

Extreme precipitation reduces reproductive output of an endangered raptor

Ryan J. Fisher^{1,2*}, Troy I. Wellicome^{1,2}, Erin M. Bayne¹, Ray G. Poulin³, L. Danielle Todd³ and Adam T. Ford⁴

¹Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada; ²Canadian Wildlife Service, Environment Canada, Edmonton, AB, Canada; ³Royal Saskatchewan Museum, Regina, SK, Canada; and

⁴Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

Summary

1. The frequency and intensity of extreme weather has increased in North America against a backdrop of anthropogenic land change. Few studies have examined how wildlife is affected by extreme weather, and none have examined whether any resulting effects are contingent upon the degree of anthropogenic landscape change.
2. Using an 8-year study in Canada (2003–2010), we examined how nest survival of burrowing owls *Athene cunicularia* varied in relation to weather, vegetation and soil type around the nest. Using a 3-year (1992, 1993 and 1996) feeding experiment, we examined whether food limitation also causes owlet mortality during inclement weather. Lastly, we examined how productivity (i.e. annual fledgling output) between 2003 and 2010 varied as a function of breeding season precipitation anomalies. Using this relationship, we estimated how productivity has changed in response to breeding season precipitation anomalies from 1960 to 2012.
3. During extreme precipitation events, nest survival decreased because of flooding. When burrow flooding did not occur, the youngest owlets in broods that were not food-supplemented had the lowest survival rates when there was precipitation, yet almost all food-supplemented owlets survived bouts of inclement weather. Accordingly, annual productivity from 2003 to 2010 varied inversely with breeding season precipitation anomalies, and we estimated that mean annual productivity decreased by 12% from 1960 to 2012.
4. *Synthesis and applications.* Extreme rainfall during the breeding season reduced reproductive success of burrowing owls. Given that many raptors experience food limitation during extreme rainfall, large-scale habitat management to increase the abundance and availability of prey may allow these species to better withstand acute food shortages. In light of predicted increases in the frequency and intensity of extreme weather, supplemental feeding could be used in triage situations for burrowing owl management and has the potential to be an effective short-term conservation measure for other raptors. Protecting or reclaiming pastures in uplands that are less prone to flooding would further buffer burrowing owls and other ground-nesting species from extreme precipitation. These actions should mitigate the negative effects of extreme rainfall in the short term; however, long-term persistence of many species will become increasingly uncertain, as climate change scenarios predict an increase in the frequency and intensity of extreme weather.

Key-words: acute weather, burrowing owl, exposure, flooding, food limitation, nestling survival, starvation

Introduction

Climate change forecasts indicate that mean annual temperature will increase across much of North America over

the next 100 years, with some projections forecasting an increase in the frequency and intensity of extreme weather (Easterling *et al.* 2009). Furthermore, historical trend analyses suggest that the frequency of short-duration heavy-precipitation events has significantly increased (Kunkel, Andsager & Easterling 1999). Unfortunately, the effect of extreme precipitation on biodiversity has received

*Correspondence author. E-mail: rjf@ualberta.ca

far less attention than the effects of changes in average climatic conditions, even though extreme weather can adversely affect wildlife (Parmesan, Root & Willig 2000).

In general, birds may be vulnerable to extreme weather during the breeding season because food provisioning for young is typically constrained by ambient conditions and most nests are directly exposed to inclement weather. Heavy, prolonged precipitation and cold temperatures can increase the probability of nestlings dying of exposure (Boersma & Rebstock 2014), reduce prey activity and foraging efficiency by adults leading to nestling starvation (Dawson & Bortolotti 2000), cause destruction of nests (Thompson & Furness 1991) or lead to nest abandonment (Griebel, Savidge & Goldstein 2007). Consequently, quantifying the influence of acute, extreme weather on avian reproductive output is urgently needed to predict the effect that increased weather variability will have on avian populations (Parmesan, Root & Willig 2000).

The effects of climate change are also unfolding against a backdrop of human-induced changes to the landscape. The Great Plains is the most disturbed landscape in North America, and reproductive success of some birds is lower in areas dominated by non-native compared to native grasses (Lloyd & Martin 2005 but see Jones & Bock 2005). Causes of lowered reproductive success or survival in these non-native grasslands compared to native grasslands include changes in the community composition and abundance of predators and brood parasites, altered prey availability, increased human disturbance and lower quality microhabitats (Perlut *et al.* 2008). Nests may be more vulnerable to flooding if human land uses alter vegetative cover, topography or soil properties (e.g. Bodhainayake & Si 2004).

Burrowing owls *Athene cunicularia* Molina are semi-fossorial raptors distributed throughout grasslands in North America and parts of Central and South America (Poulin *et al.* 2011). Burrowing owls are an Endangered Species in Canada, a Species of Special Protection in Mexico and a Species of Conservation Concern in the USA (Environment Canada 2012). The cumulative influence of threats, specifically climate change and habitat loss, during breeding, wintering and migration, is at least partially responsible for the species' decline in abundance and range contraction in Canada (Environment Canada 2012). Burrowing owl nest burrows are vulnerable to flooding during periods of intense precipitation (Griebel, Savidge & Goldstein 2007), and owlet condition deteriorates during inclement weather (Haley & Rosenberg 2013). If only some owlets do perish during inclement weather, it is unclear whether the mechanism causing owlet mortalities is exposure, starvation or both.

