Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest

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Abstract

Avian communities of arid ecosystems may be particularly vulnerable to global climate change due to the magnitude of projected change for desert regions and the inherent challenges for species residing in 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 because avian responses to climate change have primarily been studied in the relatively mesic northern temperate regions. We studied the effects of increasing air temperature and aridity on a Burrowing Owl (*Athene cunicularia*) population in the southwestern United States from 1998 to 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 to 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 7.9% mass in adult males and 10.9% mass in adult females over 16 years, and a loss of 20.0% mass in nestlings over 8 years. Taken together, these population and reproductive trends have serious implications for local population persistence. The southwestern United States 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.

Keywords: *Athene cunicularia*, body condition, Burrowing Owl, delayed breeding, nest success, population declines, precipitation, prey abundance

Introduction

Assessing species vulnerability to climate change is increasingly important for conservation and the maintenance of biodiversity, particularly for species already experiencing population declines. Although numerous studies have documented climate impacts on avian reproductive phenology and demography (Parmesan, 2006; Knudsen *et al.*, 2011; Jenouvrier, 2013), most of this research has been conducted on species residing in the relatively mesic northern temperate regions (Gordo, 2007). Few studies provide longer-term insight into the responses of arid-zone birds to rapid warming and increased drought severity and frequency (Brown *et al.*, 1999; Li & Brown, 1999; Altwegg & Anderson, 2009; Flesch, 2014), and the biotic and abiotic pressures confronting species in arid vs. north-temperate zones

may differ greatly. The southwestern United States has been identified as a climate change 'hotspot', with projections of increasing air temperature, aridity, and interannual variability (Diffenbaugh *et al.*, 2008; Seager & Vecchi, 2010; Gutzler & Robbins, 2011). Along with higher temperatures, winter precipitation is projected to decrease, and extreme events including droughts 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; Barnett *et al.*, 2008; Gutzler, 2013). In New Mexico, for example, 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). Interestingly, how these climatic changes will

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affect bird populations and communities in arid regions is poorly understood.

Increased heat and water stress can impact bird communities directly during extreme events such as heat waves and droughts and indirectly through influences on habitat quality or prey availability. The quantity and seasonal timing of precipitation strongly influence primary productivity in arid ecosystems (Sala *et al.*, 1988; Muldavin *et al.*, 2008), and vegetative growth and seed production importantly influence population growth of consumers. High air temperatures and heat stress elicit behavioral and physiological responses in desert birds, with potential impacts on fitness and 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. As arid regions are characterized by low and highly variable precipitation, high air temperatures, and high solar heat loads, increasingly extreme conditions may make arid-zone birds more vulnerable to extirpation by disrupting reproductive cycles or through direct mortality (McKechnie & Wolf, 2010).

Given these increasing stressors and the potential direct and indirect effects on avian predators, we examined the effects of rising air temperatures and drought on a Burrowing Owl (*Athene cunicularia hypugaea*) population in the desert southwest United States over a 16-year period. Western Burrowing Owls are a small (~150 g), ground-dwelling species that inhabits North American deserts and grasslands. They are unique among owls as they are active 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 Burrowing Owl populations have declined 1.1% per year since the 1960s (Sauer *et al.*, 2014). 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 prey abundance (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. To assess fine-scale population responses, owls were intensively monitored and reproductive activity quantified from 1998 to 2013 on a site in central New Mexico. We examined relationships between 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 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) How do temporal trends in phenology affect reproductive output? (3) Has the local population size declined during periods of increased air temperature and drought? (4) How 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? and (6) Have changes in nestling body 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 1573–2433 m and contains approximately 15 000 ha of suitable owl habitat. 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*, and *Pleuraphis jamesii*. Dominant shrubs include *Gutierrezia sarothrae*, *Cylindropuntia imbricata*, *Yucca* spp., *Opuntia* spp., *Atriplex canescens*, *Salsola kali*, and *Krascheninnikovia lanata*. Burrowing Owls on KAFB nest in Gunnison's prairie dog (*Cynomys gunnisoni*) 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 monthly 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 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 winter and spring, typically in low amounts.

In central New Mexico, Burrowing Owls are migratory, and the nesting period typically runs from March to June. Owls arrive on the breeding grounds late February through early April and 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. Burrowing Owls are thought to winter in the southwestern United States 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 were conducted mid-February through August from 1998 to 2013 throughout suitable grassland habitat to locate all nonbreeding and breeding Burrowing Owls in the study area. Standardized surveys conducted 5 days per week 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 2 weeks and were monitored every 1–3 days. Owls were trapped and color-banded, allowing us to identify adult movements, gather accurate counts of juveniles, and determine natal recruitment (proportion of banded juveniles returning the subsequent year) and adult return rates (proportion of banded adults returning the subsequent year). 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 fledging ≥1 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 to investigate failure and possible causes. Arrival, pair formation, nest initiation, and hatch dates were recorded 2005–2013.

To analyze prey abundance, pitfall trap arrays were installed in three sites used by breeding Burrowing Owls, and sampling occurred monthly April–August to assess the surface-active arthropod population. From 2008 to 2013, we used trapping methods modified from Smith & Conway (2007). At each site, four traps were opened for a 7-day period, producing 12 samples monthly. To increase arthropod capture, a second method was added 2010–2013 using methods modified from Crawford (1988). At each site, 20 traps were opened for a 48-h period, producing 60 samples monthly. Samples were dried, weighed, and identified, and total biomass was 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 to 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 analyses included temperature (monthly mean maximum), precipitation (monthly total), and 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 arthropod prey abundance, and to examine change over time in breeding pairs, nest success, productivity, body mass, and breeding phenology. Model fit was assessed using plot diagnostics. Significant correlations were reevaluated with residual regression of detrended bird metrics and climate variables to assess whether correlations were potentially due to co-occurring long-term trends (Grosbois *et al.*, 2008). 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. Generalized linear mixed models were used to analyze individual counts of number of fledglings from each successful pair (Poisson distribution, log link function) and binary success/failure from each breeding pair (binomial distribution, logit link function) as a function of precipitation, temperature, PMDI, prey abundance, and breeding phenology as fixed effects with year as a random effect. Akaike's Information Criterion corrected for small sample size (AICc) was used to compare alternative models. Explanatory variables were evaluated for pairwise collinearity using Pearson correlation and were used in multiple regression if correlation was relatively low ($|r| < 0.5$, Tables S1 and S2). Statistical analyses were performed in R version 3.0.1 (R Core Team, 2013); mixed models were fitted using the package lme4 (Bates *et al.*, 2014).

