R^2 = 0.36$, $P = 0.0178$) that predicted a 0.6 decrease in productivity and an 11.9% decrease in success with a 1°C increase in mean maximum breeding season temperature (Fig. 3b,e). In addition, modelling results of each nest attempt (n=440) showed a significant negative effect of warmer temperatures on the probability of success. For every 1°C increase in mean maximum March-June temperature, the log-odds of success decreased by a factor of 0.50 ($P < 0.0001$). Nest success was equally well explained by November-June precipitation and March-June mean maximum temperature (ΔAICc = 0.04) (Table 2). For each tested metric of reproduction, models including both precipitation and temperature improved fit to the data (i.e. AICc decreased), however explanatory variables were correlated (r = -0.6 – -0.7), and either temperature, precipitation, or both variables were no longer significant conditional on the other being included in the model.

Effects of drought on population and reproductive trends

Annual PMDI for the study site trended downward during the period from 1983-2013. The index showed a significant drying trend for the winter through the breeding season (Nov-Jun), with a decrease in values of -3.3 ± 2.7 since 1983. June PMDI also indicated significant drying, decreasing -4.6 ± 3.5 in index values. The 48-month period ending in June 2013 was the driest in the period of record. The Burrowing Owl population size fluctuated in relation to annual mean PMDI with a one year time lag, with population size decreasing after periods of drought ($R^2 = 0.73$, $P < 0.0001$) (Fig. 2c, Table 1). In addition, the direction and magnitude of annual percentage population change was positively correlated with previous year mean PMDI ($R^2 = 0.59$, $P = 0.0008$).

Drought severity also had an impact on Burrowing Owl reproduction. Annual productivity and success varied in a similar pattern as mean winter through breeding season (Nov-Jun) PMDI, with a decrease in mean fledglings per pair ($R^2 = 0.57$, $P = 0.0008$) and nest success ($R^2 = 0.29$, $P = 0.0365$) when drought increased in severity (Fig. 3c,f). The PMDI is a cumulative index. In order to compare singular values, June trends were examined as an indicator of breeding season drought. June PMDI represents June drought severity, but the value also captures the integrated effects of drought severity during the preceding months. The relationships between June PMDI and productivity ($R^2 = 0.54$, $P = 0.0011$) and nest success ($R^2 = 0.32$, $P = 0.0282$) were significant, and indicate reproductive rates decreased as breeding season drought increased in severity. In addition, the probability of nest success varied with the level of drought severity, with drought significantly lowering the probability of nest success. For each unit wetter in June PMDI, the log-odds of success increased by a factor of 0.21 (n=440, $P = 0.0001$). Examining fledgling counts from each successful pair, fewer fledglings were expected with higher drought severity (n=306, $P < 0.0001$) (Table 2).

Changes in prey availability

Arthropod biomass collected in pitfall traps varied monthly and annually from 2008-2013. In general, low biomass was recorded in April ($\overline{x} = 1.7$g), May ($\overline{x} = 3.4$g), and June ($\overline{x}$ = 4.6g), and a higher amount was recorded in July ($\overline{x}$ = 7.9g) and August ($\overline{x}$ = 8.3g).

Prey abundance was positively correlated with Burrowing Owl reproductive rates. The linear relationships between prey biomass collected from May-June and mean fledglings per breeding pair (R^2 = 0.69, P = 0.0396) and the probability of nest success (P = 0.0153) were significant, and indicate a decrease in reproductive output can be expected when there was a decrease in prey abundance during the nestling stage of the breeding season. For each 1g increase in May-June prey biomass, mean fledglings per pair increased by 0.09 and the log-odds of nest success increased by a factor of 0.11.

Arthropod abundance varied in relation to precipitation variability. Analysis showed cold season precipitation was an important predictor of arthropod prey availability. The linear relationship between November-March precipitation and May-June prey biomass showed an increase in prey abundance with increased cold season precipitation (R^2 = 0.71, P = 0.0345). With a 10 mm increase in cold season precipitation, arthropod biomass was predicted to increase by 3.0g. Prey abundance was not associated with amount of rainfall during the previous monsoon season (Jul–Sep) (P = 0.42).

Changes in body mass

Body mass of adult and juvenile Burrowing Owls declined significantly over the study period (Fig. 4a). Examining data of single measurements of mass of individuals during the breeding season, adult male body mass decreased -1.3g each year from 1998-2012 (n=107, P = 0.0001). After removing laying females, adult female body mass decreased -1.5g each year from 1997-2012 (n=59, P = 0.0053). Male mass on arrival to the breeding grounds significantly declined, with a loss in arrival mass of -1.9g each year since 1998 (*n*=44, $P = 0.0056$), however female arrival mass showed no trend over time (*n*=15, $P = 0.22$). We found no evidence for a change in structural size, through change in wing length (Male: *n*=21, $P = 0.71$; Female: *n*=14, $P = 0.53$) or tarsus length (Male: *n*=24, $P = 0.08$; Female: *n*=10, $P = 0.13$). Examining mass of juveniles that were fully grown but pre-fledge (28-44 days old) showed a loss of -1.3g each year from 2005-2012 (*n*=252, $P = 0.0419$). Modelling juvenile mass as a function of year, date, and age to control for juvenile growth with age, mass decreased -1.3g each year since 2005 with a 20.0% mass loss on average over 8 years ($P = 0.0318$).

Adults also lost mass as the breeding season progressed, both in owls actively provisioning young and in owls without young (Fig. 4b). The seasonal decline in mass occurred irrespective of sex or parental effort, however body mass significantly differed between owls provisioning and owls without young. Model estimates of average mass of provisioning females was 14.5g less ($P = 0.0011$) and males was 9.7g less ($P = 0.0038$) than mass of owls not feeding young. After controlling for the seasonal decline in mass, there was still a significant decrease in adult breeding mass from 1997-2012. For each increase in year, mass decreased -1.2g for females ($P = 0.0314$) and -0.9g for males ($P = 0.0130$), with an average loss in body mass of 10.9% for females and 7.9% for males over the study period.