Using data from 8 years of nest monitoring (2003–2010), we quantified daily nest survival of burrowing owls breeding in native and anthropogenic vegetation types in Saskatchewan and Alberta, Canada, in relation to extreme weather. We performed a 3-year (1992, 1993 and 1996) supplemental feeding experiment to test the exposure and starvation hypotheses for owlet mortality during inclement

weather. Using the same 8-year data set of burrowing owl nest monitoring (2003–2010), we examined productivity (as measured by the mean number of fledglings produced per year) in relation to annual breeding season precipitation anomalies. Lastly, we use these results to estimate how burrowing owl productivity, based on breeding season precipitation anomalies across the Canadian burrowing owl range, has likely changed from 1960 to 2012.

Materials and methods

DATA SETS AND STUDY AREA

We monitored nests between 2003 and 2010 in the mixed and moist-mixed grasslands of Saskatchewan and Alberta, Canada. As part of a study in Saskatchewan, we conducted a supplemental feeding experiment for 3 years (1992, 1993 and 1996) on owls breeding in artificial nest burrows (hereafter, ANBs; Wellicome 2005). Descriptions of the study areas are provided in Marsh, Wellicome & Bayne (2014) and Wellicome *et al.* (2013). In Saskatchewan and Alberta, 26% and 46%, respectively, of native grassland remains on the landscape (Environment Canada 2012). Mean annual precipitation (based on data from 1960 to 1995) in Saskatchewan and Alberta is 395 mm and 482 mm, respectively (McGinn 2010).

NEST SURVEYS

We searched for nests from 25 April to 10 May. We found nests by visiting locations reported by landowners and local conservation organizations, opportunistically detecting owls and surveying areas within an 400-m radius of burrows that had been occupied in either of the previous 2 years.

NEST AND OWLET MONITORING

We visited each nest approximately once per week. We defined three stages during the breeding season that were important for our study: (i) egg, duration = 28–33 days; (ii) owlet, duration = 35 days; and (iii) fledging, which occurs between 26 and 40 days post-hatch when owlets start moving away from their natal burrow. During the egg stage and when owlets were still underground, we examined the contents of natural burrows with an infrared video probe. When the owlets were older and above-ground, we visually monitored the nest through binoculars or a spotting scope. In both cases, visits to each nest lasted 5–30 min, except in the case of final fledgling counts. Evidence for a nesting attempt included (i) if ≥ 1 egg or owlet was observed in a nest chamber, or (ii) when our view of eggs or owlets was obscured near the nest chamber by an adult displaying aggressively or sitting in an incubating or brooding posture or (iii) if ≥ 1 owlet was observed at the burrow entrance. Wellicome (2005) and Wellicome *et al.* (2013) describe procedures for monitoring ANBs and owlet marking and monitoring.

NEST AND OWLET AGEING

We estimated the age of nests in relation to the day when the first egg was laid [i.e. clutch initiation date (CID)] in natural burrows using one of the following five methods (in order of precision): (i)

through a video probe, observing the first egg in the nest; (ii) back-dating from a mid-clutch egg count using the average lay rate of one egg per 1.5 days (Wellicome 2000); (iii) visually estimating the age of young that were <7 days post-hatch (RGP unpublished data) and then backdating from hatch another 28–33 days, depending on the maximum number of eggs observed in the nest; (iv) using the lengths of the central tail feather and 9th primary feather of trapped first-hatched owlets (Wellicome 2000) to determine their age; or (v) visually estimating the age of first-hatched young observed above-ground using a photo-reference guide (Priest 1997). In ANBs, ages of individually marked owlets and their hatching rank were determined by frequent visits near hatching.

NEST FATE, OWLET MORTALITY AND NUMBER OF FLEDGLINGS

For nests monitored from 2003 to 2010, we considered a nesting attempt successful if ≥1 owlet survived 35 days after hatch. To determine whether a nest was successful and to count the number of fledglings, we used above-ground camera systems to monitor nests for an 18- to 24-h period that encompassed at least one dusk and dawn cycle when owlets are most active (Hall & Greger 2014). If we could not access a nest with the remote camera, we visited the nest and observed the area for ≥30 min. We used maximum counts of fledglings from video or observations between 26 and 40 days post-hatch because filming or nest visits could not always be timed to exactly 35 days post-hatch. In 1992, 1993 and 1996, we monitored the fate of owlets by opening ANBs and inspecting each individual or carcass for individual markings.