We used climate data from 1983 to 2013 as a current representative of local climatology to examine recent variability and trends. Linear trend models were used to calculate trend estimates and 95% confidence intervals. Residual diagnostic plots were used to check adequacy of 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 population size (number of breeding pairs and yearly percentage change), productivity (annual mean fledglings per breeding pair and fledgling counts from each successful pair), nest success (annual proportion of breeding pairs fledging ≥1 young and success/failure from each breeding pair), and body mass. Productivity and nest success variables were selected to examine both annual and individual metrics of reproduction. 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, 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 as a function of annual precipitation and drought from the two previous years and previous year breeding season (March–June) mean maximum temperature. Reproductive rates may show an immediate or delayed response, so we tested various seasonal and interannual 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), nonmonsoon season (November–June), cold season (November–March), and owl breeding season and tested the effects of mean maximum temperature during the breeding season. In addition, we examined the effects of nest predation and recruitment rates as these variables may influence Burrowing Owl population dynamics (James *et al.*, 1997; Todd *et al.*, 2003).

Results

Breeding trends

From 1998 to 2013, 440 Burrowing Owl pairs were recorded on the study site. Annual population size ranged from a maximum of 52 pairs in 1998 to a minimum of 1 pair in 2013 ($\bar{x}$ = 27.5 ± 15.0 SD; Fig. 1a). Although there was annual variation, the population declined 98.1% over 16 years (P = 0.0340), with a pronounced decline since 2008 from 49 pairs to 1 pair. 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 ± 1.1 SD; Fig. 1b) and significantly declined since 1998 (P = 0.0398), with a sharp decline since 2007. To examine nest success trends, we removed 2013 where 100% success was misleading as it resulted from only one pair. From 1998 to 2012, success ranged from 85.0% to 14.3% ($\bar{x}$ = 65.6% ± 19.4 SD; Fig. 1c), with a significant decline since 1998 (P = 0.0016) and a sharp decline since 2007.

The observed annual growth rate of the population varied from 0.14 to 1.71 ($\bar{x}$ = 0.87 ± 0.40 SD), and growth rate increased with increasing population size (0.02 growth per pair, R^2 = 0.43, P = 0.0076). The proportion of juvenile owls recruited into the local
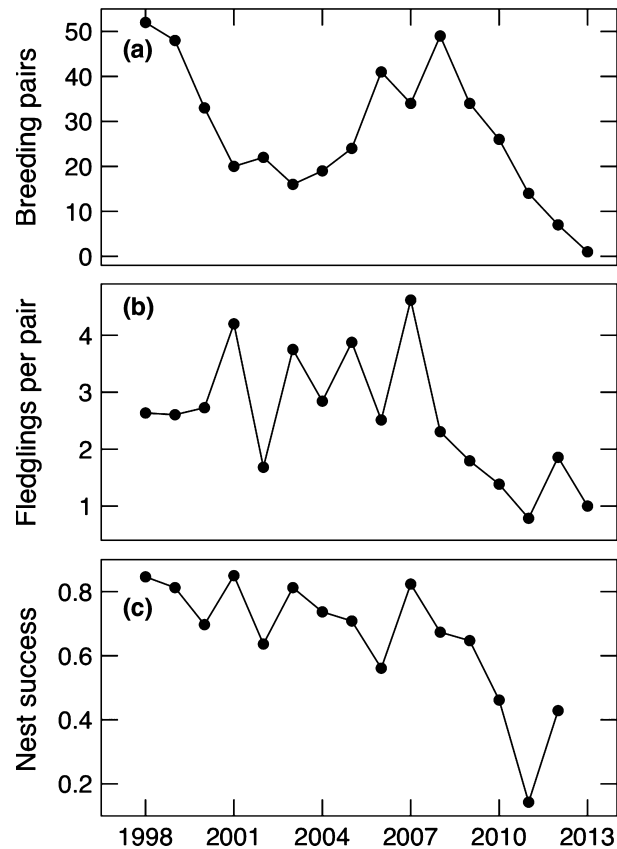

Fig. 1 Trends in Burrowing Owl (a) population size, (b) mean fledglings per breeding pair, and (c) nest success.

population the following year ranged from 0% to 18.2% ($\bar{x}$ = 7.6% ± 6.1 SD), and annual adult return rates ranged from 19.2% to 75.0% ($\bar{x}$ = 44.7% ± 18.7 SD). Natal recruitment (P = 0.36) and adult return (P = 0.17) showed no trend over time. Variation in natal recruitment and adult return rates did not explain annual population change (natal return: R^2 = 0.18, P = 0.14; adult return: R^2 = 0.09, P = 0.31), and population size was not related to proportion of adult and yearling return (R^2 = 0.07, P = 0.33). Of the nests that failed, the proportion of failure attributed to predation ranged annually from 22% to 100% ($\bar{x}$ = 64.0% ± 22.9 SD) and exhibited no trend over time (P = 0.70). There was no relationship between annual nest success and proportion of failure due to predation (R^2 = 0.05, P = 0.44), and previous year predation rates did not explain annual population change (R^2 = 0.02, P = 0.63) or population size (R^2 = 0.04, P = 0.47).