Adult body mass varied in relation to variation in precipitation, temperature, and drought. Examining the weather variables important in explaining the fluctuations in both owl reproduction and prey availability, adult mass decreased with decreasing winter and breeding season precipitation (Nov-Mar: $P < 0.0001$, Nov-Jun: $P < 0.0001$), increasing breeding season maximum temperature (Mar-Jun mean max: $P = 0.0001$), and increasing drought severity (June PMDI: $P < 0.0001$, Nov-Jun PMDI: $P < 0.0001$). Accounting for the loss of mass over time by including the year effect in the climate models, both the declining trend and the climate effects remained significant. In addition to climate variation, variation in prey availability had an effect on owl mass. The linear relationship between mean annual juvenile owl mass and arthropod biomass collected May-June showed a 1g increase in prey abundance during the nestling stage was associated with a 1.6g increase in mean juvenile owl mass ($R^2 = 0.81$, $P = 0.0374$).

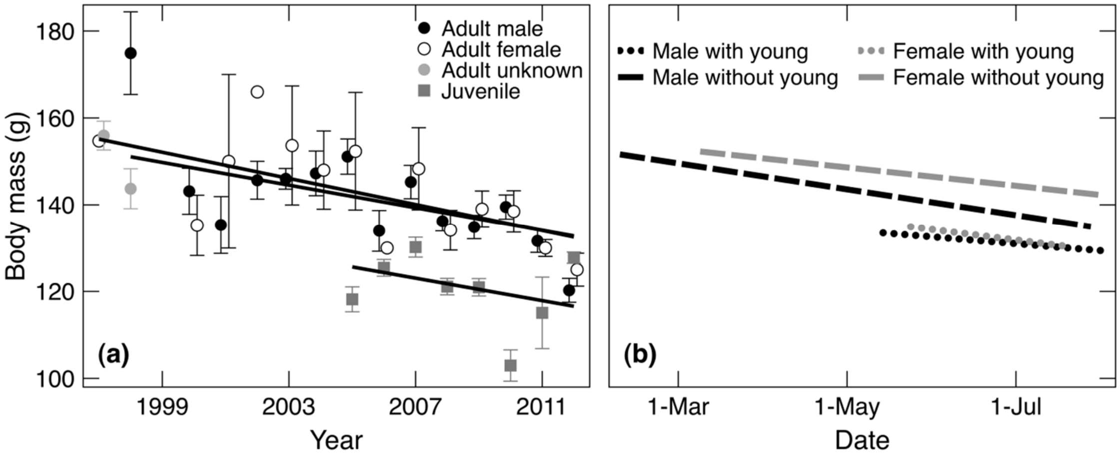

Fig. 4 Trends in Burrowing Owl body mass from 1997-2012: (a) annual loss of mass for adult males, adult females, and juveniles shown with significant linear trends on all records, annual means and standard errors (laying females removed, juvenile subset of fully grown yet not fledged 28-44 days old, and unknown sex included in grey for 1997-1998 to illustrate range of weights recorded during early years of the study when not all sexes were identified); and (b) seasonal loss of mass for adults (laying females removed) actively provisioning young and without young. Controlling for the seasonal decline, adult male mass decreased 7.9% (mass = 1961.10 – 0.90 year – 0.08 date, $P < 0.0001$, n=107) and adult female mass decreased 10.9% (mass = 2557.31 – 1.20 year – 0.08 date, $P = 0.0052$, n=59) on average over the study period. Controlling for juvenile growth with age, nestling mass decreased 20.0% (mass = 2566.01 – 1.26 year + 0.18 date + 1.41 age, $P < 0.0001$, n=252) on average over 8 years.

Changes in breeding phenology

Temporal trends in reproductive activity from 2005-2013 indicate that the breeding phenology of Burrowing Owls is increasingly delayed (Fig. 5). Examining all records of individual owls and first nesting attempts, male arrival to the breeding grounds delayed by 25.1 days on average since 2005 ($n = 230$ owls, $P < 0.0001$). Mean pair formation delayed by 22.0 days ($n = 211$ pairs, $P = 0.0001$), and mean nest initiation delayed by 13.0 days ($n = 217$ nests, $P = 0.0004$). Hatch dates also showed a delaying trend, with hatching occurring 9.4 days later on average over 9 years ($n = 177$ clutches, $P = 0.0377$). Using the first quartile as an index of the start of breeding, first arrival (1.3 days/yr, $P = 0.0236$), pair formation (1.5 days/yr, $P = 0.0060$), nest initiation (1.6 days/yr, $P = 0.0006$), and hatch dates (1.6 days/yr, $P = 0.0045$) showed significant delays over 9 years. Delaying trends were also significant when examining the interquartile range subset to remove effects of early and late breeders (male arrival: 3.1 days/yr, $P < 0.0001$; pair formation: 2.6 days/yr, $P < 0.0001$; nest initiation: 1.8 days/yr, $P < 0.0001$; hatch: 1.4 days/yr, $P = 0.0035$).

Modelling the effect of delayed phenology on reproductive success indicated that the probability of nest success decreased as the breeding season progressed. Each of the tested temporal variables were important predictors of success, with the probability of success decreasing with a later arrival ($P < 0.0001$), pair formation ($P = 0.0004$), nest initiation ($P = 0.0018$), or hatch date ($P = 0.0135$). For each day that arrival, pair formation, nest initiation or hatch were delayed, the log-odds of success decreased by a factor of 0.03. There was also a significant negative effect of delayed breeding phenology on fledgling output. Mean fledglings per pair decreased with a later male arrival ($R^2 =$

0.66, $P = 0.0146$), pair formation ($R^2 = 0.74$, $P = 0.0064$), and nest initiation ($R^2 = 0.66$, $P = 0.0137$). Examining fledgling counts, the number of fledglings from each successful pair decreased with later nest initiation ($P < 0.0001$) or hatch date ($P < 0.0001$).

