EFFECTS OF LOCAL AND LANDSCAPE PROCESSES ON ANIMAL DISTRIBUTION AND ABUNDANCE

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Effects of local and landscape processes on animal distribution and abundance

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Abstract: Investigations of processes that drive animal distribution and abundance are often approached at one of two different scales and therefore focus on different processes. At local scales, animals are thought to select home ranges or territory patches in an ideal manner by occupying them in order of their fitness potential, but a variety of processes can decouple choices from their fitness consequences and create non-ideal patterns of distribution. At landscape scales, the spatial arrangement of habitat patches and their size and isolation are thought to influence distribution patterns because extinction probability declines with increasing patch area and colonization probability declines with increasing patch isolation. Although understanding the relative effects of local and landscape processes on distribution is essential for conservation, very few studies have explicitly considered the fitness potential or quality of habitat when doing so, especially at small scales relevant to the behavioral choices of individuals. I integrated behavioral and landscape approaches for understanding distribution by assessing the relative and combined effects of habitat quality at territory-specific scales and the effects of habitat amount, habitat configuration, and matrix structure at landscape scales on long-term occupancy dynamics of Ferruginous Pygmy-Owls over 12 years. To quantify habitat quality, I considered the estimated additive and interactive effects of habitat resources, stochastic factors (e.g., weather), and conspecific density on reproductive output based on extensive demographic monitoring over 10 years in the same territory patches.

Habitat resources explained a much greater proportion of variation in reproductive output than weather or conspecifics, but realized habitat quality was best described by the interactive effects of all these factors. High-quality habitats buffered the negative effects of conspecifics and amplified the benefits of favorable weather, but did not buffer the disadvantages of harsh weather. The positive, density-independent effects of favorable weather at low conspecific densities were offset by intraspecific competition at high densities. Habitat quality had greater effects than landscape processes on patch occupancy dynamics, and its effects were best described by interactions among habitat resources, weather, and conspecifics. Nonetheless landscape factors also had important effects: habitat amount had greater effects than habitat fragmentation or matrix structure, effects that were either positive or negative depending on local habitat quality. Although metapopulation theory is the dominant paradigm upon which many conservation strategies are based, improving local habitat quality may yield greater returns, especially when the surrounding landscape context is considered.

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PREFACE

Application of ecological theory to conservation is of profound and increasing importance given global threats to biodiversity and accelerating anthropogenic changes to the biosphere. One of the most pressing questions in applied ecology involves the relative effects of local versus landscape processes in driving animal distribution and abundance. Local processes are those that affect the birth and death rates of individuals at small spatiotemporal scales such as within individual home ranges. In contrast, landscape processes are those that typically affect movement and colonization of individuals among home ranges and population persistence at much larger landscape or metapopulation spatiotemporal scales. Ecologists working at small scales have focused on how the quality or fitness potential of habitat drives settlement choices by individuals when investigating broader patterns of distribution. In contrast, those working at larger landscape scales often focus on how the area and isolation of habitat and the structure of the intervening matrix of non-habitat affect distribution. Conservation and management recommendations that result from these studies are almost entirely dependent on the processes considered. Studies at large scales, for example, often suggest that increasing habitat area or connectivity will be beneficial. In contrast, studies at small scales often recommend strategies focused on enhancing specific resources that affect settlement choices or habitat quality. Although habitat quality, habitat area, and functional connectivity among patches of habitat are now widely recognized as the core drivers of animal distribution, effective conservation strategies depend on understanding the relative importance and integrated effects of these processes. Thus, the broad goal of my work is to explore the effects of local and landscape processes in driving the distribution and abundance of animals across space and time. While this is a conceptually attractive problem, addressing it has been difficult due to logistical and methodological challenges in estimating the fitness potential of space. Here, I provide a synthetic multi-scaled approach for understanding core processes that drive animal distribution by estimating habitat quality at local patch-specific scales and the individual, relative, and combined effects of habitat quality, habitat area, and functional connectivity on distribution.