Effects of precipitation on population and reproductive trends

Climate data for the study site showed a significant decline in nonmonsoonal (November–June)

precipitation, decreasing -61.7 ± 55.9 mm from 1983 to 2013 (Fig. 2b). Monsoon precipitation exhibited no trend and showed large annual variability ranging from 35.8 to 213.2 mm ($\bar{x} = 106.3$ mm ± 43.6 SD). The Burrowing Owl population varied in relation to variation in annual precipitation, with population size following precipitation fluctuations with a 1- to 2-year lag. Both previous year's precipitation ($R^2 = 0.47$, $P = 0.0032$) and 2 year's previous precipitation ($R^2 = 0.72$, $P < 0.0001$) were significant predictors when testing effects of detrended precipitation on detrended population, indicating the correlation did not result from co-occurring trends and the variation around the overall decline in population was accounted for by precipitation variability. The strength of support of the model improved when both rainfall timescales were included (ΔAICc > 4.5), and the additive effect of rainfall during the two previous years explained 79.0% of the variation in population ($P < 0.0001$; Table 1). We also modeled yearly percentage population change in an effort to explain population fluctuations, as this approach accounted for nonindependence of population size among years. The direction and amount of annual change was positively correlated with precipitation variability during the two previous years ($R^2 = 0.34$, $P = 0.0220$; Fig. 3a).

Examining the candidate set of explanatory models for the reproductive parameters, reproductive rates were positively associated with breeding season (March–June) precipitation and cold season (November–March) precipitation; previous monsoon rainfall (July–September) was not associated with reproduction (Table 2). To include both significant predictors and remove their temporal overlap, reproductive rates were correlated with the broader timescale of winter through breeding season (November–June) precipitation. November–June rainfall was included in competitive models (ΔAICc < 2.9) predicting each tested metric of reproduction. The linear relationships between November–June precipitation and mean fledglings per pair ($R^2 = 0.48$, $P = 0.0028$) and annual nest success ($R^2 = 0.28$, $P = 0.0406$) predicted productivity to increase 0.2 and success to increase 2.1% for each 10 mm increase in precipitation (Fig. 4a, d). The relationships between detrended precipitation and productivity ($R^2 = 0.42$, $P = 0.0063$) and success ($R^2 = 0.33$, $P = 0.0247$) showed additional support for precipitation effects independent of precipitation and reproduction declines. Modeling success/failure from each of the 440 total nest attempts, the probability of success increased as precipitation increased ($P = 0.0056$). Examining fledgling counts from each of the 306 successful pairs, fledgling output increased with increasing precipitation ($P = 0.0483$).

Effects of air temperature on population and reproductive trends

Study site air temperature trended upward, with mean annual temperature increasing 1.3 ± 0.6 °C from 1983 to 2013. Mean temperature during the Burrowing Owl breeding season (March–June) increased 1.7 ± 1.1 °C (Fig. 2a). June mean temperature increased 2.5 ± 1.5 °C since 1983 and showed a significant upward trend during the 16-year study period, increasing 2.4 ± 2.0 °C since 1998. Temperature variability was negatively correlated with the owl population and reproductive fluctuations. Accounting for concurrent temperature and population trends through regression of detrended variables, population size decreased with increased previous breeding season (March–June) mean maximum temperature ($R^2 = 0.44$, $P = 0.0054$), independent of any long-term trends in temperature or population size. Modeling yearly population change predicted population size to decrease 25.0% following each 1 °C increase in temperature ($R^2 = 0.37$, $P = 0.0169$; Fig. 3b). Fitting a multiple regression model with the important detrended population predictors of detrended previous 2 years of precipitation and previous breeding season mean maximum temperature, both predictors were significant and in combination predicted unique variance in population. The combined
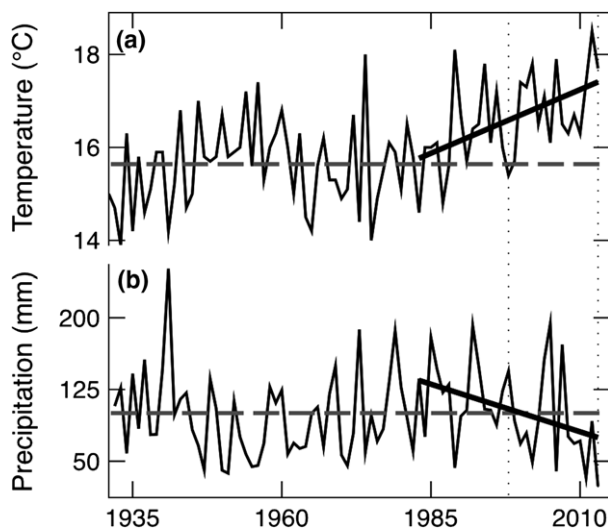

Fig. 2 Climatic trends for the central New Mexico study site from 1931 to 2013 of variables important for Burrowing Owl reproduction: annual breeding season (March–June) mean temperature (a) and winter through breeding season (November–June) precipitation (b) relative to the observed 1961–1990 climatology (dashed gray), with significant 1983–2013 trends (solid black) and vertical dotted lines outlining the 1998–2013 study period.

Table 1 Linear regression summaries and AICc ranking for tested models examining the effects of selected climate variables on Burrowing Owl population size and population change from 1998 to 2013, and climate effects after removing trends in population and environmental variables. 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