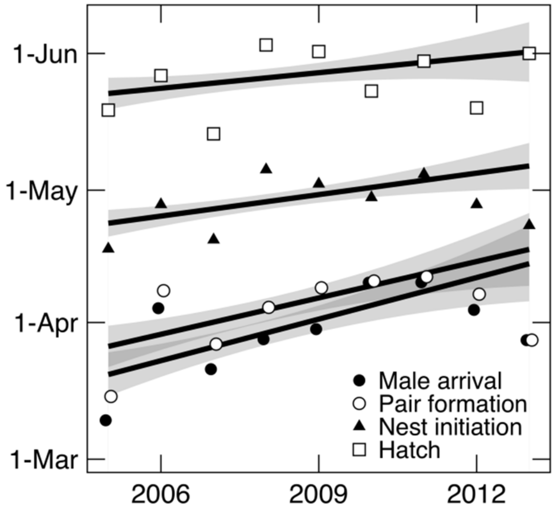

Fig. 5 Significant temporal trends in phenological events, including delays in male arrival (date = 76.06 + 3.14 year, $P < 0.0001$, n=230), pair formation (date = 82.83 + 2.75 year, $P = 0.0001$, n=211), nest initiation (date = 111.88 + 1.62 year, $P = 0.0004$, n=217), and hatch dates (date = 141.75 + 1.18 year, $P = 0.0377$, n=177), shown with annual means and the linear trends and 95% confidence intervals from all temporal records.

Discussion

Our results show a strong effect of rapid warming and drought on Burrowing Owl population dynamics and reproduction in our study population in central New Mexico. We show a dramatic population decline, a decline in productivity and nest success, as well as significant changes in body mass in both breeders and nestlings, and an unexpected delay in breeding phenology. The strong association between climate variation and owl reproductive and population trends suggests bottom-up effects on both the breeding and wintering grounds are driving Burrowing Owl demographics in this region. As Burrowing Owls are opportunistic predators and show a numerical and functional response to prey availability, they are strongly affected by seasonal and inter-annual changes in precipitation and air temperature. Because our results are significantly related to increased air temperature and aridity, we believe that they importantly signal the negative consequences for avian populations in arid landscapes under future climate change scenarios. In the following paragraphs we discuss each of our results in detail and highlight the importance of this work for understanding how increased water and heat stress may affect birds in arid ecosystems.

Decline in population size and reproductive output

We found a rapid decline in Burrowing Owl population size where the population crashed from 49 breeding pairs to a single pair over a period of six years, and our results show that this decline is strongly linked to extreme drought conditions (Fig. 2). Whether this decline represents an actual loss of breeding pairs or their movement to other regions is currently unknown. Anecdotal observations commonly suggest decreasing population trends for Burrowing Owls in New Mexico, however there are few data that document these observations and provide strong insight into the current status of this species. North American Breeding Bird Survey data show a slightly decreasing, though non-significant trend in the state from 2002-2012 (Sauer *et al.*, 2014). Although population declines can often be attributed to habitat loss, the available habitat on our site changed minimally during the study period. Our analyses indicate that the temporal variation in population size over 16 years is strongly correlated to the combined effects of precipitation and temperature variability and not to habitat loss.

Declining abundance of grassland (Bridges *et al.*, 2001; Niemuth *et al.*, 2008; Macías-Duarte *et al.*, 2009; Albright *et al.*, 2010) and arid zone (Wichmann *et al.*, 2003; Flesch, 2014) birds has been associated with drought, and this impact may be greatest in dry ecoregions where primary productivity is controlled by precipitation (Albright *et al.*, 2010). Burrowing Owls show a numerical response to prey availability through changes in demographic parameters and/or immigration rates. Small mammal irruptions have led to subsequent increases in Burrowing Owl populations (Jaksic *et al.*, 1997; Poulin *et al.*, 2001), and decreased prey abundance and poor reproduction are associated with the decline in our population. Drought duration and severity are both likely important (George *et al.*, 1992; Albright *et al.*, 2010), and the cumulative effect of the recent multi-year drought may have led to the near total loss of owls on this site.

Increasing temperature has also been implicated in declining avian populations, primarily through impacts on reproduction. Decreased reproduction due to a decline or mismatch with food resources resulting from increased temperatures can subsequently impact avian population density (Anders & Post, 2006; Both *et al.*, 2010; Pearce-Higgins *et al.*, 2010; Flesch, 2014). Increased temperatures can also impact fitness and behavior, and direct effects of heat stress and extreme temperature events have caused mass mortality in birds, with catastrophic mortality events predicted to occur more frequently with climate warming (McKechnie & Wolf, 2010). Reproductive rates of the study population declined significantly over time, and our most recent measures of productivity ($\bar{x}_{2010\text{-}2013} = 1.3$ young/nest) and nest success ($\bar{x}_{2010\text{-}2012} = 34.4\%$) were below the range of estimates reported in other studies. Values for reproductive success in other western studies ranged 63-92% (Botelho & Arrowood, 1996; Lutz & Plumpton, 1999; Restani *et al.*, 2001; Griebel & Savidge, 2007; Lantz & Conway, 2009; Berardelli *et al.*, 2010), with one reporting lower success of 47% (Bayless & Beier, 2011). Given these results, the rates of reproductive success in our population are very low. Mean annual productivity and nest success, as well as the expected count of fledglings and the probability of success also decreased with decreasing precipitation, increasing temperature, and increasing drought severity (Fig. 3). Our results suggest that the proximate cause of reduced reproductive output is the linkage between low winter precipitation and May-June arthropod abundance. Other studies also found food limitation has the greatest effect during the nestling phase of the owl's breeding cycle (Wellicome *et al.*, 2013). Abundant food resources are associated with increased productivity (Wellicome, 2000; Gervais *et al.*, 2006), fledgling size (Wellicome, 2000; Wellicome *et al.*, 2013), and high post-fledging survival (Todd *et al.*, 2003). In supplemental feeding experiments, food limitation decreased reproductive performance through poor nestling growth and low survival rates, with almost all mortality attributable to starvation (Wellicome, 2000; Haley & Rosenberg, 2013; Wellicome *et al.*, 2013). High rates of nest failure may also cause within season dispersal and low return rates to previously occupied nest sites by adult birds as well (Ronan, 2002; Catlin *et al.*, 2005; Rosier *et al.*, 2006), with serious negative population impacts. For avian populations already in decline, this trend is predicted to continue under the increasing stressors of rapid climate change (Møller *et al.*, 2008).

