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Spatiotemporal trends and drivers of population dynamics in a declining Sonoran Desert predator

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ABSTRACT

Information on population trends, population structure, and factors that drive them is useful for assessing extinction risks and for guiding conservation. In arid environments, weather often has large effects on population dynamics and climate change may be driving pervasive population declines. I used time-series data and two approaches that make different assumptions about observation error and process noise to evaluate population trends and population structure of ferruginous pygmy-owls (*Glaucidium brasilianum*) in the Sonoran Desert of northwest Mexico, and assessed how temporal variation in weather and spatial variation in vegetation and land use affected dynamics. Abundance declined over 12 years based on both approaches, but estimates from multivariate state-space models that explicitly considered observation error and process noise, were steeper (−2.8%/yr) with lower precision (SE = 3.6%) than those from mixed-effects models (−1.9%/yr, SE = 0.8%) that assumed no process noise. Annual precipitation at a two-year lag had positive effects and brooding-season temperature at a one-year lag had negative effects on abundance, and together explained 75% of variation in population dynamics that were largely synchronous across space, suggesting climate forcing. Abundance was persistently higher and varied less in areas with more nest cavities, more riparian vegetation, and lower land-use intensity, suggesting these factors are important drivers of habitat quality and good targets for managers. These results have important implications in arid regions of western North America where drought and extreme temperatures linked to climate change have prevailed over much of the last decade and where monitoring and conservation measures are needed to address these threats.

1. Introduction

Understanding processes that drive spatiotemporal variation in animal abundance is a longstanding issue in ecology (Turchin, 2003). In applied contexts, information on spatiotemporal variation in abundance is essential for assessing population trends and extinction risks. Effective management responses to observed trends, however, necessitate accurate estimates of population parameters and understanding processes that drive them. Temporal variation in weather can have large effects on vital and population growth rates, and extreme weather linked to climate change may now be driving pervasive population declines (Stenseth et al., 2002; Jenouvrier, 2013). In arid and semi-arid environments, precipitation and temperature often directly affect plant productivity and exert a range of complex direct and indirect effects on populations at varying lag times and trophic levels (Lima et al., 2002; Holmgren et al., 2006). These patterns have broad global conservation implications because arid and semi-arid regions cover >40% of land on Earth and are particularly vulnerable to climate change (Loarie et al., 2009). In arid regions of western North America, for example, recent signs of climate change are pervasive and are expected to intensify (Overpeck and Udall, 2010). Moreover, ongoing drought and extreme temperature events during the last decade have been linked to marked declines in vital or population growth rates in the few vertebrate systems that have been continuously monitored (Barrows, 2006; Moses et al., 2012; Zylstra et al., 2013; Lovich et al., 2014). Evaluating the pervasiveness of these trends and developing strategies to mitigate them requires additional data on populations and on factors that can buffer the effects of harsh weather.

Despite the importance of information on population trends and drivers, extracting accurate inferences from monitoring data is complicated by two general sources of error: observation error and process noise. Field surveys rarely reveal true abundance,

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and differences between truth and estimates produces observation error, which reduces confidence in inferences (Staples et al., 2004). Observation error includes measurement error, or differences between truth and estimates at sampled locations, and sampling error, or differences between sampled locations and the population at large. Process noise resulting from demographic and environmental stochasticity can produce short-term declines in populations that are actually stable over the long term (Dennis et al., 2006). Because they explicitly consider both sources of error, state-space models (SSM) are being used increasingly to model population dynamics but are complex and may have lower precision and power to detect declines than more conventional approaches (Dennis et al., 2006; Wilson et al., 2011a). These issues are especially relevant when assessing the dynamics of rare or at-risk populations where sample sizes and time-series length are often limited and where low precision complicates detecting patterns more likely to have serious consequences. Nonetheless, there are few comparisons of techniques (e.g., Wilson et al., 2011a). Moreover, because populations with low process noise and high levels of structure (e.g., numerous independent subpopulations with asynchronous dynamics) are less vulnerable to extinction, unbiased forecasts of extinction risk necessitate accurate inferences on these parameters (Heino et al., 1997; Holmes et al., 2007).

I evaluated population trends and population structure of a predatory bird in an arid region of northwest Mexico where drought and extreme temperature events, which have prevailed over much of western North America over the last decade, may be driving population declines. To do so, I compared inferences from multivariate state-space models (mSSM) that explicitly consider uncertainty due to both observation error and process noise with those from more conventional mixed-effects models of observed counts that assume no process noise. Despite few examples of their application, mSSM offer multiple advantages over their univariate counterparts because they facilitate simultaneous estimation of spatiotemporal variation in trends, process variance, and covariance, which are important for understanding population dynamics and forecasting extinction risk (Hinrichsen and Holmes, 2010). Moreover, I assessed the effects of weather on population dynamics by evaluating hypothesized relationships between temporal variation in abundance and weather based on the biology of the system. Finally, because understanding factors that can buffer the effects of harsh weather on populations can guide managers, I assessed the effects of spatial variation in vegetation and land use on spatiotemporal variation in abundance.