| Environmental metric	Population size (n = 16 years)					Population change (n = 15 years)					Detrended population size and environmental metrics (n = 16 years)				
	ΔAICc	Rank	β	R^2	P	ΔAICc	Rank	β	R^2	P	ΔAICc	Rank	β	R^2	P
Precipitation															
Previous year annual	16.19	6	1.67	0.53	0.0014	8.18	5	3.51	0.30	0.0358	16.27	5	1.42	0.47	0.0032
Two year's previous annual	9.79	4	2.00	0.69	<0.0001	9.46				0.07	6.15	3	1.80	0.72	<0.0001
Combined two previous years' annual	3.47	2	1.19	0.79	<0.0001	7.18	3	2.12	0.34	0.0220	1.60	2	1.08	0.79	<0.0001
Temperature															
Previous breeding season mean maximum (March–June)	15.70	5	−11.30	0.55	0.0011	6.62	2	−25.04	0.37	0.0169	17.38	6	−9.58	0.44	0.0054
Palmer Modified Drought Index															
Previous year annual	7.33	3	6.32	0.73	<0.0001	0	1	15.09	0.59	0.0008	6.56	4	5.63	0.71	<0.0001
Precipitation + Temperature															
Combined two previous years' annual + Previous breeding season mean maximum (March–June)	0	1	0.93, −5.17	0.86	<0.0001	8.06	4	1.31, −16.86	0.46	0.0251	0	1	0.90, −4.08	0.85	<0.0001
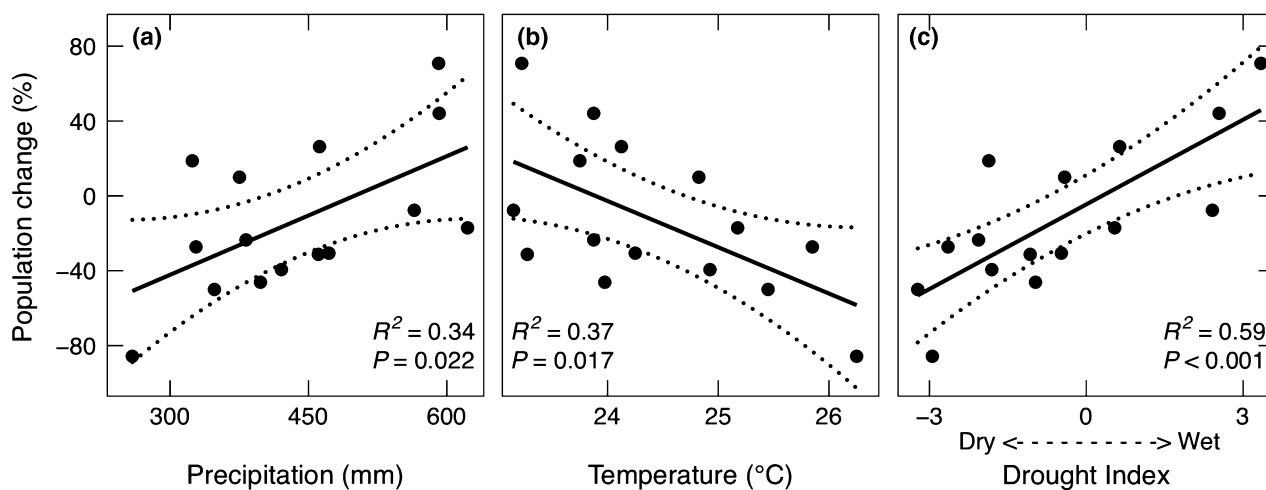
Fig. 3 Annual population change as a function of (a) previous 2 years of precipitation, (b) previous breeding season (March–June) mean maximum temperature, and (c) previous year mean Palmer Modified Drought Index.

effects of temperature and precipitation explained 84.8% of the variation in population ($P < 0.0001$; Table 1), indicating the temporal variation in population over 16 years was largely explained by climate variability.

Analyses of reproduction as a function of temperature indicate reproductive rates decreased as breeding season temperature increased. The negative linear relationships between mean maximum March–June temperature and mean fledglings per pair ($R^2 = 0.25$, $P = 0.0498$) and annual nest success ($R^2 = 0.36$, $P = 0.0178$) predicted productivity to decrease 0.6 and success to decrease 11.9% for each 1 °C increase in temperature (Fig. 4b, e). Removing temporal trends in reproduction and temperature, the relationship between detrended temperature and productivity was not significant ($P = 0.19$) and success was marginal ($P = 0.0510$) in the presence of a trend effect. Modeling success/failure of each nest attempt ($n = 440$), the probability of success decreased with increased temperatures ($P = 0.0042$). Success probability was equally well explained by November–June precipitation and March–June mean maximum temperature (ΔAICc = 0.62; 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; Table S2), 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 toward more negative values from 1983 to 2013. The index showed a significant drying trend for the winter through breeding season (November–June), decreasing -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 June 2013 was the driest in the period of record. The Burrowing Owl population fluctuated in relation to annual mean PMDI with a 1-year time lag, with population size decreasing after periods of drought. The relationship between detrended PMDI and detrended population ($R^2 = 0.71$, $P < 0.0001$) showed drought variability explained a significant amount of annual variation in population, independent of temporal trends. In addition, the direction and magnitude of annual population change was positively correlated with previous year mean PMDI ($R^2 = 0.59$, $P = 0.0008$; Fig. 3c, Table 1).

Drought severity also impacted reproduction (Table 2), with mean fledglings per pair ($R^2 = 0.57$, $P = 0.0008$) and annual nest success ($R^2 = 0.29$, $P = 0.0365$) decreasing when winter through breeding season (November–June) mean PMDI increased in severity. PMDI is a cumulative index. 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 success ($R^2 = 0.32$, $P = 0.0282$) indicate reproductive rates decreased as breeding season drought increased in severity (Fig. 4c, f). Relationships between detrended PMDI and detrended productivity ($R^2 = 0.47$, $P = 0.0035$) and success ($R^2 = 0.32$, $P = 0.0281$) showed further support for drought effects after accounting for trends over time. In addition, increased drought

Table 2 Generalized linear model and mixed model summaries and AICc ranking for tested models examining the effects of selected climate variables on Burrowing Owl reproductive parameters, including success/failure from each breeding pair, annual nest success, and annual mean fledglings per breeding pair, from 1998 to 2013. Success/Failure and Fledgling Output models include year as a random effect. 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