Delayed phenology

Our arrival and breeding phenology data for Burrowing Owls show large, significant delays over 9 years ranging from 25.1 days for arrival to 9.4 days for hatch (Fig. 5), with significant negative consequences for reproduction. Our observations of delayed breeding may represent a long-term trend for owls in central New Mexico. While the start of egg laying between 2005-2013 shifted from the first to the third week of April, a study conducted between 1970-1971 observed laying starting in the third week of March (Martin, 1973). These data suggest a longer term trend towards later breeding for Burrowing Owl populations in this region. Our results contrast with most avian studies that show the vast majority of bird species with shifting phenology trend toward earlier arrival (Butler, 2003; Cotton, 2003; Hüppop & Hüppop, 2003) and egg laying (Crick *et al.*, 1997; Brown *et al.*, 1999; Dunn & Winkler, 1999; Fletcher *et al.*, 2013). Although uncommon, delays have also been reported (Mason, 1995; Oglesby & Smith, 1995; Peñuelas *et al.*, 2002; Laaksonen *et al.*, 2006; Wanless *et al.*, 2009), and have been attributed to winter drought (Gordo *et al.*, 2005) and population declines (Lee *et al.*, 2011). Avian response to climate change may be species-specific (Vegvari *et al.*, 2010) and not all species exhibit changing phenology despite regional climatic changes (Bradley *et al.*, 1999; Wilson & Arcese, 2003). With warmer spring temperatures, earlier green up of vegetation, and earlier spring emergence of insects, bird populations may suffer if their timing does not shift concurrently. Adverse effects on abundance and reproduction may occur due to asynchrony or mismatch with food resources (Visser *et al.*, 1998, 2006; Pearce-Higgins *et al.*, 2005; Both *et al.*, 2010). Møller *et al.* (2008) showed that migratory birds with stable or increasing population trends had advanced spring arrival while declining species had delayed or had not shown a phenological response to climate warming. Significantly delayed phenology may also be indicative of declining populations (Miller-Rushing *et al.*, 2008; Lee *et al.*, 2011).

Consequences of later breeding have been well documented in birds and include reduced clutch size (Dijkstra *et al.*, 1982; Murphy, 1986; Perrins & McCleery, 1989; Rowe *et al.*, 1994), nesting success (Perrins, 1970; Newton & Marquiss, 1984), and nestling body condition (Møller, 1994; Griebel & Savidge, 2003; Smith & Moore, 2005). Studies reporting effects of timing of reproduction for Burrowing Owls have produced conflicting results. With later arrival and breeding, smaller clutch sizes and fewer fledglings have been reported (Wellicome, 2000; Griebel & Savidge, 2007); in contrast, Lantz and Conway (2009) reported an increased probability of nest survival with later breeding. Our results indicate that delayed breeding has a negative effect on reproduction, with both fledgling output and the probability of nest success decreasing as the breeding season progresses.

The delayed breeding observed in our Burrowing Owl population may be related to poor body condition or habitat condition on the wintering grounds as discussed below. In migratory birds, winter habitat quality influences arrival on the breeding grounds, with early arriving birds wintering in high quality habitat (Norris *et al.*, 2004) and maintaining higher body condition (Marra *et al.*, 1998; Gill *et al.*, 2001). Wintering grassland birds are also strongly influenced by precipitation (Macías-Duarte *et al.*, 2009), and the impacts of drought and reduced prey availability may contribute to declining body condition and survival on the owl's wintering grounds. Food-limited birds may delay their spring migration due to low body mass (Studds & Marra, 2007). The effects of decreased rainfall and food availability on the wintering grounds can carry-over to the breeding season by delaying arrival and breeding and lowering reproductive rates (Saino *et al.*, 2004; Studds & Marra, 2011; Rockwell *et al.*, 2012), and precipitation effects in dry wintering regions may be particularly important in explaining delayed phenology (Gordo *et al.*, 2005). Where Burrowing Owls from the study population winter and the conditions on the wintering sites are currently unknown, but our data show potentially adverse effects of these sites on arrival condition.

Loss of body condition during the breeding cycle

We found significant declines in adult body mass over time, with male breeding mass declining by 7.9% and female breeding mass declining by 10.9% over 16 years (Fig. 4a). These trends indicate that owls from more recent breeding seasons are in poorer body condition than observed in earlier years of the study and have important implications for survivorship and reproduction. Reduced mass and adult body condition has been linked to smaller clutch sizes, lowered parental investment and provisioning rates, less productivity and success, and lowered fecundity and survival (Drent & Daan, 1980; Martin, 1987; Price *et al.*, 1988; Rowe *et al.*, 1994). Male owls also arrived on the breeding grounds in poorer condition whereas female arrival mass showed no change, however the sample size of females trapped on arrival (n=15) may have been too small to detect a trend. The poor condition of males on arrival provides additional support for food limitation or poor habitat quality on the wintering grounds. In addition to the loss of condition over time, owls also lost mass during the breeding cycle (Fig. 4b). This mass loss is partially an expected seasonal trend as peak adult energy demand occurs during the nestling and fledgling stages of reproduction in many species (Klomp, 1970; Bryant, 1979; Newton *et al.*, 1983), however this additional decline in condition in combination with the lighter breeding masses is likely to importantly impact the survival and return rates of adult birds in our population. The trade-off between maintaining physical condition and parental effort has been well documented in birds (Nur, 1984; Martin, 1987; Owens & Bennett, 1994), and this cost of reproduction is well illustrated by our data: male owls actively provisioning young are approximately 10g (6.4%) lighter than owls without young; females under the same circumstances are 15g (9.4%) lighter than their non-reproductive counterparts (Fig. 4b).