2. Methods

2.1. Study species and area

I considered populations of ferruginous pygmy-owls (*Glaucidium brasilianum*) in four watershed regions in the Sonoran Desert of northwest Mexico directly south of Arizona, USA (see Flesch and Steidl, 2006 for details on study sites). In these arid environments, pygmy-owls are generalist predators and residents in woodlands associated with giant columnar saguaro cacti (*Carnegiea gigantea*) that provide nest cavities. Pygmy-owls were once considered common in portions of the Sonoran Desert in Arizona but were extirpated from much of their range, listed as endangered in 1997, then delisted for reasons unrelated to recovery in 2006 (USFWS, 2011). In neighboring northwest Mexico, pygmy-owls are more common but thought to be declining for unknown reasons (Flesch and Steidl, 2006). Thus, current information on population trends and factors that drive them are important for conservation and management in this system and more generally for understanding how vertebrate populations in arid regions of western North America are responding to extreme weather.

The study area included both major vegetation communities occupied by pygmy-owls in the northern Sonoran Desert, the Arizona Upland subdivision of the Sonoran Desert and semi-desert grassland (Brown, 1982). Arizona Uplands are dominated by woodlands and scrub of short leguminous trees such as mesquite (*Prosopis velutina*) and saguaros. Semi-desert grasslands are dominated by open mesquite woodlands, bunchgrasses, sub-shrubs, and often support lower densities of saguaros. Riparian areas in both communities are dominated by mesquite woodlands. Annual precipitation in this region is bimodal and dominated by a summer monsoon in late June–September and winter storms that are most intense during the warm phase of the El Niño Southern Oscillation.

2.2. Sampling and survey design

I estimated abundance by repeatedly surveying the same locations across time. In spring 2000, I surveyed 71 transects that I selected randomly. After these initial surveys, I randomly selected 18 transects in landscapes occupied by pygmy-owls and surveyed these transects each spring for the next 11 years. Transects were located within 75 km of the US–Mexico border and totaled 54 km in length. I placed transects along drainage channels and elicited responses by broadcasting territorial calls at 5–10 stations per transect, which yields nearly perfect detection probability of territorial males (Flesch and Steidl, 2006, 2007). To minimize chances of double-counting individuals, which typically move toward broadcasts, I increased station spacing after initial detection of each male, used response distance, direction, and timing to estimate abundance, and occasionally repeated surveys at some stations.

2.3. Trend analyses

To estimate population trends and population structure, I used autoregressive mSSM,

$$x_t = Bx_{t-1} + u + v_t, \quad v_t \sim \text{MVN}(0, Q) \tag{1}$$

$$y_t = Zx_t + a + w_t, \quad w_t \sim \text{MVN}(0, R) \tag{2}$$

where x_t is a vector of log+1 transformed unknown true abundances in year t, B is an autoregressive parameter estimating density dependence, u is a trend parameter, and v is process error that has a multivariate normal (MVN) distribution with mean zero and variance Q that measures process variance (Hinrichsen and Holmes, 2010). In Eq. (2), y_t is a vector of log+1 transformed counts of males on each transect, Z is a $n \times m$ design matrix identifying time series (n) associated with each state process (m), which models population structure, a is a vector of $n - 1$ intercept-like parameters, and w is observation error that has a MVN distribution with mean zero and variance R that measures observation error. Data enter the model as y's and x's are estimated. I assumed initial abundance (x_0) was not at equilibrium and assumed density independence ($B = 1$) because estimates of B from parametric bootstrap likelihood ratio tests (Dennis and Taper, 1994) and the best mSSM were $\geqslant 0.96$. To estimate the unknown parameters (u, Q, R, x_0), I used maximum likelihood (ML) methods and the expectation-maximization and Kalman filter algorithms implemented by the MARSS library in R to estimate parameters and parametric bootstraps to estimate standard errors (R Core Development Team, 2013).

Univariate and mSSM are similar but by considering multiple time series simultaneously, mSSM do not require condensing data from each sample into a single population-wide estimate for each time step. Therefore, variation in trends and process errors among population units in different strata and covariance among errors can be estimated, and inferences reported here are based on the full 18 transect ×12 year sample. To assess evidence of population structure, I considered three model structures: (1) time series for each transect as independent samples from one larger population with one trend and process error, (2) regional subpopulations ($m = 4$) with equal trends and equal or varying process errors with covariance, and (3) regional subpopulations with varying trends and equal or varying process errors with covariance. In models that considered regional population structure, the number of estimated parameters (K) included both variances and covariances. Because likelihood profiles of parameters in SSM can have multiple local maxima and low estimablility, I initiated parameter searches from random sets of starting values and evaluated profile likelihoods across a range of parameter values.

To compare inferences on trends and population structure between mSSM and a more conventional approach that did not partition observation and process error, I fit a similar set of linear mixed-effects models (LMEM)

$$y_{it} = (\beta_0 + b_{0i}) + \beta_1 x_{it} + \varepsilon_{it}, \quad \varepsilon_{it} \sim N(0, \sigma^2) \tag{3}$$

where y_{it} is the observed data as in Eq. (2), β_0 is an intercept for the population, b_{0i} is a vector of random intercepts for each transect, β_1 is a trend parameter for a fixed time effect, x_{it} indicates the year of each observation for the i^{th} transect centered at 0, and ε_{it} is an error term that has a normal distribution with a mean of zero and variance σ^2 that measures observation variance. Whereas mSSM explicitly separate observation and process variance, both variances are confounded in LMEM of count data and all variance is assumed to be observation error.