As a study system, I considered Ferruginous Pygmy-Owls (*Glaucidium brasilianum*) in the Sonoran Desert region of northwest Mexico, which is immediately south of Arizona. This system has a number of advantageous properties. First, because detectability is nearly perfect, patch occupancy and abundance can be efficiently estimated with standardized techniques. Second, landscape processes should affect distribution in this system because pygmy-owls are non-migratory, disperse relatively short distances, and because movement behavior and colonization success during dispersal are affected by landscape structures such as roadways and agricultural fields. Finally, because pygmy-owls have declined to endangered levels in adjacent Arizona despite the presence of habitat, understanding the relative roles of local and landscape processes in driving distribution has important implications for management and recovery. In Arizona, pygmy-owls were listed as endangered in 1997, delisted for reasons unrelated to recovery in 2006, and are the focal species behind a major controversy between land developers and conservationists. In the late 1990s, a large proportion of the Arizona population of pygmy-owls that was known at the time, occupied developed and undeveloped areas around Tucson on lands of high economic and conservation value. Although the controversy has largely subsided with the loss of federal regulations linked to endangered status, the Arizona population is extremely small and has been extirpated around Tucson since 2006. Nonetheless, the pygmy-owl remains a focal species in regional conservation plans in southern Arizona and many unresolved questions regarding their ecology remain. This dissertation addresses some of these questions.

Each chapter I present builds on the preceding one by providing information and support upon which new questions are asked and answered. The research described herein relies heavily on papers I published during my second year in the graduate program at the University of Montana. These papers, which are not presented here, described the patterns and consequences of resource selection and showed that resource choices in this system are largely adaptive (Flesch and Steidl 2010), and assessed movement behavior and colonization success of dispersing individuals and showed that anthropogenic disturbance and landscape structure affect these parameters (Flesch et al. 2010; see Chapter 1 for literature cited). The chapters in this dissertation are formatted as individual publications for specific peer-reviewed scientific journals. Because one chapter was largely a collaborative effort (Chapter 2), I have listed collaborators as co-authors and use the collective “we” in that chapter.

The first paper (Chapter 1) entitled “Spatiotemporal trends and drivers of population dynamics in a declining Neotropical owl” describes population trends and population structure over a 12-year period and shows how temporal variation in weather and spatial variation in habitat and land use affected population dynamics. The second paper (Chapter 2) entitled “Spatial, temporal, and density-dependent components of habitat quality for Ferruginous Pygmy-Owls” explicitly estimates the fitness potential of space at the scale of individual territory patches by considering the effects of important habitat resources, temporal factors such as weather and primary productivity, and conspecific density. Although habitat quality is a fundamental concept in ecology, and is essential for understanding distribution, the relative and interactive effects of habitat resources, weather, and conspecifics in driving it are rarely investigated simultaneously in wild animal populations. This chapter, which is a long paper intended to be published as monograph, also addresses the relative importance of food and predation in driving performance, how the effects of conspecifics vary at different spatial scales, and how interactive relationships between habitat resources and weather can inform conservation and management in changing climates. The third paper (Chapter 3) entitled “Integrating behavioral and landscape approaches for understanding animal distribution” assesses the relative and combined effects of local (habitat quality, ecological traps) and landscape (habitat area, habitat fragmentation, matrix structure) processes on the distribution of owls across space. To address this problem, I consider long-term occupancy dynamics of owls measured over 12 years in 112 territory patches across broad gradients in habitat quality and landscape structure in a large number of independent landscapes. My approach is novel because I explicitly estimated the fitness potential or quality of space based on the effects of important habitat resources, stochastic factors, and conspecific density on vital rates at the scale of individual territory patches while simultaneously assessing the effects of landscape processes. During the last decade, landscape and metapopulation approaches have suggested an important role of habitat quality in driving animal distribution, thereby broadening the area-isolation focus that has dominated these approaches. Nonetheless, virtually all studies that consider habitat quality use indirect proxies based on resources that are thought to be important in driving vital rates rather than direct estimates of vital rates, which as I show has likely underestimated the role of habitat quality in driving distribution.