| Environmental metric	Success/Failure (n = 440 total pairs)				Fledgling output (n = 306 successful pairs)				Annual nest success (n = 15 years)					Mean fledglings per pair (n = 16 years)				
	ΔAICc	Rank	β	P	ΔAICc	Rank	β	P	ΔAICc	Rank	β	R^2	P	ΔAICc	Rank	β	R^2	P
Precipitation																		
Breeding season (March–June)	0	1	0.16	0.0016	3.62			0.21	0.17	2	0.04	0.35	0.0193	5.19	5	0.22	0.40	0.0084
Cold season (November–March)	3.13	6	0.10	0.0214	3.35			0.18	3.20				0.09	6.81	6	0.17	0.34	0.0183
Winter, breeding season (November–June)	1.57	4	0.09	0.0056	1.65	4	0.02	0.0483	1.70	5	0.02	0.28	0.0406	2.86	4	0.15	0.48	0.0028
Previous monsoon (July–September)	7.48			0.94	4.89			0.63	6.71				0.92	12.74				0.46
Temperature																		
Breeding season mean maximum (March–June)	0.95	2	−0.51	0.0042	5.11			0.89	0	1	−0.12	0.36	0.0178	8.84	7	−0.57	0.25	0.0498
Palmer Modified Drought Index																		
June	1.22	3	0.16	0.0049	0.79	3	0.04	0.0255	0.95	3	0.04	0.32	0.0282	0.83	2	0.28	0.54	0.0011
Cold season (November–March)	3.42	7	0.22	0.0277	0.01	2	0.07	0.0151	3.02				0.08	2.44	3	0.41	0.50	0.0023
Winter, breeding season (November–June)	1.74	5	0.21	0.0074	0	1	0.06	0.0150	1.48	4	0.05	0.29	0.0365	0	1	0.38	0.57	0.0008
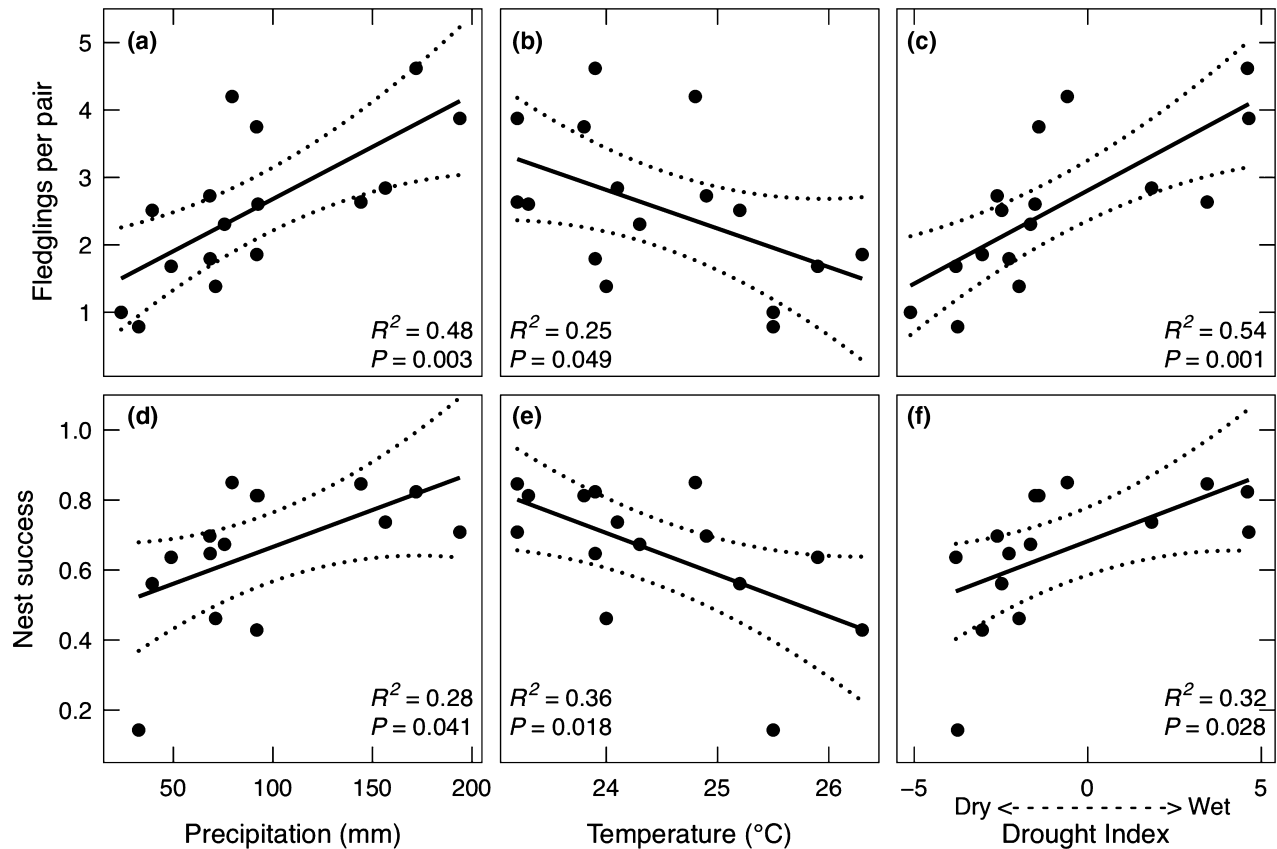
Fig. 4 Annual variation in mean fledglings per breeding pair (a, b, c) and nest success (d, e, f) as a function of winter through breeding season (November–June) precipitation, breeding season (March–June) mean maximum temperature, and June Palmer Modified Drought Index.

severity significantly lowered the probability of nest success ($n = 440$ pairs, $P = 0.0049$) and number of fledglings produced ($n = 306$ successful pairs, $P = 0.0255$).

Changes in prey availability

Arthropod biomass collected in pitfall traps varied monthly and annually 2008–2013. In general, low biomass was recorded in April ($\bar{x} = 1.7$ g $\pm$ 1.3 SD), May ($\bar{x} = 3.4$ g $\pm$ 2.6 SD), and June ($\bar{x} = 4.6$ g $\pm$ 3.7 SD), and a higher amount was recorded in July ($\bar{x} = 7.9$ g $\pm$ 5.5 SD) and August ($\bar{x} = 8.3$ g $\pm$ 3.3 SD). Prey abundance was positively correlated with Burrowing Owl reproduction. The relationships between arthropod biomass collected May–June and mean fledglings per breeding pair ($R^2 = 0.69$, $P = 0.0396$) and probability of nest success ($P = 0.0153$) indicate reproductive output decreased with decreased prey abundance during the nestling stage of the breeding season. Mean fledglings per pair increased 0.09 for each 1 g increase in prey.