To assess population structure, I specified additional models analogous to those for mSSM. To assess regional variation in intercepts, I replaced b_{0i} in Eq. (3) with a vector of random intercepts for regions (b_{0j}) and a vector of random intercepts for transects nested within regions ($b_{0j(i)}$). To assess regional variation in trends, I fit a random slope for region (b_{1j}). To assess spatial variation in observation error, I fit three additional models that estimated observation variances for each region. To model covariance in observation error, I considered first-order autoregressive [AR(1)] and autoregressive-moving-average structures; AR(1) was supported in all cases and reported. I used restricted ML when assessing models with different random effects, ML to estimate fixed effects, and fit models with the nlme library in R. To evaluate support among models in each set, I used AIC$_c$ and model averaging where there was support (e.g., AIC$_c$ within 2 points) for >1 model (Burnham and Anderson, 2002).

2.4. Environmental drivers

Temporal variation in weather could affect owl abundance directly through energetic and thermoregulatory constraints or indirectly by affecting prey. Low winter temperatures could cause direct mortality of owls or prey, or reduce body condition necessary to establish territories. Thus, the winter stress hypothesis predicts that lower average minimum temperatures during winter (November–March) reduce owl abundance the following spring. High temperatures during nesting could limit prey activity or reduce nestling condition or survival, which could reduce owl productivity and abundance the following year. Thus, the nestling stress hypothesis predicts that high average maximum temperatures reduce owl abundance one year later. In arid environments, precipitation can augment prey abundance directly and positively during the same year or indirectly by augmenting insect or plant resources that are important to prey and create lagged effects. Thus, the direct prey enhancement hypothesis predicts owl abundance in year t increases with precipitation in year $t-1$, and the delayed prey enhancement hypothesis predicts owl abundance in year t increases with precipitation in year t–2. Because the effects of annual vs. seasonal precipitation, and incubation- vs. brooding-season temperature could vary, I considered cool-season (October–May), warm-season (June–September), and annual (October–September) precipitation when evaluating prey enhancement hypotheses, and temperature during incubation (April) and brooding (May–June) when evaluating the nestling stress hypothesis and used factors that minimized AIC$_c$ to represent hypotheses. Correlations between weather factors associated with different hypotheses were relatively low ($r = -0.41$–0.38). All weather data were from stations near Sasabe, which is at the north-central edge of the study area 5-75 km from transects (Western Regional Climate Center, 2012).

Spatial variation in factors that affect resources important to owls could explain variation in population dynamics. To address this question, I quantified vegetation and land use around survey stations and averaged measurements within transects (see Flesch and Steidl, 2006). I quantified amount of riparian vegetation by measuring the width of riparian vegetation corridors. To describe vegetation structure, I measured woodland cover, canopy height, and vegetation volume in riparian areas, and canopy height and vegetation volume in uplands. I estimated abundance of potential nest sites by measuring the proportion of stations where mature saguaros were present, which were the only substrates used for nesting. I ranked land-use intensity from 0 to 3 (none, low, moderate, high) in five categories (agriculture, woodcutting, exotic-grass planting, livestock grazing, housing) and summed ranks across categories. I measured vegetation at the beginning of the study because it was largely static and land use each year because it occasionally varied. Because some attributes of vegetation structure were correlated, I used principal components analysis to generate synthetic variables. A component representing riparian vegetation structure was positively correlated with woodland cover ($r = 0.66$), canopy height ($r = 0.52$), and vegetation volume in strata >3-m above ground ($r \geqslant 0.34$) in riparian areas, whereas a component representing upland vegetation structure was positively correlated with canopy height ($r = 0.65$) and vegetation volume ⩾1-m above ground ($r \geqslant 0.90$) in uplands. Correlations between vegetation and land-use factors were relatively low ($r = -0.40$ to 0.52).

To evaluate the effects of weather, vegetation, and land-use factors, I added fixed covariate terms to Eq. (3), used the most parsimonious structures for the random effects and σ^2, and used AIC$_c$ to assess support among models. When evaluating support among weather hypotheses, I considered each hypothesis independently and biologically plausible combinations of hypotheses. To evaluate the effects of spatial factors, I developed nine candidate models representing the effects of five potential covariates and considered abundance of potential nest sites in all models because they are critical for reproduction. Because inferences were very similar based on both modeling approaches, all reported effects are from LMEM.

Individuals in high-quality habitat may be less susceptible to harsh weather (Franklin et al., 2000). Moreover, theoretical models and data on habitat selection indicate the highest quality places are selected first and used more consistently over time (Fretwell and Lucas, 1969; Sergio and Newton, 2003). Therefore, transects with more persistent populations and thus lower coefficients of variation in abundance (CV$_a$) across time should support higher quality habitat independent of local carrying capacity. Hence, to identify factors associated with habitat quality, I regressed vegetation and land-use factors against CV$_a$.

3. Results

3.1. Trends and variances

Abundance declined across time based on both modeling approaches (Fig. 1). Two top-ranked mSSM estimated declines of 2.6–2.8%/yr, or 25.2–26.5% over 12 years. A top-ranked LMEM estimated a decline of 1.9%/yr or 19.2% overall (Tables 1 and 2). Despite similar trend estimates, precision was low for mSSM (SE = 3.6%) and 95% confidence intervals overlapped zero. Abundance was high initially (55 males), declined steadily to 2008 (21 males), increased in 2009 and 2010 (36–39 males), then decreased somewhat during the final year (34 males). Although dynamics varied somewhat regionally (Fig. 1), there was no evidence that trends varied regionally ($\Delta AIC_c \geqslant 6.6$; Table 1).