We classified nest failures based on several criteria: if plucked adult feathers were observed at or near the nest, we classified the nest as failed due to avian predation; if signs of digging, fresh scat or hairs were observed at or near a burrow, we classified the nest as depredated by a mammal; if the nest chamber was partially or totally filled by water or the burrow was wet inside, we considered the nest to have flooded; burrows sometimes collapsed and caused nest failures; and we classified the nest as failed due to human destruction if vehicle tracks were observed on or near the burrow mound or if we found adults killed by vehicles.

NESTING HABITAT TYPE AND SOIL TEXTURE

We classified the habitat type within a 10-m radius of the nest burrow. We defined four habitat categories: native pasture (i.e. native, grazed vegetation), tame pasture (i.e. planted with exotic grasses and forbs grazed by cattle), roadside (i.e. on a roadside or in an adjacent ditch or median that is typically mowed or hayed and planted with exotic grasses) and lawns (i.e. mowed lawns that were part of a golf course or home).

Using a GIS (ArcMap v10.0; ESRI Inc., Redlands, CA, USA), we determined soil texture at nests using the Soil Landscapes of Canada v3.1 (Soil Classification Working Group 1998). Soil texture was classified into three categories: soil textures 1 and 2 (category 1, fine texture), textures 3 and 4 (category 2) and textures 5, 6 and 7 (category 3, coarse texture; Stevens, Bayne & Wellicome 2011).

SUPPLEMENTAL FEEDING EXPERIMENT

We performed a feeding experiment at 75 nests in ANBs over 3 years (1992, 1993 and 1996) to test the starvation and exposure hypotheses regarding owlet survival under inclement weather.

Owl pairs were assigned to three treatment groups that had similar CIDs: nests that were fed during the owlet stage ($n = 23$), nests fed during the egg and owlet stages ($n = 30$), and unfed control pairs ($n = 22$; Wellicome *et al.* 2013 for further details).

PRECIPITATION AND TEMPERATURE DATA

For analyses examining daily nest (2003–2010) and owlet survival (1992, 1993, 1996), we gathered information on daily temperature (°C) and precipitation (mm) from Environment Canada's National Climate Data and Information Archive (<http://www.climate.weatheroffice.gc.ca>, accessed 10 February 2011). To ensure conditions at weather stations approximated conditions at the nest, we included data from all weather stations within 50 km of a nest (mean 22 km, range 1–44 km). For each time interval between nest visits, we calculated an inverse distance-weighted maximum daily precipitation (all precipitation indices are in mm), average daily precipitation, total precipitation, the number of days with ≥7 mm or ≥1 mm precipitation, and the number of consecutive 3-day blocks where each day had ≥7 mm precipitation. We also calculated the inverse distance-weighted minimum, average and maximum daily temperatures for each interval.

To examine the effects of breeding season precipitation on productivity, as measured by the number of fledglings produced per nest annually, from 2003 to 2010, we used monthly precipitation data for nest locations that were derived from ClimateWNA (Wang *et al.* 2012). For each location with data on owl productivity, we calculated total precipitation for May, June and July for the year the nest was active. We defined the breeding season precipitation anomaly (mm) as the long-term normal (calculated from 1961 to 1990) May, June and July total precipitation subtracted from the year-specific May, June and July total precipitation value for each location.

To examine trends in historical breeding season precipitation anomalies that were relevant for breeding burrowing owls, we used the same breeding season precipitation anomaly metric from ClimateWNA for 1456 locations historically and currently occupied by burrowing owls in Saskatchewan and Alberta. We calculated annual breeding season precipitation anomalies for each location from 1960 to 2012 (the most recent year that is available from ClimateWNA).

DATA ANALYSES

Nest survival

We modelled daily nest survival from 2003 to 2010 using proc NLMixed (SAS 9.2) and used Akaike's Information Criterion corrected for small sample sizes (AIC_c) for model selection (Rotella *et al.* 2007). We excluded nests in 1992, 1993 and 1996 because the supplemental feeding experiments occurred during these years. Nests in ANBs were also removed because they may experience different rates of predation or flooding compared to natural burrows.

We predicted that precipitation would have a linear, negative effect on nest survival. All of the precipitation metrics (see Precipitation and temperature data above) were highly correlated ($r > 0.70$), so we separately examined the effect of each on nest survival and selected the metric producing a model with the lowest AIC_c. We predicted that low temperatures would reduce nest survival via reduction in prey availability or exposure, while high

temperatures may influence nest survival via effects on nest defence (Fisher *et al.* 2004). We therefore examined both a linear and quadratic response of daily nest survival in relation to temperature. We considered each temperature metric (minimum, average and maximum daily temperature) univariately and selected the metric that produced a model with the lowest AIC_c. Quadratic models were all >2 ΔAIC_c units from the linear models, so we included a linear effect of minimum daily temperature on daily nest survival in further multivariate analyses.