After accounting for juvenile growth with age, nestling Burrowing Owls also show a loss of body mass, with a mass loss of 20.0% over 8 years (Fig. 4a). Nestling body condition has important future fitness implications and is positively associated with survival (Todd *et al.*, 2003; Schwagmeyer & Mock, 2008), subsequent reproduction (Lindström, 1999) and population growth (Todd *et al.*, 2003). As juvenile Burrowing Owls have high mortality in general (Todd *et al.*, 2003; Davies & Restani, 2006), impacts of this significant loss of mass may be substantial. Although brood size is inversely correlated to nestling growth rates and body condition (Landry, 1979; Dijkstra *et al.*, 1990; Bellocq, 1997), Burrowing Owls on this site are having smaller broods yet the nestlings are in poor condition. Concomitant with the poor adult condition, the production of fewer young of poorer quality indicates a reduced investment in reproduction. This conflicts, in part, with the loss of condition during the breeding season observed in adults and suggests that they are still investing heavily in reproduction at the potential cost of future survival. We also found a seasonal decline in mass in adults that were not feeding young, which may reflect insufficient food resources to support either reproduction or body condition. These impacts of breeding season food limitation on body condition may be intensified by winter food limitation (Martin, 1987); therefore the decline in physical condition may reflect poor breeding as well as wintering habitat quality.

Despite the strong downward trends, body mass varied with fluctuations in winter precipitation and breeding season temperature. Drought and increasing temperatures may impact owl body condition through impacts on prey abundance. Our results show arthropod abundance during the nestling period has a significant, positive effect on juvenile body mass, and the correlation between low winter precipitation and low insect abundance may explain some of the loss of adult and juvenile condition. In addition, increased temperatures can negatively impact body condition due to the physiological demands of temperature regulation. In an arid zone passerine, Cunningham et al. (2013) showed fledging body mass decreased with an increase in days during nestling growth with maximum temperatures above a critical threshold of 33°C, which authors attributed to a decrease in parental provisioning and direct physiological costs of high temperatures. Although the possibility of threshold temperatures for Burrowing Owls has not been studied, temperatures regularly exceed 33°C during the nestling period in this region of New Mexico. Nest burrows provide juvenile owls with a refuge from thermal stress associated with high air temperatures, but adults face increased predation risk when inside burrows from nest predators including badgers, coyotes, and snakes. As a consequence, during the nestling period adults experience high solar heat loads because they spend most of their time alert and outside of the burrow in full sunlight or in partial shade of sparse grassland vegetation. Burrowing Owls in Canada significantly reduced nest defense behaviors at high air temperatures of 23-31°C (Fisher *et al.*, 2004), suggesting thermal constraints at maximum temperatures routine in the desert southwest may be considerable.

Furthermore, recent studies have suggested burrow-dwelling might not provide sufficient thermal refuge with increasing temperatures, and shallow desert burrows can be quite hot (Walsberg, 2000; Tracy & Walsberg, 2002; Moses *et al.*, 2012). Indeed, higher summer daytime temperatures have negative effects on survival of the banner-tailed kangaroo rat (*Dipodomys spectabilis*), a nocturnal burrower found in central New Mexico (Moses *et al.*, 2012). Burrow temperatures in the owl nest chambers have not been described, however, air temperatures at a depth of 30cm within nest burrows did not differ from the burrow entrance (Coulombe, 1971). Therefore it is possible that both adult and nestling owls will experience significant and increasing heat stress with climate warming with potential fitness costs.

Conclusions

Burrowing Owls breeding in arid zones may be highly vulnerable to climate change. In the population we monitored, Burrowing Owl population size and reproductive dynamics are strongly associated with climate. We found rapid and profound decreases in population size with increasing air temperatures, decreased precipitation and severe drought. In addition, we found that owls were arriving and breeding later and that the arrival and breeding masses of owls were significantly lower as the study progressed. These and other factors, such as reduced prey abundance and increased physiological stress produced a significant decline in the reproductive output of

Burrowing Owls. Not only did owls produce fewer young, but nestling mass declined during the study period. Our results demonstrate the importance of resource limitation in driving population processes in arid environments. Bottom-up effects of precipitation on prey abundance limit the reproductive potential of owls at our site. The strength of the bottom-up controls may be more pervasive during periods of extreme resource limitation, such as during the recent severe drought, leading to the sharp decreases in reproductive output and population size in recent years and additional constraints on owl fitness and survival.

Taken together, the Burrowing Owl population and reproductive declines we have described have serious implications for population persistence. Reduced nestling body mass leads to decreased survival probability, poor adult condition, and decreased populations in subsequent seasons. Poor adult condition leads to decreased reproduction and survival, further influencing the future population size. The relatively poor body condition on arrival and delayed breeding may suggest owls are occupying less than optimal habitats on the wintering grounds. Reduced body condition may be a cause and/or a consequence of the delayed breeding. Owls in poor condition on the winter grounds may delay migration and therefore breeding arrival. Delayed breeding is shifting the nestling period into the hottest part of the summer, leading to increased physiological costs and potentially a poorer body condition. The fitness costs of later breeding include: fewer young, reduced nest success, and poor condition. All of these negative trends indicate environmental conditions both on the breeding and wintering grounds are stressing Burrowing Owls populations.