The top-ranked mSSM was for a single population with one trend and process variance. A model with regional covariance in process variance ($r = 0.58$) had less support ($\Delta AIC_c = 1.49$). In contrast, the top-ranked LMEM indicated regional differences in observation error (range = 0.082–0.13) but not intercepts ($\Delta AIC_c \geqslant 2.12$). Residuals separated by one year were moderately correlated ($r = 0.29$) whereas observations from the same transects across time were highly correlated ($r = 0.71$).

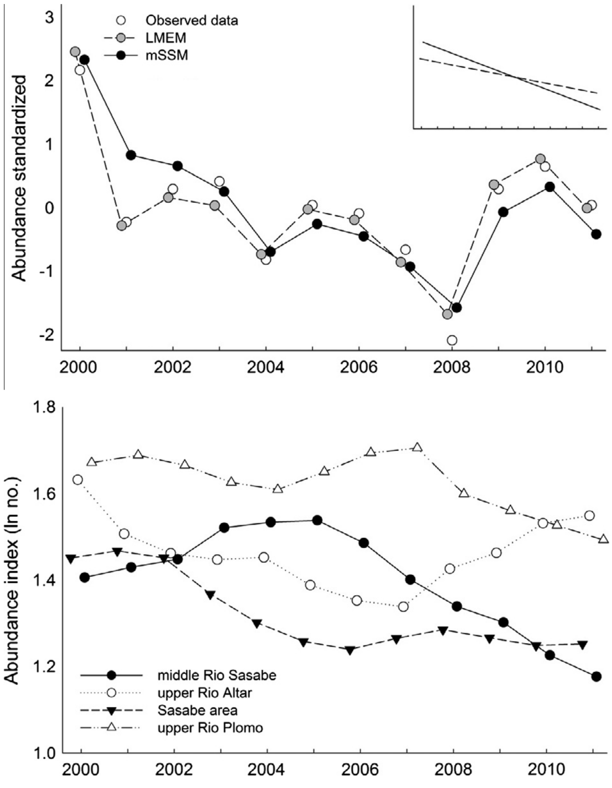

Fig. 1. Temporal variation and trends in abundance of ferruginous pygmy-owls in the Sonoran Desert of northwest Mexico, 2000–2011. Top figure shows annual estimates of log abundance based on the observed data (open points), fitted values from a top-ranked linear mixed-effect model (LMEM; gray points-dashed line), and smoothed state estimates from a top-ranked multivariate state-space model (mSSM black points-solid line) on a standardized scale (e.g., subtract mean and divide by standard deviation). Inset figure shows estimated trends based on each modeling approach. Bottom figure shows spatiotemporal variation in abundance among four regions based on smoothed state estimates from a mSSM that considered spatial population structure and was parameterized with an equal growth rate, equal process error, and regional covariance in process error among subpopulation units in each region. Spatiotemporal variation in abundance is represented by an abundance index because estimates are scaled to the first observation time series in each region, which I selected to be the time series with the lowest mean abundance across time.

Estimates of process variance from mSSM (0.015) were much lower than observation error (0.086; Table 2). Profile likelihoods of observation variance suggested it was highly estimable but less so for the trend parameter and process variance (Appendix A). Estimates of observation error from LMEM (0.094) were similar to the sum of both variances from mSSM.

3.2. Environmental drivers

Owl abundance varied markedly with weather but support among hypotheses differed. Support for the nestling stress hypothesis with brooding-season temperature and for the delayed prey enhancement hypothesis with annual precipitation, were highest (Table 3). Temporal variation in abundance closely tracked annual precipitation at a lag time of two years (Fig. 2A) and abundance increased by an average of 0.42 ± 0.17% (±SE) with each 1-cm increase in precipitation. Abundance also closely deviated from mean maximum temperature during the brooding season at a lag time of one year (Fig. 2C) and abundance decreased by an average of 8.5 ± 2.9% with each 1 °C increase in temperature. Together, both of these weather factors explained 75% of temporal variation in abundance across the population based on a simple linear model. Importantly, maximum brooding-season temperature was higher and annual precipitation was lower than long-term averages during all but two years of the study (Appendix B). Warm-season precipitation at a 1-year lag also had a strong effect but there was little support for an effect of cool-season precipitation ($\Delta AIC_c \geqslant 7.14$) or for the winter stress hypothesis (Table 3).

Spatial variation in vegetation and land use had large effects on spatiotemporal variation in abundance. A top-ranked model included positive effects of abundance of potential nest sites, structural complexity and amount of riparian vegetation, and a negative effect of land-use intensity, but there was little support for an effect of upland vegetation structure once these other factors were considered (Table 3; Fig. 3). Moreover, most vegetation and land-use factors that explained spatiotemporal variation in abundance were associated with CV_a in the predicted directions (Fig. 3).

4. Discussion

Abundance of ferruginous pygmy-owls in the Sonoran Desert of northwest Mexico declined by an estimated 19–27% over 12 years and temporal changes in owl abundance was highly associated with variation in precipitation and temperature. These patterns suggest that owl declines have been driven by drought and extreme temperature events that have dominated the climate of southwestern North America in recent years, and that are expected to intensify (Seager et al., 2007; Overpeck and Udall, 2010; Appendix B). Because patterns I observed in northwest Mexico conform generally to those observed for abundance or vital rates in the few vertebrate systems that have been monitored over the same period in other arid regions of western North America (Barrows, 2006; Flesch, 2008; Moses et al., 2012; Zylstra et al., 2013; Lovich et al., 2014), they have alarming implications for conservation. For ferruginous pygmy-owls, these implications are especially troublesome because populations have already declined to endangered levels in the neighboring USA and because both temperature and precipitation were associated with marked changes in abundance and have strong multiplicative effects on reproductive output that are likely driven by different mechanisms (Flesch, 2013). Despite these alarming trends, additional monitoring is needed to assess whether they represent short-term natural variation in abundance or an actual systematic long-term decline.