To identify the best-fitting model, we first developed a null model predicting a constant daily nest survival. This null model is unlikely to represent the typical fluctuations in daily nest survival during the breeding season; therefore, we developed a model that included a quadratic effect of nest age and an effect of CID on daily nest survival (INTRINSIC model). Next, we examined nest survival in relation to temperature and precipitation (WEATHER model; temperature + precipitation + temperature × precipitation), habitat type (HABITAT model; one covariate with three categories, including native pasture, tame pasture and roadside), soil texture (SOIL model; one covariate, with three categories), precipitation interacting with habitat type (Precipitation × HABITAT) and precipitation interacting with soil texture (Precipitation × SOIL). We assumed there would be no interactions between habitat type, soil, and temperature. We added each of these models to the INTRINSIC model and compared them to the null model using AIC_c. Year was included as a random effect in all models.

To verify that we did not include uninformative parameters in the top model, we calculated the ratio of $\beta : SE$ in all explanatory variables included in the top model ($\Delta AIC_c = 0$) and sequentially removed variables that had the lowest ratio of $\beta : SE$. We then recalculated AIC_c for this reduced model and continued this process until the AIC_c of the reduced model increased from a more parameterized model (Pagano & Arnold 2009). We evaluated goodness-of-fit of the final model using methods in Sturdivant, Rotella & Russell (2007).

To prevent the undue influence of a small number of observations, we produced 1000 bootstrapped resamples, with replacement up to the original sample size in each habitat type, of the original data set (Bentzen, Powell & Suydam 2008). For each bootstrapped resample, we ran the top model that was identified from the previous step using the same proc NLMixed procedure, acquired parameter estimates for each explanatory variable for every bootstrapped sample run and calculated 95% CIs around the bootstrapped parameter estimates using the bias-corrected method (Carpenter & Bithell 2000). The most important covariates influencing daily survival were those that had bias-corrected bootstrapped 95% CIs that did not include zero.

Nest survival quantifies the probability of nest success, but the binary nature of these data does not provide information about how those nests failed. Therefore, we conducted two separate nest survival analyses using two data sets: (i) all successful and all failed nesting attempts and (ii) all successful nesting attempts and all nests that failed due to flooding. These analyses allowed us to address three questions: (i) What is the relative influence of habitat type, weather, and soil on nest survival? (ii) What level of precipitation is correlated with nest flooding? And (iii) to what extent is nest flooding exacerbated or mediated in different habitat types? The analysis using only flooded nests had small sample sizes, so we simplified models and did not include INTRINSIC (nest age and CID should not influence probability of flooding)

or random effects. All parameter estimates are presented with 95% CI.

Owlet survival

To examine variation in individual owlet mortality attributed to weather, habitat and supplemental feeding, we quantified daily owlet survival using the same statistics as above (Rotella *et al.* 2007), but using data from 1992, 1993 and 1996. We included a random effect of the nest to account for non-independence of owlet mortality within a nest. As an INTRINSIC model, used to account for variance contributed by factors not directly relevant to our hypotheses, we included a quadratic effect of owlet age, brood size (total number of owlets remaining in the brood on each visit) and hatching rank (rank 1 = first-hatched owlet, rank 2 = second-hatched owlet, etc.). Of all precipitation and temperature metrics that we examined (see Precipitation and Temperature Data above), average daily precipitation and minimum daily temperature between nest visits produced the owlet survival model with the lowest AIC_c. Our WEATHER model included Temperature + Precipitation + Temperature × Precipitation. We included treatment group as an explanatory variable (TREATMENT model). As we had a limited sample of nests in different habitat types, we examined owlet mortality in grazed pastures (native plus tame pastures: $n = 56$ nests) vs. mowed lawns ($n = 19$ nests; HABITAT model, one covariate with two categories). We examined all additive models and a null model predicting constant daily owlet survival, as well as TREATMENT × precipitation, TREATMENT × temperature, TREATMENT × HABITAT and HABITAT × precipitation interactions. All parameter estimates are presented with 95% CI.

Productivity and recent precipitation trends

For each year of nest monitoring from 2003 to 2010, we calculated the mean number of fledglings produced per nesting attempt (hereafter, annual productivity). Using the precipitation data from ClimateWNA, we calculated a mean annual breeding season precipitation anomaly for these nests. We used a linear regression (R version 3.1.1; R Core Team 2014) to examine the relationship between mean annual breeding season precipitation anomaly (mm) and mean annual productivity. We included the inverse variance of mean annual productivity as a weight to account for unequal variances around the estimate of mean annual productivity. We considered precipitation to be important if the model including breeding season precipitation anomaly was >2.0 AIC_c units lower than a null model. We also conducted a correlation analysis (Pearson's r) between annual average breeding season precipitation anomaly for each location and the number of days with ≥ 20 mm of daily rainfall (see Results) calculated for each nest in the same year. The number of days where daily rainfall exceeded 20 mm was calculated using Environment Canada weather station data (see Precipitation and Temperature Data). This analysis allowed us to verify that breeding season precipitation anomaly was correlated with daily precipitation metrics we used in the nest and owlet survival analyses.