CHAPTER 1

SPATIOTEMPORAL TRENDS AND DRIVERS OF POPULATION DYNAMICS IN A DECLINING NEOTROPICAL OWL

Abstract. Estimates of population trends are useful for managers, but understanding processes that drive trends is vital for guiding management, especially of rare or at-risk species. Inferences on population trends an extinction risk are often affected by observation error and process noise and, thus, approaches for addressing these sources of error have important implications for trend detection and management. 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 northwest Mexico over 12 years. I also assessed how temporal variation in weather and spatial variation in habitat affected dynamics, which has important implications for managers, especially in adjacent Arizona where pygmy-owls have declined to endangered levels. Both approaches revealed declining trends in abundance but estimates from multivariate state-space models, which explicitly partitioned observation error and process noise were steeper (-2.8%/yr) with much lower precision (SE=3.6%) than those from mixed-effects models (-1.9%/yr, SE=0.8%), which assumed no process noise and indicated higher levels of population structure. Abundance increased markedly with annual precipitation at a lag time of two years and decreased with brooding-season temperature at a lag time of one year, and dynamics were largely synchronous across space, which is typical in climate-forced systems. Abundance was consistently higher and varied less across time in areas with more potential nest cavities, greater structural complexity and quantity of riparian vegetation, and lower intensity of anthropogenic land use, suggesting these factors are important drivers of habitat quality and good targets for managers. Given predictions for intensifying drought and warming temperatures associated with climate change, these results suggest active measures to enhance habitat quality can augment recovery

prospects.

Key words: ferruginous pygmy-owl, habitat quality, observation error, population trends, process error, state-space models, weather.

INTRODUCTION

Understanding temporal variation in animal abundance is a longstanding issue in ecology (Turchin 1995). In applied contexts, information on temporal variation in abundance is important for assessing population trends and extinction risk. Effective management responses to observed trends, however, also require understanding factors that drive population dynamics, especially for rare or at-risk species. A broad range of exogenous factors such as weather, predation, and habitat loss can drive population dynamics and these effects may depend on intrinsic factors such as age structure or population density (Turchin 2003). Given these complexities, identifying mechanisms that drive population dynamics may require experimental approaches in field settings that are logistically difficult (Bjørnstad and Grenfell 2001). Most data on populations, however, exist in the form of time series of abundance estimates and associated environmental data, which can provide important insights into processes that drive dynamics, especially when guided by hypotheses based on the biology of a system.

Time-series data indicate strong associations between weather and population dynamics in a broad range of systems (Stenseth et al. 2002). In arid environments, for example, precipitation can directly affect plant productivity and exert complex indirect effects on populations at various trophic levels and lag times (Holmgren et al. 2006). Even when weather is important, however, intrinsic factors can mediate its effects (Pelletier et al. 2012). One aspect of individual heterogeneity that has received less attention in the context of population dynamics but that has important implications for management is spatial variation in resources available to different individuals in a population (Reid et al. 2006, Ozgul et al. 2007). Because individuals with access to high-quality habitat may be less susceptible to harsh weather (Franklin et al. 2000), identifying resources that explain temporal variation in abundance should help focus managers, especially in changing climates.

Despite the importance of information on population dynamics and factors that drive it, two general sources of variation can affect inferences: observation error and process noise. Field surveys rarely reveal true abundance, and differences between truth and estimates produces observation error, which reduces confidence in trend estimates (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 partition both sources of error, state-space models (SSM) are being used increasingly to model population dynamics but are computationally complex, require long time series to estimate parameters, and may have lower precision and power to detect declines than more conventional approaches (Dennis et al. 2006, Wilson et al. 2011*a*). These issues are especially relevant when estimating trends and extinction probabilities for rare or at-risk populations where sample sizes and time-series length are often limited and where low precision and power complicate detecting patterns that have serious consequences.