Table 1
Rankings and descriptions of models of population dynamics and population structure of ferruginous pygmy-owls in northwest Mexico, 2000–2011. Multivariate state-space models (mSSM) estimated population growth rate (u), observation variance (R), and process variance (Q), and linear mixed-effects models (LMEM) estimated trend (β_1), observation variance (σ^2), and random intercepts for each region (b_{0j}) in time-series abundance data. In mSSM that considered regional subpopulation structure, each estimated process error and covariance was considered an estimated parameter (K).

Model Description	K	ΔAIC_c	w_i
mSSM			
One population, one u, equal Q	21	0.00	0.67
Regional subpopulations, one u, equal Q	22	1.49	0.32
Regional subpopulations, one u, varying Q	30	8.48	0.01
Regional subpopulations, varying u, equal Q	25	8.92	0.01
Regional subpopulations, varying u, varying Q	33	16.44	0.00
LMEM			
Regional subpopulations, one β_1, varying σ^2, same b_{0j}	8	0.00	0.72
Regional subpopulations, one β_1, varying σ^2, varying b_{0j}	9	2.18	0.24
Regional subpopulations, varying β_1, varying σ^2, varying b_{0j}	11	6.60	0.03
One population, one β_1, equal σ^2, same b_{0j}	5	8.69	0.01
Regional subpopulations, one β_1, equal σ^2, varying b_{0j}	6	10.81	0.00
Regional subpopulations, varying β_1, equal σ^2, varying b_{0j}	8	15.10	0.00

4.1. Trends and variances

Although trend estimates based on both approaches were negative, estimates from multivariate state-space models (mSSM) were steeper (2.8%/yr) with much lower precision than those from linear-mixed effects models (LMEM; 1.9%/yr). Because process noise can produce autocorrelated residuals and may drive short-term declines in populations that are actually stable, estimates of decline from SSM tend to be higher than those from generalized linear models of observed counts (Wilson et al., 2011b). Nonetheless, by assuming no process noise, generalized linear models underestimate true uncertainty in population trends. Although confidence interval coverage in SSM improves with time-series length (Humbert et al., 2009), estimates of precision from mSSM based on longer time series (22–28 years at 6–13 sites) are similar to those reported here based on a 12-year time series at 18 sites, suggesting much longer time series are needed to augment precision (Hinrichsen and Holmes, 2010; Ward et al., 2010). Despite uncertainty, the fact that both approaches produced similar estimates matches results from the only other comparison of similar techniques of which I am aware (Wilson et al., 2011a) and increases confidence that populations have indeed declined.

Table 2
Parameter estimates from top-ranked models of population dynamics and population structure of ferruginous pygmy-owls in northwest Mexico, 2000–2011. Multivariate state-space models (mSSM) estimated population growth rate (u), observation variance (R), process variance (Q), and linear mixed-effects models (LMEM) estimated trend (β_1), observation variance (σ^2), and random intercepts for each region (b_{0j}) in time-series abundance data.

Model	u/β_1		R/σ^2		Q	
Description	Estimate	SE	Estimate	SE	Estimate	SE
mSSM						
One population, one u, equal Q	−0.026	0.036	0.091	0.0091	0.013	0.0093
Regional subpopulations, one u, equal Q	−0.028	0.036	0.082	0.0089	0.019	0.010
Model averaged estimates and unconditional SE	−0.026	0.036	0.086	0.0099	0.015	0.0097
LMEM						
Regional subpopulations, one β_1, varying σ^2, same b_{0j}	−0.019	0.0079	0.094	0.021		

Table 3
Model rankings and parameter estimates for the effects of weather and habitat factors on abundance (log +1) of ferruginous pygmy-owls along 18 transects in northwest Mexico, 2000–2011. Parameter estimates are on a percent scale and based on linear mixed-effects models with residual variances estimated for each region. Predicted effects of precipitation (P, cm) and temperature (T, °C) considered lag times of one ($t-1$) and two ($t-2$) years and annual (October–September), brooding-season (May–June), warm-season (June–September), and winter (November–March) periods. Habitat factors include cavity abundance (%), riparian vegetation structure (principal component correlated with vegetation height, volume, and woodland cover in riparian areas), width of riparian vegetation zone ($\log m$), upland vegetation structure (principal component correlated with vegetation height and volume in upland areas), and land-use intensity (sum of ranks across categories; 0-none, 1-low, 2-mod., 3-high). Parameter estimates and standard errors are in parentheses.