We used the regression equation from the analysis of annual productivity and breeding season precipitation anomalies between 2003 and 2010 (see above) to estimate burrowing owl productivity for each year from 1960 to 2012. We did not have field data on burrowing owl productivity or daily precipitation metrics for

the entire period from 1960 to 2012, necessitating this analysis. We used a linear regression and AIC_c (R version 3.1.1; R Core Team 2014) to determine whether there was a statistical trend in estimated annual productivity from 1960 to 2012. To account for variation around estimated annual productivity based on the linear regression equation, we used an inverse variance weighting. This analysis does not account for additional factors (e.g. food abundance) that are also known to influence burrowing owl productivity.

Results

NEST SURVIVAL

We monitored 964 nesting attempts between 2003 and 2010 and acquired weather data and information on nest fate for 754 of these. Of those 754 nesting attempts, 621 were in native pastures, 82 in tame pastures and 51 in roadsides. The mean age when nests were found was 13 days after CID; 44% of nesting attempts were monitored beginning 1–3 days after CID and an additional 45% were found prior to 40 days after CID. This large sample of nests that were monitored almost immediately after CID greatly reduces any potential biases associated with left-censored nest survival data. The mean interval between nest visits was 6 days.

Of the 754 nests, 589 were successful and 165 failed. Of those 165 failures, 19% were caused by flooding, 12% were due to poor weather conditions (periods of intense rain followed by abandonment), 21% were depredated by mammalian predators, 3% were due to adult mortality from avian predators, 1% were depredated by snakes, 2% due to unknown predators, 2% due to human destruction, 5% because of burrow collapse and 2% because adults died during the breeding season. The remaining 32% failed for unknown reasons. An additional 1% of nests in the ‘unknown’ category may have failed due to weather because these nests were exposed to ≥ 30 mm of rain in a 1-day period prior to failing.

The top model explaining variation in daily nest survival included INTRINSIC, precipitation and HABITAT

effects (Table 1). Despite being included in the WEATHER model, parameter estimates of minimum temperature and the precipitation \times temperature interaction had 95% CIs that included 0, indicating they had low explanatory power (Table 1). Although HABITAT was included in the top model, bootstrapping revealed that this effect was driven by a few influential nests in tame pastures; removal of single nests from the tame pasture category resulted in non-significant effects of habitat [$\beta_{\text{Tame}} = -0.542$ (-0.962 , 0.066), $\beta_{\text{Road}} = -0.022$ (-0.588 , -0.784), native pastures are the reference category]. Thus, we based our inferences on a bootstrapped model that contained INTRINSIC and precipitation effects. Daily nest survival was lowest 40–45 days after clutch initiation [$\beta_{\text{age}} = -0.071$ (-0.11 , -0.0034), $\beta_{\text{age}^2} = 0.001$ (0.0001 , 0.002)]. Nests initiated later in the breeding season had a lower daily survival rate compared to nests initiated earlier [$\beta_{\text{CID}} = -0.033$ (-0.049 , -0.019)]. Daily nest survival decreased as maximum 1-day precipitation between visits increased [$\beta = -0.016$ (-0.029 , -0.005)].

Twenty-eight nests failed due to flooding and were included in the daily nest survival analysis that compared successful nests ($n = 589$) with those that flooded. Model-predicted estimates and 95% CIs of daily nest survival at 20 mm precipitation had no overlap with those at 0 mm precipitation, suggesting that this is the point where flooding occurs more frequently [$\beta = -0.039$ (-0.057 , -0.018); Fig. 1]. However, daily nest survival continued to decline when daily precipitation exceeded 20 mm (Fig. 1). Although the precipitation \times habitat interaction was included in the best performing model (Table 2), bootstrapped parameter estimates of habitat type and precipitation \times habitat type all had 95% CIs that included zero.

OWLET SURVIVAL

We monitored 604 owlets from 75 nests in 1992, 1993 and 1996; 461 owlets survived to 35 days post-hatch. Of these 75 nests, all individual owlets eventually died in only

Table 1. Models in the 90% confidence set describing daily nest survival of burrowing owls from 2003 to 2010 in Alberta and Saskatchewan, Canada. All models include a random effect of Year. The ‘INTRINSIC’ model included clutch initiation date and a quadratic effect of nest age. HABITAT was the nest habitat type, WEATHER included temperature + precipitation + temperature \times precipitation, and SOIL contained soil texture. Temperature and the temperature \times precipitation interaction were included in the WEATHER model, but were removed from subsequent models because the 95% CIs of their parameter estimates included zero. Included is the goodness-of-fit of the top model (GOF)

Model	K	AIC_c	ΔAIC_c	w_i	GOF
INTRINSIC + Precip + HABITAT	8	1377.99	0.00	0.26	$P = 0.89$
INTRINSIC + Temp + Precip + HABITAT	9	1378.44	0.45	0.21	
INTRINSIC + Precip	6	1378.88	0.89	0.17	
INTRINSIC + WEATHER + HABITAT	10	1379.71	1.72	0.11	
INTRINSIC + WEATHER + HABITAT + HABITAT \times Precip	12	1380.30	2.31	0.08	
INTRINSIC + WEATHER	8	1380.69	2.70	0.07	
INTRINSIC	5	1383.11	5.12	0.02	
Null	2	1405.63	27.64	0.00	