Our site-specific climate records for the last 16 years show increasing temperatures throughout the year with significant warming in June, and large annual and seasonal variability in precipitation accompanied by severe drought, with the period between July 2009 and June 2013 the driest 48-month period in the instrumental record. Although air temperatures are projected to continue to increase, trends for precipitation are likely to vary and projections are uncertain. Nonetheless, increased evapotranspiration associated with warming and decreased winter precipitation will likely lead to increased aridity in the southwestern U.S. by the mid-21st century (Seager & Vecchi, 2010; Gutzler & Robbins, 2011). An increasingly warm and dry climate may contribute to this species' decline, and may already be a driving force of decline in the desert southwest. Of further concern, Burrowing Owls are severely declining at the northern periphery of their range. If climate effects are contributing to declines in the southern arid zone, we may see larger declines range-wide in the future.

References

Albright TP, Pidgeon AM, Rittenhouse CD et al. (2010) Effects of drought on avian community structure. *Global Change Biology*, **16**, 2158–2170.

Anders AD, Post E (2006) Distribution-wide effects of climate on population densities of a declining migratory landbird. *Journal of Animal Ecology*, **75**, 221–227.

Andreadis KM, Lettenmaier DP (2006) Trends in 20th century drought over the continental United States. *Geophysical Research Letters*, **33**, L10403.

Bale JS, Masters GJ, Hodkinson ID et al. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.

Barnett TP, Pierce DW, Hidalgo HG et al. (2008) Human-induced changes in the hydrology of the western United States. *Science*, **319**, 1080–1083.

Bayless TA, Beier P (2011) Occurrence and habitat characteristics of Burrowing Owl nests in Gunnison's prairie dog colonies of Northeastern Arizona. *Journal of the Arizona-Nevada Academy of Sciences*, **42**, 65–74.

Bellocq MI (1997) Ecology of the Burrowing Owl in agrosystems of Central Argentina. *Journal of Raptor Research Report*, **9**, 52–57.

Berardelli D, Desmond MJ, Murray L (2010) Reproductive success of Burrowing Owls in urban and grassland habitats in southern New Mexico. *The Wilson Journal of Ornithology*, **122**, 51–59.

Bolger DT, Patten MA, Bostock DC (2005) Avian reproductive failure in response to an extreme climatic event. *Oecologia*, **142**, 398–406.

Botelho ES, Arrowood PC (1996) Nesting success of Western Burrowing Owls in natural and human-altered environments. In: *Raptors in human landscapes: adaptations to built and cultivated environments* (eds Bird DM, Varland DE, Negro JJ), pp. 61–68. Academic Press, San Diego, California.

Both C, Van Turnhout C, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1259–1266.

Bradley NL, Leopold AC, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 9701–9704.

Bridges AS, Peterson MJ, Silvy NJ, Smeins FE, Wu XB (2001) Differential influence of weather on regional quail abundance in Texas. *Journal of Wildlife Management*, **65**, 10–18.

Brown JL, Li S, Bhagabati N (1999) Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 5565–5569.

Bryant DM (1979) Reproductive costs in the House Martin (*Delichon urbica*). *Journal of Animal Ecology*, **48**, 655–675.

Butler CJ (2003) The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis*, **145**, 484–495.

Catlin DH, Rosenberg DK, Haley KL (2005) The effects of nesting success and mate fidelity on breeding dispersal in Burrowing Owls. *Canadian Journal of Zoology*, **83**, 1574–1580.

Cayan DR, Das T, Pierce DW, Barnett TP, Tyree M, Gershunov A (2010) Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21271–21276.

Conway CJ, Simon JC (2003) Comparison of detection probability associated with Burrowing Owl survey methods. *Journal of Wildlife Management*, **67**, 501–511.

Cotton PA (2003) Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 12219–12222.

Coulombe HN (1971) Behavior and population ecology of the Burrowing Owl, *Speotyto cunicularia*, in the Imperial Valley of California. *The Condor*, **73**, 162–176.

Crawford CS (1988) Surface-active arthropods in a desert landscape: influences of microclimate, vegetation, and soil texture on assemblage structure. *Pedobiologia*, **32**, 373–385.

Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526.

Cunningham SJ, Martin RO, Hojem CL, Hockey P a R (2013) Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. *Plos One*, **8**, e74613.

Davies JM, Restani M (2006) Survival and movements of juvenile burrowing owls during the postfledging period. *The Condor*, **108**, 282–291.

Diffenbaugh NS, Giorgi F, Pal JS (2008) Climate change hotspots in the United States. *Geophysical Research Letters*, **35**, L16709.

Dijkstra C, Vuursteen L, Daan S, Masman D (1982) Clutch size and laying date in the kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis*, **124**, 210–213.

Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra M (1990) Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology*, **59**, 269–285.

Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.

Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of Tree Swallows throughout North America. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 2487–2490.

Ernest SKM, Brown JH, Parmenter RR (2000) Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos*, **88**, 470–482.

Fisher RJ, Poulin RG, Todd LD, Brigham RM (2004) Nest stage, wind speed, and air temperature affect the nest defence behaviours of burrowing owls. *Canadian Journal of Zoology*, **82**, 707–713.

Flesch AD (2014) Spatiotemporal trends and drivers of population dynamics in a declining Sonoran Desert predator. *Biological Conservation*, **175**, 110–118.

Fletcher K, Howarth D, Kirby A, Dunn R, Smith A (2013) Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis*, **155**, 456–463.

George TL, Fowler AC, Knight RL, McEwen LC (1992) Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications*, **2**, 275–284.

Gervais JA, Hunter CM, Anthony RG (2006) Interactive effects of prey and p,p'-DDE on Burrowing Owl population dynamics. *Ecological Applications*, **16**, 666–677.

Gill JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, Sutherland WJ (2001) The buffer effect and large-scale population regulation in migratory birds. *Nature*, **412**, 436–438.

Gordo O, Brotons L, Ferrer X, Comas P (2005) Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology*, **11**, 12–21.