Model and estimates	K	AIC_c	ΔAIC_c	w_i
Weather Hypotheses {Factor (β_1 ± SE)}				
Nestling Stress + Indirect Prey Enhancement {T-avg. max. brooding $t-1$ (−8.5 ± 2.9), P-annual $t-2$ (0.42 ± 0.17)}	10	175.95	0.00	0.73
Nestling Stress {T-avg. max. brooding $t-1$ (−11.2 ± 2.8)}	9	179.78	3.83	0.11
Nestling Stress + Direct Prey Enhancement {T-avg. max. brooding $t-1$ (−9.5 ± 3.0), P-warm season $t-1$ (0.51 ± 0.39)}	10	180.28	4.33	0.08
Indirect Prey Enhancement {P-annual t-2 (0.59 ± 0.16)}	9	181.72	5.77	0.04
Nestling Stress + Winter Stress {T-avg. max. brooding $t-1$ (−11.2 ± 2.8), T-avg. min. winter (0.23 ± 2.7)}	10	181.97	6.02	0.04
Direct prey enhancement {P-warm season $t-1$ (1.0 ± 0.36)}	9	187.24	11.29	0.00
Null {time, intercepts, ${\sigma^2}_j$}	8	192.47	16.52	0.00
Winter stress {T-avg. min. winter (0.56 ± 2.8)}	9	194.62	18.67	0.00
Habitat Models and Factors (β_1 ± SE)				
Cavities (1.3 ± 0.3) + Rip. veg. structure (19.2 ± 5.8) + Rip. width (26.8 ± 7.7) + Land use (−18.0 ± 8.6)	14	158.50	0.00	0.40
Cavities (1.4 ± 0.3) + Rip. veg. structure (22.8 ± 6.6) + Rip. width (25.9 ± 7.6) + Land use (−15.5 ± 8.7) + Up. veg. structure (−4.6 ± 4.4)	15	159.72	1.22	0.22
Cavities (1.4 ± 0.3) + Rip. veg. structure (22.6 ± 6.2) + Rip. width (22.4 ± 8.3)	13	160.26	1.76	0.17
Cavities (1.5 ± 0.3) + Rip. veg. structure (27.1 ± 6.7) + Rip. width (22.0 ± 7.8) + Up. veg. structure (−6.7 ± 4.6)	14	160.48	1.98	0.15
Cavities (1.4 ± 0.4) + Rip. veg. structure (17.2 ± 7.0)	12	164.18	5.68	0.02
Cavities (1.5 ± 0.4) + Rip. veg. structure (22.1 ± 7.7) + Up. veg. structure (−7.1 ± 5.5)	13	164.85	6.35	0.02
Cavities (1.4 ± 0.4) + Rip. veg. structure (14.8 ± 7.3) + Land use (−10.1 ± 10.7)	13	165.54	7.05	0.01
Cavities (1.6 ± 0.4)	11	167.36	8.86	0.00
Cavities (1.6 ± 0.5) + Up. veg. structure (0.83 ± 5.8)	12	169.58	11.08	0.00
Null {time, weather, intercepts, σ_j^2}	10	175.95	17.45	0.00

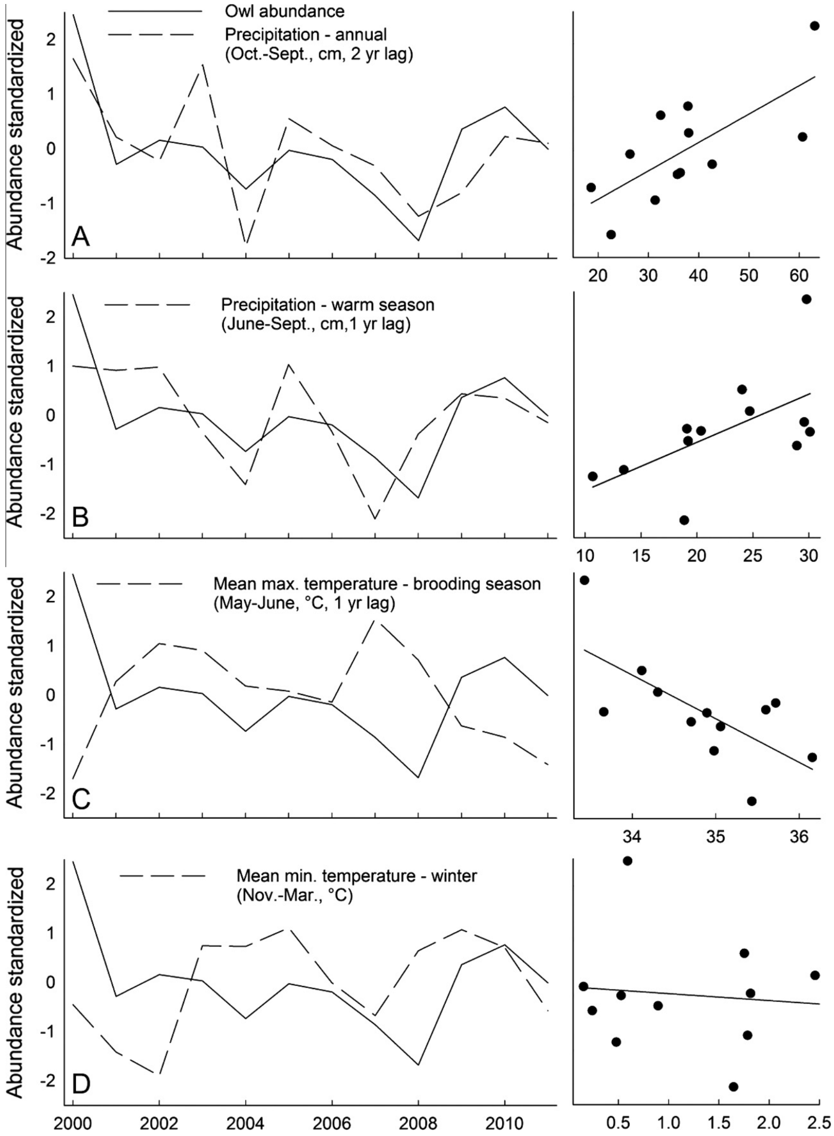

Fig. 2. Associations between abundance of ferruginous pygmy-owls and weather factors in the Sonoran Desert of northwest Mexico, 2000–2011. Left panel shows how variation in annual estimates of owl abundance tracked different weather factors across time on a standardized scale. Right panel shows associations between annual estimates of owl abundance and the weather factor depicted in the adjacent figure on the left panel on the observed scale. Lines are based on linear models.