Ferruginous Pygmy-Owls (*Glaucidium brasilianum*) were once considered common in portions of the Sonoran Desert in southern Arizona but were extirpated from much of their historic range due likely to habitat loss (Johnson et al. 2003). Consequently, pygmy-owls were listed as endangered in Arizona in 1997 but delisted for reasons unrelated to recovery in 2006 when less than 10 pairs were known (USFWS 2011). In neighboring northwest Mexico, pygmy-owls are more common, found in similar environments where riparian woodlands occur near stands of giant saguaro cacti (*Carnegiea gigantea*), which provide nest cavities, and were thought to be declining for unknown reasons (Flesch and Steidl 2006). Mexican populations of pygmy-owls are important for recovery in Arizona because natural or facilitated dispersal from Mexico can augment populations, especially when coupled with habitat restoration, and because information on factors that drive population dynamics can guide management. Despite the importance of Mexican populations, current data on population trends and factors that drive them are unavailable.

I evaluated population trends and population structure of pygmy-owls in northwest Mexico by comparing inferences from multivariate state-space models (mSSM), which explicitly estimate observation error and process noise, and more conventional mixed-effects models of observed counts, which assume no process noise. Understanding how assumptions regarding these sources of error affect inferences is important for guiding monitoring and management in this and a broad range of other systems despite few comparisons of techniques (e.g., Wilson et al. 2011*a*). Moreover, unbiased forecasts of extinction risk require explicit estimates of process noise and information on population structure because populations with low process noise and high levels of structure (e.g., numerous independent subpopulations with asynchronous dynamics) are less vulnerable to extinction (Heino et al. 1997, Holmes et al. 2007). Because information on factors that explain population dynamics can guide managers and because weather often affects population dynamics in arid environments but may be less influential in high-quality habitat, I evaluated hypothesized relationships between population dynamics and temporal variation in weather and assessed the effects of spatial variation in vegetation and land use.

METHODS

I considered a region in northwest Mexico that is within 120 km of Arizona and includes both major vegetation communities occupied by pygmy-owls, the Arizona Upland subdivision of the Sonoran Desert and semi-desert grassland. 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, and sub-shrubs. 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-Sept and winter storms that are most intense during the El Niño Southern Oscillation.

Sampling and survey design

I estimated abundance by repeatedly surveying the same locations across time. In spring of 2000, I surveyed a random sample of 71 transects. After these initial surveys, I selected 18 transects that were occupied by pygmy-owls and surveyed them each spring for the next 11 years. Survey effort was focused in 4 regions and totaled 54 km/yr (*see* Flesch and Steidl 2006). 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 (*see* Flesch and Steidl 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.

Trend analyses

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

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

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

where x_t is a vector of $\log_e$+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 distribution with mean zero and variance Q that measures process variance (Hinrichsen and Holmes 2010). In eq. 2, y_t is a vector of $\log_e$+1 transformed counts of male pygmy-owls 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–1intercept-like parameters, and w is observation error that has a multivariate normal distribution with mean zero and variance R that measures observation variance. Data enter the model as y's and x's are estimated. I assumed initial abundance was not at equilibrium and density independence (B=1) because estimates of B based on parametric bootstrap likelihood ratio tests (Dennis and Taper 1994) and the best mSS model were ≥0.96 (Sabo et al. 2004). 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 mSSM consider multiple time series simultaneously and do not require condensing data from each sample into a single population-wide estimate for each time step, which allows variation in growth rates and process errors among population units in different spatial strata and covariance among errors to be estimated. Thus, parameter estimates were based on the full 18 time series by

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 growth rate and process error, 2) regional subpopulations (m=4) with a common growth rate and equal or varying process errors, and 3) regional subpopulations with varying growth rates and equal or varying process errors. 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 does not partition observation and process error, I fit a similar set of linear mixed-effects models (LMEM)

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

where 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, ε_{it} is an error term that has a normal distribution with a mean of zero and variance σ^2, which measures what is assumed to be observation variance, and y_{it} is the observed data as in eq. 2. 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 is reported. I used restricted maximum likelihood when assessing models with different random effects, ML methods 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 for >1 model (Burnham and Anderson 2002).