Cold season precipitation was an important predictor of prey availability. The positive linear relationship between November–March precipitation and May–June arthropod biomass predicted prey to increase 3.0 g with each 10 mm increase in precipitation ($R^2 = 0.71$, $P = 0.0345$). Prey abundance was not associated with rainfall during the previous monsoon season (July–September; $P = 0.42$).

Changes in body mass

Body mass of adult and juvenile Burrowing Owls declined significantly over the study period (Fig. 5a). Examining data on single body mass measurements of individuals during the breeding season, adult male mass decreased −1.3 g annually 1998–2012 ($n = 107$, $P = 0.0001$). Removing laying females, adult female mass decreased −1.5 g annually 1997–2012 ($n = 59$, $P = 0.0053$). Male mass on arrival to the breeding grounds declined −1.9 g annually ($n = 44$, $P = 0.0056$); female arrival mass showed no trend ($n = 15$, $P = 0.22$). We found no evidence for a change in structural size,
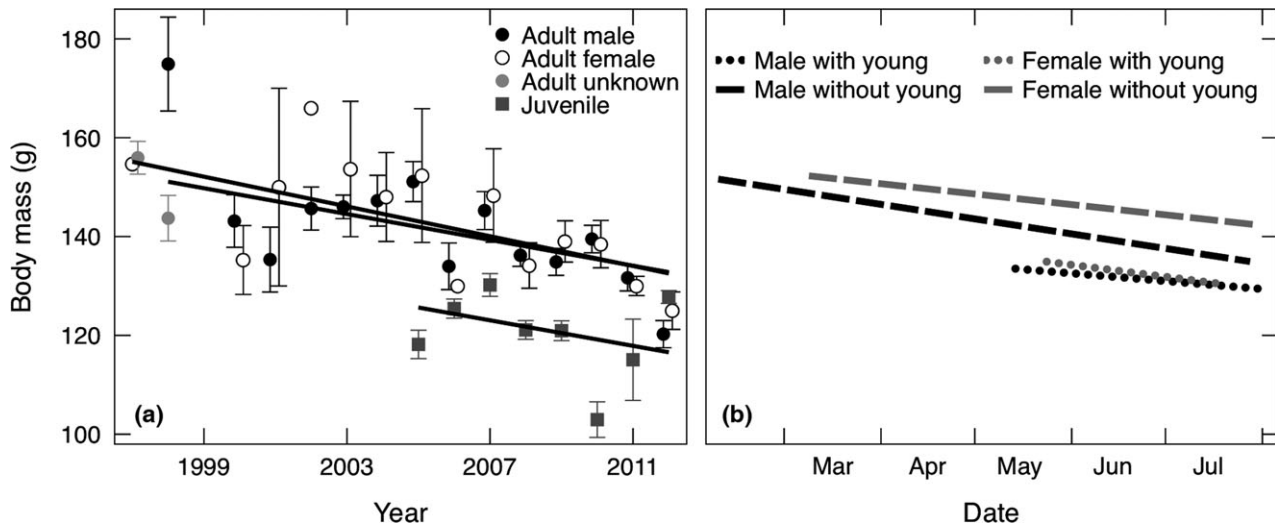
Fig. 5 Trends in Burrowing Owl body mass: (a) annual loss of mass for adult males, adult females, and juveniles shown with significant linear trends on all records, annual means, and standard errors (laying females removed, juvenile subset of fully grown yet not fledged 28–44 days old, and unknown sex included in gray 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 (adult male mass = $1961.10 - 0.90$ year $- 0.08$ date, $P < 0.0001$, $n = 107$; adult female mass = $2557.31 - 1.20$ year $- 0.08$ date, $P = 0.0052$, $n = 59$; juvenile mass = $2566.01 - 1.26$ year $+ 0.18$ date $+ 1.41$ age, $P < 0.0001$, $n = 252$).

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 fully grown but prefledge (28–44 days old) showed a loss of -1.3 g annually 2005–2012 ($n = 252$, $P = 0.0419$). Modeling juvenile mass as a function of year, date, and age to control for juvenile growth with age, mass decreased 20.0% on average over 8 years (-1.3 g yr^{-1}, $P = 0.0318$).

Adults also lost mass as the breeding season progressed (Fig. 5b). The seasonal decline occurred irrespective of sex or parental effort; however, body mass significantly differed between owls provisioning young and owls without young. Model estimates of average mass of provisioning females was 14.5 g less ($P = 0.0011$) and males was 9.7 g less ($P = 0.0038$) than mass of owls not feeding young. Controlling for the seasonal decline in mass, female mass decreased 10.9% (-1.2 g yr^{-1}, $P = 0.0314$) and male mass decreased 7.9% (-0.9 g yr^{-1}, $P = 0.0130$) on average over the study period.

Adult body mass varied in relation to variation in precipitation, temperature, and drought. Examining weather variables important in explaining fluctuations in both owl reproduction and prey availability, adult mass decreased with decreased winter and breeding season precipitation (November–March: $P < 0.0001$, detrended $P = 0.0004$; November–June: $P < 0.0001$, detrended $P = 0.0002$), increased breeding season maxi-

mum temperature (March–June mean max: $P = 0.0001$, detrended $P < 0.0001$), and increased drought severity (June PMDI: $P < 0.0001$, detrended $P < 0.0001$; November–June PMDI: $P < 0.0001$, detrended $P = 0.0001$). 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. Variation in prey availability also had an effect on owl mass. The linear relationship between juvenile owl mass and May–June arthropod biomass showed a 1 g increase in prey abundance during the nestling stage was associated with a 1.6 g increase in mean juvenile owl mass ($R^2 = 0.81$, $P = 0.0374$).