By explicitly estimating both observation error and process noise, SSM can provide more reliable inferences on population trends, especially in noisy systems or situations where sampling methods are unstandardized. Nonetheless, when data are too sparse to reliably separate process noise from observation error, using SSM at a cost of precision may not be a useful tradeoff, especially when sampling effort is high and measurement error and process noise are known or suspected to be low *a priori.* In these situations, more conventional approaches such as LMEM may be preferred.

Estimates of process noise (0.015) were relatively low, within the range reported for other vertebrates, similar to estimates for other non-passerine birds, and higher than for many large mammals (Sabo et al., 2004; Holmes et al., 2007). Although precision was also low given the relatively short time series (Lindley, 2003), estimates of process noise are useful for forecasting extinction risks, especially for species of conservation concern such as pygmy-owls where no prior information existed. In contrast, estimates of observation error (0.086) were higher, more precise, similar to or lower than those for other non-passerine birds, and higher than those for long-lived mammals (Lindley, 2003; Staples et al., 2004; Ward et al., 2010).

Trends did not vary regionally based on either approach but other aspects of population structure varied. When no process noise was assumed, observation error varied regionally suggesting higher levels of population structure than mSSM. When observation error and process noise were partitioned, process noise did not vary regionally but year-to-year deviations in population growth were moderately correlated among regions indicating largely synchronous dynamics across space. Whereas mSSM are useful for evaluating population structure (Ward et al., 2010), determining what drives this structure is more complex. Synchronized dynamics can be driven by dispersal, climate forcing, and spatial autocorrelation in important environmental factors (Ranta et al., 1995). Although regions I monitored were roughly equidistant, the region with the most disparate dynamics was isolated by mountains that can limit dispersal (Flesch et al., 2010). Climate forcing combined with local weather variation could drive synchrony at levels observed here and is suggested by marked weather effects. Moderate levels of synchrony have important

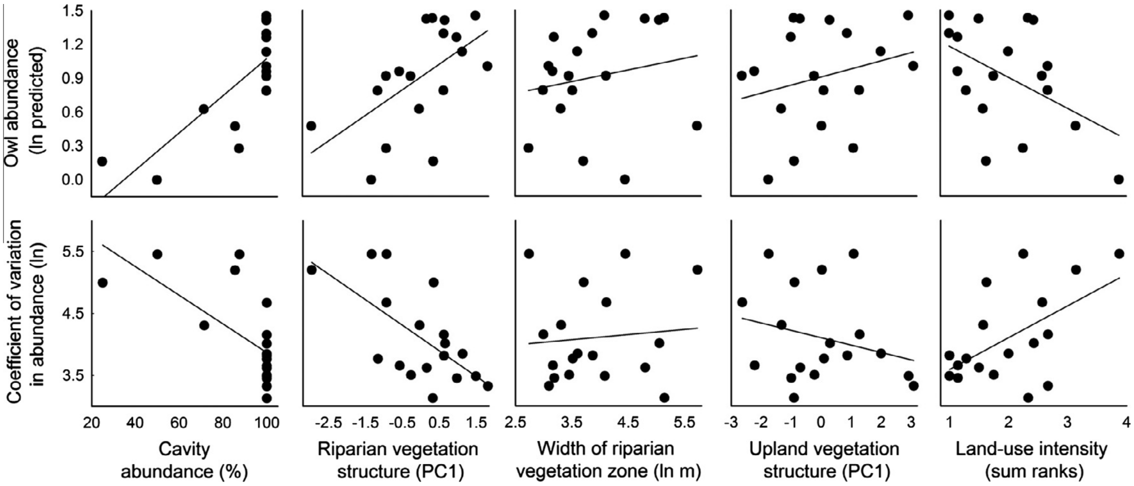

Fig. 3. Associations between spatial factors and abundance of ferruginous pygmy-owls along 18 transects in the Sonoran Desert of northwest Mexico, 2000–2011. Top panel shows average predicted abundances along each transect across gradients in five vegetation or land-use factors measured along transects, and are based on estimates from a linear mixed-effect model that included habitat and weather factors in the top-ranked model and a linear time effect. Bottom panel shows coefficients of variation in owl abundance (CV_a) across time for each transect vs. gradients in these same vegetation and land-use factors. Riparian vegetation structure was quantified based on a principal component (PC1) that was positively correlated with vegetation height, volume, and woodland cover in riparian areas, and upland vegetation structure was quantified based on a PC that was positively correlated with vegetation height and volume in upland areas. Parameter estimates (±SE) for each factor on abundance and CV_a are as follows: cavity abundance (1.6 ± 0.4, −2.3 ± 0.7), riparian vegetation structure (0.23 ± 0.08, −0.41 ± 0.12), width of riparian zone (0.10 ± 0.13, 0.08 ± 0.22), upland vegetation structure (0.07 ± 0.07, −0.12 ± 0.11), land-use intensity (−0.28 ± 0.12, 0.51 ± 0.19). Lines are based on linear models.

implications for persistence because highly synchronized populations face greater extinction risks (Heino et al., 1997).