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 (Nov-Mar) 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 abundance of prey 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 (Oct-May), warm-season (June-Sept), and annual (Oct-Sept) precipitation when evaluating prey enhancement hypotheses, and temperature during incubation (Apr) and brooding (May-June) when evaluating the nestling stress hypothesis and used factors that minimized AIC_c to represent each hypotheses. Correlations between weather factors representing hypotheses were low (r = -0.41-0.38). All weather data were taken from stations near Sasabe, Arizona, which is 5-75 km from transects (WRCC 2011).

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 amounts of riparian vegetation by measuring the width of riparian corridors. To describe vegetation structure, I measured woodland cover, canopy height, and vegetation volume in riparian areas, and canopy height and vegetation volume in adjacent uplands. I estimated abundance of potential nest sites by measuring the proportion of stations where mature saguaros were present, which were the only substrate 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 >3-m above ground ($r \geq 0.34$), whereas a component representing upland vegetation structure was positively correlated with canopy height (r=0.65) and vegetation volume ≥1-m above ground (r≥0.90). Correlations between most vegetation and land-use factors were low (r = -0.40-0.52).

To evaluate the effects of temporal (weather) and spatial (habitat and land use) factors on population dynamics, 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 that represented the effects of five potential covariates and considered abundance of potential nest sites in all models because safe nests are critical for reproduction. Because inferences were similar based on both modeling approaches, all reported effects are from LMEM.

Theoretical models of habitat selection predict the highest quality places are selected first and used more consistently over time (Fretwell and Lucas 1969). 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 vegetation and land-use factors associated with habitat quality, I regressed spatial factors against CV_a.

RESULTS

Trends and variances

Abundance declined across time based on both modeling approaches (Fig. 1). Two top-ranked mSSM estimated negative growth rates of 2.6-2.8%/yr, a 25.2-26.5% decline over 12 years. A top-ranked LMEM estimated a declining trend of 1.9%/yr or 19.2% overall (Tables 1-2). Despite similar 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), then increased. Although dynamics varied somewhat regionally (Fig. 1), there was no evidence that trends varied among regions ($\Delta AIC_c \geq 6.6$; Table 1).

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

Estimates of process variance from mSSM (0.015) were much lower than observation variance (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 variance from LMEM (0.094) were similar to the sum of both variances from mSSM.

Environmental drivers

Temporal variation in weather explained owl abundance in the predicted directions but support among hypotheses varied. Support for the delayed prey enhancement hypothesis with annual precipitation and the nestling stress hypothesis with brooding-season temperature 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. Additionally, temporal variation in abundance closely deviated from average maximum temperatures 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-ºC increase in temperature.

Annual precipitation at a lag time of two years has stronger effects than warm-season precipitation at a lag time of one year. There was little support for an effect of cool-season precipitation ($\Delta \mathrm{AIC_c} \geq 7.14$) or for the winter stress hypothesis (Table 3; Fig. 2).

Spatial variation in vegetation and land use had large effects on local temporal variation in abundance. A top-ranked model included positive effects of abundance of potential nest sites and structural complexity and amount of riparian vegetation, and a negative effect of land-use intensity, but there was little support for an effect of structural complexity of upland vegetation once these factors were considered (Table 3; Fig. 3). Most vegetation and land-use factors that explained local variation in abundance were associated with $\mathrm{CV_a}$ in the predicted directions (Fig. 3). Abundance of potential nest sites ($\beta_1 \pm \mathrm{SE} = -2.3 \pm 0.7$) and structural complexity of riparian vegetation (-0.41±0.12) decreased with increasing $\mathrm{CV_a}$ whereas land-use intensity increased (0.51±0.19).