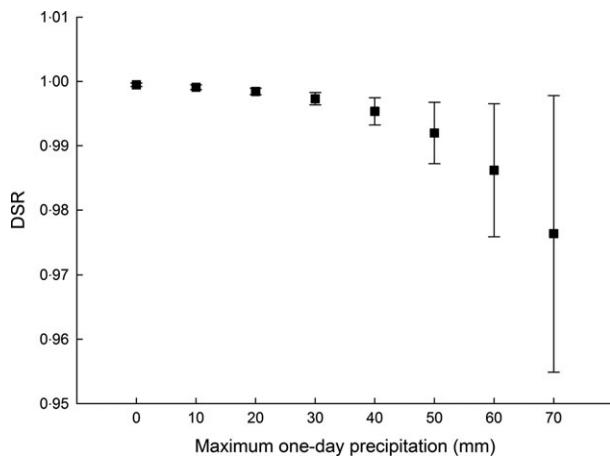


Fig. 1. Burrowing owl daily nest survival (with 95% CI) from 2003 to 2010 in relation to maximum 1-day precipitation (mm) when comparing successful nests to those that were flooded.

three, though not all brood members died at once. The top model (INTRINSIC + TREATMENT + Precipitation + Precipitation \times TREATMENT) describing owlet survival had an AIC_c weight of 0.99 (GOF, $P = 0.50$) and no other models were within 10 ΔAIC_c units. To account for variation caused by age of the owlet and the brood size (number of owlets remaining in brood at each visit), age [$\beta_{Age} = -0.035$ (-0.135 , 0.064), $\beta_{Age}^2 = 0.002$ (-0.0008 , 0.004)] and brood size [$\beta = 0.212$ (0.082 , 0.343)] were retained in all models. Owlets hatching later than their counterparts (i.e. high hatching rank) had comparatively lower survival [$\beta = -0.38$ (-0.47 , -0.30); Fig. 2]. Regardless of hatching rank, owlets reared in broods that received supplemental food had the highest survival under any amount of precipitation, whereas owlet survival in broods that were unfed decreased as precipitation increased [β_{Fed} from lay to fledge \times precipitation = 0.096 (0.008, 0.185), β_{Fed} from hatch to fledge \times precipitation = 0.123 (0.042, 0.205); Fig. 2].

PRODUCTIVITY AND RECENT PRECIPITATION TRENDS

Annual productivity from 2003 to 2010 was negatively related to breeding season precipitation anomaly [adjusted $R^2 = 0.63$, $\beta = -0.013$ (-0.022 , -0.004), $AIC = 9.88$ (AIC of null model = 17.53); Fig. 3]. Breeding season precipitation anomaly was correlated with the number of days with precipitation ≥ 20 mm ($r = 0.79$). There was a

negative trend in estimated annual productivity between 1960 and 2012 [adjusted $R^2 = 0.03$, $\beta = -0.008$ (-0.017 , 0.001); $AIC = 87.4$ (AIC of null model = 88.3); Fig. 4], although the 95% CIs of the parameter estimate included zero. Based on this analysis, annual productivity is estimated to have declined since 1960 by 12% [range 3–18% (determined by dividing 2012 productivity estimates and upper and lower 95% CIs by the productivity estimate in 1960); Fig. 4].

Discussion

Burrowing owl nest and owlet survival declined, and hence annual productivity declined, as a function of exposure to extreme precipitation. These heavy precipitation events occurred in June, when burrowing owl renesting is unlikely. In our study area, the mean CID for renesting is 19 May (range 30 April–9 June), suggesting that these extreme events lead to a complete loss of annual reproductive output for pairs that fail. Burrowing owls' susceptibility to extreme precipitation is not limited to our study area, as other studies have reported burrow flooding (MacCracken, Uresk & Hansen 1985; Millsap & Bear 2000; Griebel, Savidge & Goldstein 2007) and reduced owlet body condition (Griebel & Savidge 2003) and survival (Haley & Rosenberg 2013) after inclement weather. Furthermore, the effects of inclement weather on reproductive success have been reported in a wide range of other birds occupying a broad spectrum of habitats (Dinsmore, White & Knopf 2002; Skagen & Adams 2012; Anctil, Franke & Béty 2014; Öberg *et al.* 2014). The rate at which daily precipitation decreases nest or nestling survival likely differs among species; nevertheless, future increases in the frequency and intensity of extreme precipitation during the breeding season could have significant negative effects on reproduction of many birds.