Changes in breeding phenology

Temporal trends in reproductive activity from 2005 to 2013 indicate Burrowing Owl breeding phenology was increasingly delayed (Fig. 6). Examining all records of individual owls and first nesting attempts, male arrival to the breeding grounds delayed 25.1 days on average since 2005 ($n = 230$ owls, $P < 0.0001$). Mean pair formation delayed 22.0 days ($n = 211$ pairs, $P = 0.0001$), and mean nest initiation delayed 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
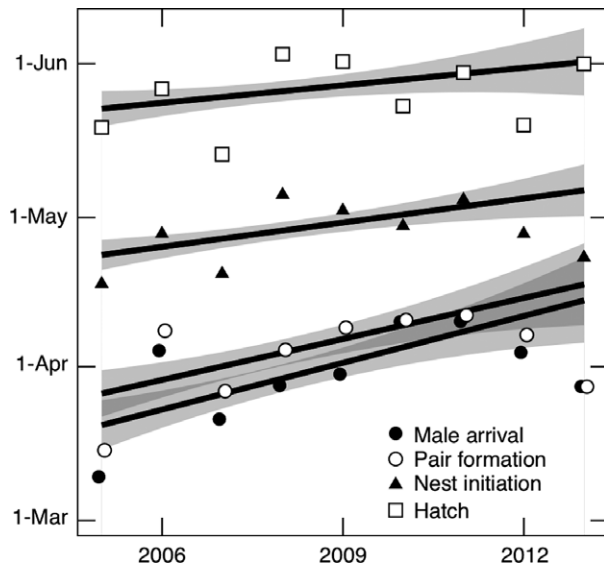
Fig. 6 Temporal trends in phenological events, including delays in male arrival (date = 76.06 + 3.14 year, $P < 0.0001$, $n = 230$), pair formation (date = 82.83 + 2.75 year, $P = 0.0001$, $n = 211$), nest initiation (date = 111.88 + 1.62 year, $P = 0.0004$, $n = 217$), and hatch dates (date = 141.75 + 1.18 year, $P = 0.0377$, $n = 177$), shown with annual means and the linear trends and 95% confidence intervals from all temporal records.

breeding, first arrival (1.3 days yr^{-1}, $P = 0.0236$), pair formation (1.5 days yr^{-1}, $P = 0.0060$), nest initiation (1.6 days yr^{-1}, $P = 0.0006$), and hatch dates (1.6 days yr^{-1}, $P = 0.0045$) 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^{-1}, $P < 0.0001$; pair formation: 2.6 days yr^{-1}, $P < 0.0001$; nest initiation: 1.8 days yr^{-1}, $P < 0.0001$; hatch: 1.4 days yr^{-1}, $P = 0.0035$).

Modeling effects of breeding phenology on nest success showed the probability of success decreased as the breeding season progressed. Each of the tested temporal variables were important predictors of success, with success decreasing with later arrival ($P = 0.0005$), pair formation ($P = 0.0013$), nest initiation ($P = 0.0025$), or hatch date ($P = 0.0449$). Mean fledglings per pair also decreased with later male arrival ($R^2 = 0.66$, $P = 0.0146$), pair formation ($R^2 = 0.74$, $P = 0.0064$), nest initiation ($R^2 = 0.66$, $P = 0.0137$), or hatch date ($R^2 = 0.66$, $P = 0.0145$). Removing temporal trends in productivity and phenology, the relationships between detrended productivity and male arrival ($P = 0.11$) and pair formation ($P = 0.07$) were not significant, and nest initiation ($P = 0.0338$) and hatch date ($P = 0.0139$) remained significant in the presence of a trend effect. Examining fledgling counts, the number of fledglings from each successful pair

decreased with later nest initiation ($P = 0.0092$) or hatch date ($P = 0.0070$).

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, significant changes in body mass in both breeders and nestlings, and an unexpected delay in breeding phenology. Because our results are significantly related to increased air temperature and aridity, we believe 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 strongly linked to extreme drought conditions, where the population crashed from 49 pairs to a single pair over a 6-year period (Figs 1 and 3). Whether this decline represents actual loss of breeding pairs or emigration is currently unknown. Anecdotal observations frequently suggest decreasing population trends for Burrowing Owls in New Mexico; however, there are few data that vet these observations and provide strong insight into the current status of this species. Although population declines are broadly attributed to habitat loss and degradation through grassland conversion and the loss of nest burrows (Poulin *et al.*, 2011), growth and development on our site remained relatively static during the study period. Systematic data have not been collected on trends in prairie dog abundance on the study site, but there have been regional declines associated with drought (Davidson *et al.*, 2014). Nevertheless active prairie dog colonies remained widely distributed during the study, and in recent years many potential nest burrows that were previously occupied by owls remained unused. While variation in predation and return rates may also explain population change, they were unrelated in this study. Despite minimal loss of suitable habitat, continued availability of active prairie dog burrows, and lack of influence of predation and return rates, the owl population dramatically declined. Our analyses indicate the temporal variation in population size over 16 years was largely

explained by the combined effects of precipitation and temperature variability.

The declining abundance of grassland (Bridges *et al.*, 2001; Niemuth *et al.*, 2008; Macías-Duarte *et al.*, 2009) and arid-zone birds (Wichmann *et al.*, 2003; Flesch, 2014) has been associated with drought, and this impact may be greatest in dry ecoregions (Albright *et al.*, 2010). Small mammal irruptions have led to subsequent increases in Burrowing Owl populations through changes in demographic parameters and/or immigration rates (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 multiyear drought may have led to the near total loss of owls on this site. Reproductive rates declined during the study (Fig. 1b, c), with very low productivity in the latter years ($\bar{x}_{2010-2013}$ = 1.3 fledglings per nest) and recent nest success ($\bar{x}_{2010-2012}$ = 34.4%) below the 63–92% range observed in most studies for Burrowing Owls in western United States (Botelho & Arrowood, 1996; Lutz & Plumpton, 1999; Restani *et al.*, 2001; Griebel & Savidge, 2007; Lantz & Conway, 2009; Berardelli *et al.*, 2010). Productivity and success also decreased with decreasing precipitation, increasing temperature, and increasing drought severity (Fig. 4). The strong association between climate variation and owl reproductive and population trends suggests bottom-up resource effects are driving Burrowing Owl demographics in this region, and time lags of the biological responses to variation in temperature and precipitation indicate both direct and indirect effects operate in this system (Flesch, 2014). Our results suggest the proximate cause of reduced reproduction is the linkage between low winter precipitation and May–June prey abundance. In other Burrowing Owl studies, food limitation had the greatest effect during the nestling phase of the breeding cycle (Wellicome *et al.*, 2013). Abundant food resources were associated with increased productivity, fledgling size, and high postfledging survival (Wellicome, 2000; Todd *et al.*, 2003; Gervais *et al.*, 2006). In supplemental feeding experiments, food limitation decreased reproductive performance through poor nestling growth and starvation (Haley & Rosenberg, 2013; Wellicome *et al.*, 2013). High rates of nest failure may also cause within season dispersal and low adult return to previously occupied nest sites (Ronan, 2002; Catlin *et al.*, 2005; Rosier *et al.*, 2006), with serious negative local 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 breeding phenology results show large, significant delays over 9 years ranging from 25.1 days for arrival to 9.4 days for hatch (Fig. 6), with negative consequences for reproduction. While the start of egg laying shifted from the first to the third week of April from 2005 to 2013 on our site, a study conducted in 1970–1971 observed laying starting the third week of March (Martin, 1973). These data suggest a longer-term trend toward later breeding for owl populations in this region and contrast with the advances in avian phenology that have been widely observed (Gordo, 2007; Rubolini *et al.*, 2007; Dunn & Winkler, 2010). Although uncommon, reproductive delays have been reported in other birds (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; McCreedy & van Riper, 2015) and population declines (Lee *et al.*, 2011). Significantly delayed phenology may also be indicative of declining populations (Miller-Rushing *et al.*, 2008; Lee *et al.*, 2011; Gordo & Doi, 2012).