Griebel RL, Savidge JA (2003) Factors related to body condition of nestling Burrowing Owls in Buffalo Gap National Grassland, South Dakota. *The Wilson Bulletin*, **115**, 477–480.

Griebel RL, Savidge JA (2007) Factors influencing Burrowing Owl reproductive performance in contiguous shortgrass prairie. *Journal of Raptor Research*, **41**, 212–221.

Guthery FS, Rybak AR, Fuhlendorf SD, Hiller TL, Smith SG, Puckett WH, Baker RA (2005) Aspects of the thermal ecology of bobwhites in north Texas. *Wildlife Monographs*, 1–36.

Gutzler DS (2013) Regional climatic considerations for borderlands sustainability. *Ecosphere*, **4**, 1–12.

Gutzler DS, Robbins TO (2011) Climate variability and projected change in the western United States: regional downscaling and drought statistics. *Climate Dynamics*, **37**, 835–849.

Haley KL, Rosenberg DK (2013) Influence of food limitation on reproductive performance of Burrowing Owls. *Journal of Raptor Research*, **47**, 365–376.

Holroyd GL, Trefry HE, Duxbury JM (2010) Winter destinations and habitats of Canadian Burrowing Owls. *Journal of Raptor Research*, **44**, 294–299.

Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 233–240.

Jaksic FM, Silva SI, Meserve PL, Gutierrez JR (1997) A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos*, **78**, 341–354.

Johnson NK (1994) Pioneering and natural expansion of breeding distributions in western North American birds. *Studies in Avian Biology*, **15**, 27–44.

Jones J, Doran PJ, Holmes RT (2003) Climate and food synchronize regional forest bird abundances. *Ecology*, **84**, 3024–3032.

Klomp H (1970) The determination of clutch size in birds: a review. *Ardea*, **58**, 1–124.

Laaksonen T, Ahola M, Eeva T, Vaisanen RA, Lehikoinen E (2006) Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos*, **114**, 277–290.

Landry RE (1979) *Growth and development of the Burrowing Owl (*Athene cunicularia*).* MS Thesis, California State University.

Lantz SJ, Conway CJ (2009) Factors affecting daily nest survival of Burrowing Owls within black-tailed prairie dog colonies. *Journal of Wildlife Management*, **73**, 232–241.

Lee SD, Ellwood ER, Park S, Primack RB (2011) Late-arriving Barn Swallows linked to population declines. *Biological Conservation*, **144**, 2182–2187.

Lima M, Ernest SKM, Brown JH, Belgrano A, Stenseth NC (2008) Chihuahuan Desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. *Ecology*, **89**, 2594–2603.

Lindström J (1999) Early development and fitness in birds and mammals. *Trends in Ecology and Evolution*, **14**, 343–348.

Lutz R., Plumpton DL (1999) Philopatry and nest site reuse by Burrowing Owls: implications for productivity. *Journal of Raptor Research*, **33**, 149–153.

Macías-Duarte A, Montoya AB, Méndez-González CE, Rodríguez-Salazar JR, Hunt WG, Krannitz PG (2009) Factors influencing habitat use by migratory grassland birds in the state of Chihuahua, Mexico. *The Auk*, **126**, 896–905.

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.

Martin DJ (1973) Selected aspects of Burrowing Owl ecology and behavior. *The Condor*, **75**, 446–456.

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.

Mason CF (1995) Long-term trends in the arrival dates of spring migrants. *Bird Study*, **42**, 182–189.

Masters GJ, Brown VK, Clarke IP, Whittaker JB, Hollier JA (1998) Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology*, **23**, 45–52.

McKechnie AE, Wolf BO (2010) Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, **6**, 253–256.

Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st Century. *Science*, **305**, 994–997.

Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P (2008) Bird migration times, climate change, and changing population sizes. *Global Change Biology*, **14**, 1959–1972.

Møller AP (1994) Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology*, **35**, 115–122.

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 16195–16200.

Moses MR, Frey JK, Roemer GW (2012) Elevated surface temperature depresses survival of banner-tailed kangaroo rats: will climate change cook a desert icon? *Oecologia*, **168**, 257–268.

Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*, **155**, 123–132.

Murphy MT (1986) Temporal components of reproductive variability in Eastern Kingbirds (*Tyrannus tyrannus*). *Ecology*, **67**, 1483–1492.

New Mexico Burrowing Owl Working Group (NMBOWG) (2005) Recommended Burrowing Owl survey and monitoring protocol. http://www.nmburrowingowl.com.

NOAA National Climatic Data Center (2013) Available at http://www.ncdc.noaa.gov.

Newton I, Marquiss M (1984) Seasonal trend in the breeding performance of Sparrowhawks. *Journal of Animal Ecology*, **53**, 809–829.

Newton I, Marquiss M, Village A (1983) Weights, breeding, and survival in European Sparrowhawks. *The Auk*, **100**, 344–354.

Niemuth ND, Solberg JW, Shaffer TL (2008) Influence of moisture on density and distribution of grassland birds in North Dakota. *The Condor*, **110**, 211–222.

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 59–64.

Nur N (1984) The consequences of brood size for breeding Blue Tits I. Adult survival, weight change and the cost of reproduction. *Journal of Animal Ecology*, **53**, 479–496.

Oglesby RT, Smith CR (1995) Climate change in the northeast. In: *Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems.* (eds LaRoe ET, Farris GS, Puckett CE, Doran PD, Mac MJ), pp. 390–391. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Owens IPF, Bennett PM (1994) Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society B: Biological Sciences*, **257**, 1–8.

Pearce-Higgins JW, Yalden DW, Whittingham MJ (2005) Warmer springs advance the breeding phenology of Golden Plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia*, **143**, 470–476.

Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW (2010) 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*, **16**, 12–23.

Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531–544.

Perrins CM (1970) Timing of birds' breeding seasons. *Ibis*, **112**, 242–255.