Extreme precipitation in the USA has increased 10–20% across much of the Great Plains over the past 50 years, with a projected increase in the frequency of the heaviest rainfall events of 15–40% (Karl *et al.* 2009). Unfortunately, comparable precipitation trend analyses in Canada do not extend past 2000 (Akinremi, McGinn & Cutforth 1999; Kunkel, Andsager & Easterling 1999), but in the last 14 years (2000–2014) there have been four summers ranked in the top 10 wettest on record since 1948 (2002, 2005, 2010 and 2014; Environment Canada 2014).

Table 2. Models comparing daily nest survival of successful burrowing owl nests to nests that failed due to flooding. This analysis allowed us to determine what levels of daily precipitation reduced daily nest survival. Model abbreviations and column headings are the same as Table 1

	K	AIC_c	ΔAIC_c	w_i	GOF
HABITAT + Precip + HABITAT \times Precip	6	372.63	0.00	0.72	$P = 0.46$
HABITAT + Precip	4	374.57	1.94	0.27	
Precip	2	383.49	10.86		
HABITAT	3	399.10	26.46	0.00	
Null	1	407.57	34.93	0.00	

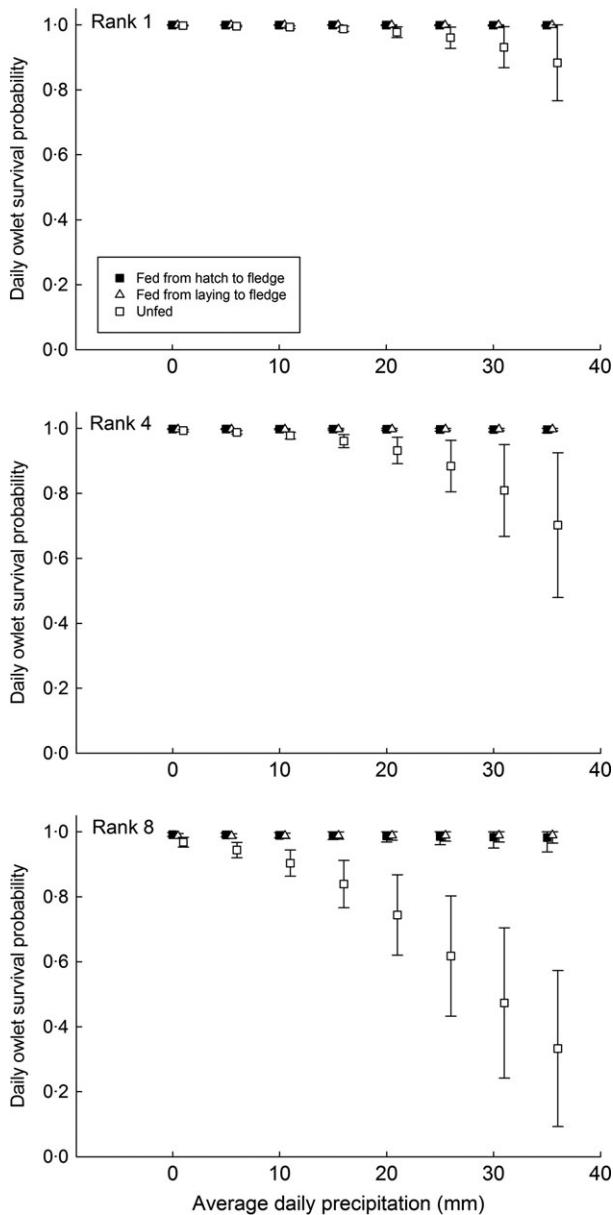


Fig. 2. Daily owlet survival (with 95% CI) in 1992, 1993 and 1996 in relation to supplemental feeding treatments, average daily precipitation (mm) between nest visits, and hatching rank [rank 1 (oldest), rank 4 and rank 8 (youngest)].

In the preceding 40 years, there were only two such years (1963 and 1993; Environment Canada 2014).

Neither vegetation type surrounding the nest nor soil texture altered the effect of extreme precipitation. We did not have access to data on local topography around nests, despite the likelihood that topography plays a role in the susceptibility of a nest to flooding (MacCracken, Uresk & Hansen 1985). A larger issue, however, may be at the landscape scale in prairie Canada, where pastures are typically located in areas that have poor agricultural capacity (i.e. poor soils; Rashford, Walker & Bastian 2011) or where terrain has hindered pasture conversion (Simonson & Johnson 2005). Whether non-random placement of

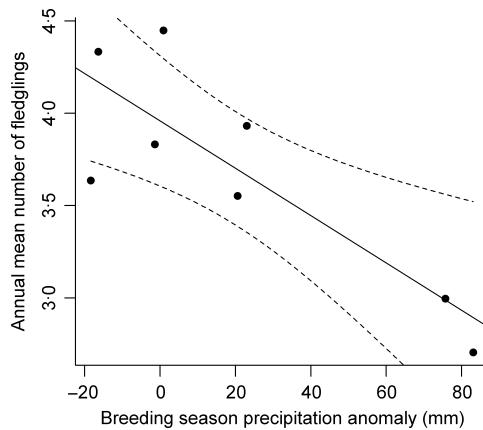


Fig. 3. Mean number of burrowing owl fledglings produced annually per nesting attempt (95% CI, dashed lines) from 2003 to 2010 in Alberta and Saskatchewan, Canada, in relation to breeding season precipitation (mm) anomaly.