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). In this study, both the number of fledgling produced and the probability of success decreased as the breeding season progressed. For some avian species, shifting phenology has led to population and reproductive declines due to asynchrony with food resource peaks (Visser *et al.*, 1998, 2006; Pearce-Higgins *et al.*, 2005; Both *et al.*, 2010). However, the Burrowing Owl population and reproductive declines are not explained by predator–prey mismatch. Burrowing Owls are generalist, opportunistic feeders, and desert environments are not characterized by the strong peak in seasonally available prey of temperate regions where mismatches have occurred with climate warming. While in this study arthropod abundance increased in July–August as expected with the arrival of the monsoon, this comes after breeding and thus should not influence reproductive output. Decreased reproductive output with delayed breeding may be mediated through increased physical and ecological stressors with high late-season temperatures, including decreased survival, abundance, or activity of vertebrate prey (Sinervo *et al.*, 2010; Moses *et al.*, 2012) and direct physiological costs for adult and juvenile owls of water loss and heat stress (Wolf, 2000; du Plessis *et al.*, 2012).

The delayed breeding observed in this population may be related to poor body condition mediated by conditions on the wintering grounds. In some migratory birds, winter habitat quality influences arrival times 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 owls' 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.

Changes in body condition

We found significant declines in breeding adult body mass, with male mass declining 7.9% and female mass declining 10.9% over 16 years (Fig. 5a). These trends indicate owls are in poorer body condition than observed in earlier years of the study (Brown, 1996) and have important implications for survivorship and reproduction. Reduced mass and condition have 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 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 decline over time, owls lost mass during the breeding cycle (Fig. 5b). This 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 lighter breeding masses is likely to importantly impact the survival 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 our data are consistent with this cost of reproduction: male owls actively provisioning young are approximately 10 g (6.4%) lighter, and females are 15 g (9.4%) lighter, than owls without young (Fig. 5b).

Nestling Burrowing Owls showed a 20.0% loss of body mass over 8 years (Fig. 5a). Nestling body condition has important 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 with nestling growth rates and body condition (Landry, 1979; Dijkstra *et al.*, 1990; Bellocq, 1997), owls on this site are having smaller broods, yet nestlings are in poor condition. Production of fewer young of poorer quality indicates reduced parental reproductive investment. However, we still observed a decline in adult condition during the breeding cycle, which suggests that adults are still investing heavily in reproduction at the potential cost of self-maintenance and future survival. We also found a seasonal decline in mass in adults without young, which may reflect insufficient food resources to support either reproduction or self-maintenance. Impacts of breeding season food limitation on body condition may be intensified by winter food shortages (Martin, 1987), and by the energetic costs of migration and/or the quality of migratory stopover sites (Klaassen *et al.*, 2012). In addition, reduced nestling body mass may translate into poor adult condition (Cunningham *et al.*, 2013), as developmental and carryover effects of poor natal and breeding sites lead to reduced body condition and reproductive performance in subsequent seasons.

Despite strong downward trends, body mass varied with fluctuations in winter precipitation and breeding season temperature. Our results show nestling-period arthropod abundance has a significant, positive effect on juvenile mass, and the correlation between low winter precipitation and low prey 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 nestling mass decreased with an increase in days with maximum temperatures above a critical threshold of 33 °C, which authors attributed to decreased 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 refuge from the thermal stress of high air temperatures, but adults face increased predation risk when inside burrows from badgers, coyotes, and snakes. Consequently, during the nestling period, adults experience high solar heat loads because they spend most time alert and outside 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's nest chamber have not been described; however, air temperatures at a depth of 30 cm within nest burrows did not differ from the burrow entrance (Coulombe, 1971). Therefore, it is possible 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 global warming. In the population we monitored, population size and reproductive dynamics were strongly associated with climate. We found rapid, profound decreases in population size with increasing air temperatures, decreased precipitation, and severe drought. In addition, we found owls were arriving and breeding later, and the arrival and breeding masses 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 reproductive output. 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. Our data are most consistent with bottom-up effects of precipitation on prey abundance limiting the reproductive potential of owls at our site. The strength of 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 trends 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 on wintering grounds are stressing Burrowing Owl populations.

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 increasing, 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 United States by the mid-21st century (Seager & Vecchi, 2010; Gutzler & Robbins, 2011; Williams *et al.*, 2013). 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 rangewide in the future.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Pearson correlation coefficients among the candidate explanatory variables used to test effects of climate variability on Burrowing Owl population metrics.

Table S2. Pearson correlation coefficients among the candidate explanatory variables used to test the effects of climate variability on Burrowing Owl reproductive metrics.