DISCUSSION

Abundance of Ferruginous Pygmy-Owls in the Sonoran Desert of northwest Mexico declined by an estimated 1.9%/yr or 19% over 12 years based on linear-mixed effects models (LMEM) that assumed no process noise, and by up to 2.8%/yr or 27% overall based on multivariate state-space models (mSSM) that explicitly considered process noise and observation error. Despite similar trend estimates, precision varied and confidence intervals from mSSM were broad and included positive values. Because process noise can produce autocorrelated residuals and may suggest 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. 2011*b*). In comparison, by assuming no process noise, generalized linear models of observed counts underestimate true uncertainty in trend estimates. 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 required to generate precise trend estimates (Hinrichsen and Holmes 2010, Ward et al. 2010). Because detection probability of pygmy-owls is nearly perfect and thus measurement error is low (Flesch and Steidl 2007), any effect of observation error on uncertainty was due largely to sampling error. 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 and increases confidence that populations have indeed declined (Wilson et al. 2011*a*).

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 in situations where 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 of counts may be preferred.

Estimates of process noise (0.015) were fairly 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, Ward et al. 2010). Although precision was also low, given the relatively short time series (Lindley 2003), estimates of process noise are critical for assessing extinction probability (Holmes et al. 2007), especially for at-risk species such as pygmy-owls for which no prior information existed. In contrast, estimates of observation variance (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 inferences regarding population structure differed. When no process noise was assumed, estimates of observation error varied regionally suggesting higher levels of population structure than indicated by mSSM. When observation error and process noise were partitioned, however, process noise did not vary regionally but year-to-year deviations in population growth were moderately correlated among regions suggesting somewhat synchronous dynamics across space. mSSM are useful for evaluating population structure (Ward et al. 2010) but 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 considered were roughly equidistant, one region with the most disparate dynamics was isolated by mountains that can limit dispersal (Flesch et al. 2010). Climate forcing combined with local variation in weather could drive synchrony at levels observed here, especially given marked weather effects. Moderate levels of synchrony have important implications for persistence because highly synchronized populations face greater extinction risks (Heino et al. 1997).

Weather was associated with marked changes in abundance, and important factors and lag times identified were consistent with the ecology of this system and arid systems in general. Precipitation had large effects on owl abundance and annual precipitation at a lag time of two years had larger effects than warm-season precipitation at a lag time of one year. In arid environments, precipitation drives rapid increases in plant biomass, seed production, and insect abundance, and these resource pulses directly bolster food availability for small vertebrates, which increases their productivity and abundance 6-12 months later (Jaksic 2001, Lima et al. 2002, 2008). Consequently, predator populations are often separated from the direct effects of precipitation and exhibit numerical responses two years later (Jaksic et al. 1992, Dennis and Otten 2000, Lima et al. 2002, Letnic et al. 2005, this study). In the Sonoran Desert, pygmy-owls are generalists that primarily consume lizards and secondarily large arthropods (Flesch, *unpubl. data*), which explains why precipitation had stronger effects at lag times of two vs. one year. Wide-ranging effects of precipitation on the dynamics of small vertebrate and predator populations have been observed on at least three continents (Holmgren et al. 2006) with this study providing a rare example from the Sonoran Desert (Rosen 2000). Because weather factors and lag times identified here are consistent with the ecology of this system and similar systems worldwide, these patterns suggest weather-mediated trophic interactions and the ongoing drought drove observed declines.

In contrast with other arid systems (Holmgren et al. 2006), 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 had large effects on precipitation. In the Sonoran Desert, summer rather than winter precipitation drives increases in lizard abundance (Rosen 2000) 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 as average maximum temperatures during the brooding season increased 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). The role of direct effects is suggested by the fact that use of hotter west-facing nest cavities in this system declines from cool to hot regions, and that nest success increases in cavities with cooler microclimates (Flesch and Steidl 2010). Alternatively, indirect effects are also plausible because temperatures >20-30ºC reduce activity levels of lizard species that are commonly depredated by pygmy-owls (Flesch, *unpubl. data*). Regardless of the mechanism, negative effects of high temperatures has disturbing implications given predictions for increasing temperatures associated with climate change.