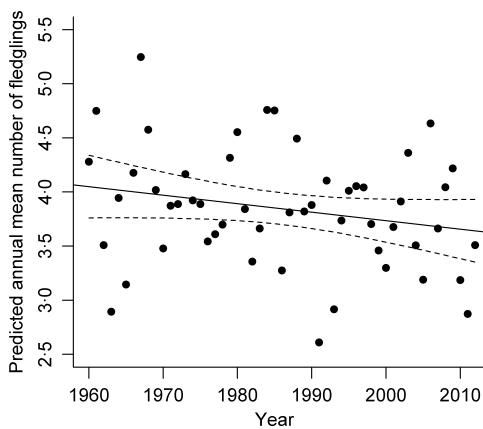


Fig. 4. Estimated annual mean fledglings produced per nesting attempt (95% CI, dashed lines), based on linear regression equation derived from Fig. 3 and annual breeding season precipitation anomalies, from 1960 to 2012, in Alberta and Saskatchewan, Canada.

remaining pastures has made ground nests and burrows within these habitat types more susceptible to flooding compared to historical nesting locations remains to be determined. Preserving remaining upland pastures and restoring cropland to pastureland in upland areas would help to retain and create areas for burrow-creating mammals and areas where nest flooding would be unlikely for burrowing owls and other ground nesters. Proper placement of ANBs, which are frequently used for burrowing owl industrial mitigation and conservation, is critical to ensure the probability of burrow flooding is low.

Studies have documented the negative impacts of inclement weather on nestling survival and body condition in many raptors (Rodríguez & Bustamante 2003; McDonald, Olsen & Cockburn 2004; Haley & Rosenberg 2013). Our feeding experiment demonstrated that owlets, including the youngest members of each brood,

did not die during inclement weather if they received supplemental food. Burrowing owls cache food (Wellcome 2005), providing an ‘insurance policy’ against periods of acute food shortage (Korpimaki 1987), and these caches are largest in years with high prey abundance (Poulin, Wellicome & Todd 2001). Furthermore, Poulin (2003) demonstrated that burrowing owl prey cache size was positively related to burrowing owl population size the following year (burrowing owls often breed in the first year after hatch; Mitchell *et al.* 2011). Unfortunately, prey outbreaks in Canada are linked to winter weather conditions (Heisler, Somers & Poulin 2014), which cannot be managed. However, habitat management actions promoting abundant and accessible prey in non-outbreak years should increase burrowing owl prey caches, thereby allowing owls to better withstand periods of acute food shortage during inclement weather and presumably increase their productivity. While the management strategies below concentrate on increasing abundance and accessibility of prey for burrowing owls, ensuring abundant and accessible prey for many other raptors will be especially important in the light of predicted increases in the frequency and intensity of extreme breeding season precipitation.

Burrowing owls successfully capture a variety of small mammalian prey in a multitude of habitat types and typically forage >500 m from their nest; however, within these varied habitat types, burrowing owls successfully capture prey in sites with low vegetation density and ground cover (Marsh, Wellicome & Bayne 2014). Management strategies (i.e. grazing, mowing, haying) that create heterogeneous vegetation structure in grasslands would promote both abundant (tall and dense vegetation) and available (short and sparse vegetation) small mammalian prey (Marsh, Wellicome & Bayne 2014), such as deer mice *Peromyscus maniculatus* Wagner, meadow voles *Microtus pennsylvanicus* Ord and sagebrush voles *Lemmiscus curtatus* Cope (Heisler, Somers & Poulin 2014). Management actions to increase prey abundance and availability in other habitat types remain more elusive. One suggestion to promote heterogeneous vegetation structure is to leave some areas in cropland unseeded (Marsh, Wellicome & Bayne 2014) or to harvest some strips within cropland, hayland or roadside ditches earlier than others, thereby creating a mosaic of areas with tall overhead cover for small mammals and adjacent shorter areas, where owls can access prey. Although these habitat management strategies will not reduce burrow flooding, they would potentially reduce owlet mortalities from starvation by allowing adults to maximize cache sizes prior to inclement weather. Supplemental feeding could be considered as a short-term stopgap conservation measure for burrowing owls (e.g. Mitchell *et al.* 2011) and other raptors (Gonzalez *et al.* 2006) displaying acute food limitation during inclement weather, but could not be accomplished at a scale sufficient to arrest or reverse widespread declines in burrowing owl populations.

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Data accessibility

The data in the present study have not been archived because they could reveal sensitive information about a protected species that is listed in Canada as Endangered under the federal *Species-At-Risk Act* and is listed as Endangered under the respective Wildlife Acts of the provinces of Alberta and Saskatchewan, Canada.

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