Perrins CM, McCleery RH (1989) Laying dates and clutch size in the Great Tit. *The Wilson Bulletin*, **101**, 236–253.

Du Plessis KL, Martin RO, Hockey PAR, Cunningham SJ, Ridley AR (2012) The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, **18**, 3063–3070.

Polis GA, Hurd SD, Jackson CT, Piñero FS (1997) El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology*, **78**, 1884–1897.

Poulin RL, Todd D, Haug EA, Millsap BA, Martell MS (2011) Burrowing Owl (*Athene cunicularia*). In: The Birds of North America Online (ed Poole A). Cornell Lab of Ornithology, Ithaca.

Poulin RG, Wellicome TI, Todd LD (2001) Synchronous and delayed numerical responses of a predatory bird community to a vole outbreak on the Canadian prairies. *Journal of Raptor Research*, **35**, 288–295.

Price T, Kirkpatrick M, Arnold SJ (1988) Directional selection and the evolution of breeding date in birds. *Science*, **240**, 798–799.

Priest JE (1997) Age identification of nestling Burrowing Owls. *Journal of Raptor Research Report*, **9**, 125–127.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Restani M, Rau LR, Flath DL (2001) Nesting ecology of Burrowing Owls occupying black-tailed prairie dog towns in southeastern Montana. *Journal of Raptor Research*, **35**, 296–303.

Rockwell SM, Bocetti CI, Marra PP (2012) Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (Setophaga kirtlandii). *The Auk*, **129**, 744–752.

Romero-Lankao P, Smith JB, Davidson DJ et al. (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B. Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (eds Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, Maccracken S, Mastrandrea PR, White LL), Cambridge, United Kingdom and New York, NY, USA.

Ronan NA (2002) *Habitat selection, reproductive success, and site fidelity of Burrowing Owls in a grassland ecosystem*. MS Thesis, Oregon State University.

Rosier JR, Ronan NA, Rosenberg DK (2006) Post-breeding dispersal of Burrowing Owls in an extensive California grassland. *American Midland Naturalist*, **155**, 162–167.

Rowe L, Ludwig D, Schluter D (1994) Time, condition, and the seasonal decline of avian clutch size. *The American Naturalist*, **143**, 698–722.

Saino N, Szep T, Romano M, Rubolini D, Spina F, Møller AP (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters*, **7**, 21–25.

Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJ, Link WA (2014) *The North American Breeding Bird Survey, results and analysis 1966 - 2012*. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schwagmeyer PL, Mock DW (2008) Parental provisioning and offspring fitness: size matters. *Animal Behaviour*, **75**, 291–298.

Seager R, Vecchi GA (2010) Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21277–21282.

Seager R, Ting M, Held I et al. (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, **316**, 1181–1184.

Sheffield J, Wood EF (2008) Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Climate Dynamics*, **31**, 79–105.

Silva SI, Lazo I, Silva-Aranguiz E, Jaksic FM, Meserve PL, Gutierrez JR (1995) Numerical and functional response of Burrowing Owls to long-term mammal fluctuations in Chile. *Journal of Raptor Research*, **29**, 250–255.

Sinervo B, Méndez-de-la-Cruz F, Miles DB et al. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, **328**, 894–899.

Smith MD, Conway CJ (2007) Use of mammal manure by nesting burrowing owls: a test of four functional hypotheses. *Animal Behaviour*, **73**, 65–73.

Smith RJ, Moore FR (2005) Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology*, **57**, 231–239.

Studds CE, Marra PP (2007) Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, Setophaga ruticilla. *Climate Research*, **35**, 115–122.

Studds CE, Marra PP (2011) Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3437–3443.

Thibault KM, Ernest SKM, White EP, Brown JH, Goheen JR (2010) Long-term insights into the influence of precipitation on community dynamics in desert rodents. *Journal of Mammalogy*, **91**, 787–797.

Todd LD, Poulin RG, Wellicome TI, Brigham RM (2003) Post-fledging survival of Burrowing Owls in Saskatchewan. *Journal of Wildlife Management*, **67**, 512–519.

Tracy RL, Walsberg GE (2002) Kangaroo rats revisited: re-evaluating a classic case of desert survival. *Oecologia*, **133**, 449–457.

Vegvari Z, Bokony V, Barta Z, Kovacs G (2010) Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biology*, **16**, 1–11.

Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, **265**, 1867–1870.

Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, **147**, 164–172.

Walsberg GE (2000) Small mammals in hot deserts: some generalizations revisited. *BioScience*, **50**, 109–120.

Wanless S, Frederiksen M, Walton J, Harris MP (2009) Long-term changes in breeding phenology at two seabird colonies in the western North Sea. *Ibis*, **151**, 274–285.

Weiss JL, Castro CL, Overpeck JT (2009) Distinguishing pronounced droughts in the southwestern United States: seasonality and effects of warmer temperatures. *Journal of Climate*, **22**, 5918–5932.

Wellicome TI (2000) *Effects of food on reproduction in burrowing owls (*Athene cunicularia*) during three stages of the breeding season*. PhD Thesis, University of Alberta.

Wellicome TI, Todd LD, Poulin RG, Holroyd GL, Fisher RJ (2013) Comparing food limitation among three stages of nesting: supplementation experiments with the burrowing owl. *Ecology and Evolution*, **3**, 2684–2695.

Wichmann MC, Jeltsch F, Dean WRJ, Moloney KA, Wissel C (2003) Implication of climate change for the persistence of raptors in arid savanna. *Oikos*, **102**, 186–202.

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 of the United States of America*, **100**, 11139–11142.

Wolf B (2000) Global warming and avian occupancy of hot deserts; a physiological and behavioral perspective. *Revista Chilena de Historia Natural*, **73**, 395–400.

Zarn M (1974) *Habitat Management Series for Unique or Endagered Species: Burrowing Owl*. Bureau of Land Management, Denver, CO.