4.2. Environmental drivers

Precipitation was strongly associated with temporal changes in abundance but annual precipitation at a two-year lag had greater effects than warm-season precipitation at a one-year lag, which is consistent with the ecology of this system and other arid systems in general. In arid environments, precipitation often drives rapid increases in plant biomass, seed production, and insect abundance, and these resource pulses directly bolster food availability for small vertebrates thus increasing their abundances 6–12 months later (Jaksic, 2001; Lima et al., 2002, 2008). Consequently, predator populations are often affected indirectly and respond two years later (Jaksic et al., 1992; Dennis and Otten, 2000; Lima et al., 2002; Letnic et al., 2005). In the Sonoran Desert, pygmy-owls primarily consume lizards and secondarily large arthropods (unpublished data), which explains why precipitation had stronger effects at a lag time of two vs. one year. Wide-ranging effects of precipitation on the dynamics of vertebrate populations have been observed on at least three continents (Holmgren et al., 2006) with this study providing a rare example from the Sonoran Desert (Flesch, 2008). Because observed effects and lag times are consistent with the ecology of this system and similar systems worldwide, they strongly suggest weather-mediated trophic interactions driven by drought contributed to declines.

In contrast with other arid systems (e.g., Holmgren et al., 2006), high winter precipitation driven by the El Niño Southern Oscillation (ENSO) may not be the principal driver of bottom-up dynamics in this system, even though ENSO events in early years affected annual precipitation. In the Sonoran Desert, summer rather than winter precipitation drives increases in lizard abundance (Flesch, 2008) and causes marked late-summer pulses in primary productivity when young pygmy-owls are recruiting into the adult population.

Weather can have indirect effects on populations by affecting resources or direct physiological effects (Stenseth et al., 2002). Owl abundance decreased with increasing average maximum temperatures during the brooding season at a lag time of one year, which suggests both direct and indirect processes operate in this system. Heat stress can directly affect the behavior and physiology of desert birds (Wolf, 2000) and its potential effect on small owls is plausible given they have lower thermal tolerances than other desert birds (Ligon, 1969). Direct effects are also suggested by the facts that use of hotter west-facing nest cavities by pygmy-owls declines from relatively cool to hot regions of the Sonoran Desert, and nest success is higher in cavities that produce cooler microclimates (Flesch and Steidl, 2010). Alternatively, indirect effects are also likely because high temperatures limit activity levels of lizard species that are commonly depredated by pygmy-owls (Flesch, 2008). Regardless of the mechanism, the observed negative effects of both high temperature and low precipitation has disturbing implications given future forecasts associated with climate change in this region (Seager et al., 2007; Appendix B).

Despite marked weather effects, spatial variation in vegetation and land use also had important effects on owl abundance. Abundance was higher on average in areas with more potential nest cavities, greater structural complexity and quantity of riparian vegetation, and lower intensity of livestock grazing and other land uses. Moreover, abundance also varied less across time with many of these same factors, suggesting they are important drivers of habitat quality. Higher nest-site abundance can enhance habitat quality by reducing predator efficiency (Martin, 1993) and by providing more optimal nest cavities that mitigate predation risk and thermal stress (Flesch and Steidl, 2010). Larger area and greater structural complexity of riparian vegetation also enhances reproductive performance of pygmy-owls (Flesch and Steidl, 2010; Flesch, 2013) whereas higher grazing intensity can degrade prey resources and cover (Fleischner, 1994). Thus, while the bottom-up effects of weather may have driven declines across the region, high-quality habitat seemed to promote local persistence. Although studies of population dynamics often focus on deterministic changes in abundance over large areas, spatial variation in local resources can explain variation in dynamics that is often assumed to be noise (Bjørnstad and Grenfell, 2001).

4.3. Conservation implications

Conserving vertebrate populations in arid environments in a changing climate poses a range of challenges for managers. For pygmy-owls, these challenges are especially complex in the USA where widespread degradation and fragmentation of riparian woodlands and urban growth have likely driven major population declines during the last century (USFWS, 2011) and where habitat restoration combined with natural or facilitated dispersal from Mexico may be needed for recovery. Although declines I describe in adjacent Mexico were not accompanied by any obvious changes in vegetation or land use, if they continue, recovery strategies that depend on dispersal from Mexico will be less effective and persistence of pygmy-owls in the northern Sonoran Desert could be jeopardized. Nonetheless, even in systems where weather has large effects, understanding other factors that affect population dynamics can help guide conservation. In this system, abundance was higher and varied less over time in areas with more nest cavities, greater structural complexity and amount of riparian vegetation, and lower land-use intensity, suggesting these factors are important drivers of habitat quality and good targets for managers. Thus, augmenting nest cavities by erecting nest boxes and translocating saguaros, restoring mesquite woodlands in riparian areas, which have been lost or degraded across large areas of the Sonoran Desert, and mitigating the effects of land use on important resources should augment habitat quality and recovery prospects for pygmy-owls. More broadly, because high-quality habitats can buffer the negative effects of harsh weather or amplify the benefits of favorable weather on vital and population growth rates (Franklin et al., 2000; Flesch, 2013) enhancing habitat quality offers a promising potential strategy for mitigating the effects of climate change. Understanding the extent to which habitat quality can mediate weather effects is important in the wake of anticipated climate change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.04.021.

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