Spatial variation in vegetation and land use may have affected population dynamics in important ways. Abundance was higher on average in areas with higher abundance of potential nest cavities, greater structural complexity and quantity of riparian vegetation, and lower intensity of 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 abundance of potential nest cavities 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 quantities and greater structural complexity of riparian vegetation also enhances reproductive performance of pygmy-owls (Flesch and Steidl 2010) whereas higher grazing intensity and other land uses can degrade resources (Fleischner 1994). Thus, while bottom-up effects of weather may have driven declines, high-quality habitat can 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.

Conserving populations of pygmy-owls in Arizona has been a major focus of managers since they were first listed as endangered. If declines in abundance described here continue, recovery strategies that depend on dispersal from Mexico will be less effective and persistence of pygmy-owls in the Sonoran Desert could be jeopardized. Although active recovery strategies such as facilitated dispersal from Mexico have been considered, these efforts should not remove individuals from populations that are declining. Quantitative trend estimates for pygmy-owls in Arizona are unavailable, but historic information and recent surveys suggest widespread loses of riparian woodlands drove major contractions in distribution over the last century (Johnson et al. 2003, USFWS 2011). Thus, declines I described in adjacent Mexico are notable because they were not accompanied by any obvious changes in vegetation or land use.

Understanding factors that drive population dynamics at local scales can help guide conservation efforts. In this system, abundance was higher and varied less over time in areas with more nest cavities and riparian vegetation, and less intensive land use. Thus, management focused on these factors should enhance recovery prospects. For example, augmenting nest cavities (e.g., nest boxes or saguaro translocation) and restoring mesquite woodlands in riparian areas, which have been lost or degraded across vast portions of southern Arizona and northwest Mexico, should simultaneously enhance habitat quality and habitat area. Despite these recommendations, predictions for increasing temperature and decreasing precipitation due to climate change (Seager et al. 2007) could make habitat management less effective. Although some local factors seemed to promote habitat quality, the relative effects of habitat vs. weather are unknown because they were each measured at different scales. Understanding the extent to which high-quality habitat can buffer the effects of harsh weather is important in this and many other systems in the wake of anticipated climate change.

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SUPPLEMENTAL MATERIAL

Appendix A

A figure illustrating profile log-likelihoods of parameter estimates from the top-ranked multivariate state-space model.

Appendix B

A figure illustrating variation in temperature and precipitation between 1960 and 2011 in the study region.

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 (Q), 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.

Model Description	K	$\Delta\text{AIC}_\text{c}$	w_i
mSSM			
One population, equal u, equal Q	21	0.00	0.67
Regional subpopulations, equal u, equal Q	22	1.49	0.32
Regional subpopulations, equal 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, equal β_1, varying σ^2, same b_{0j}	8	0.00	0.72
Regional subpopulations, equal 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, equal β_1, equal σ^2, same b_{0j}	5	8.69	0.01
Regional subpopulations, equal 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

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 trends (β_1), observation variance (σ^2), and random intercepts for each region (b_{0j}) in time-series abundance data.

Model	u / β_1		R		Q	
Description	Estimate	SE	Estimate	SE	Estimate	SE
mSSM						
One population, equal u, equal Q	-0.026	0.036	0.091	0.0091	0.013	0.0093
Regional subpopulations, equal u, equal Q	-0.028	0.036	0.082	0.0089	0.019	0.010
Model averaged estimates, unconditional SE	-0.026	0.036	0.086	0.0099	0.015	0.0097
LMEM						
Regional subpopulations, equal 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. Hypothesized precipitation (P, cm) and temperature (T, ºC) effects consider lag times of one (*t*-1) and two (*t*-2) years, and annual (Oct-Sept), brooding-season (May-June), warm-season (June-Sept), and winter (Nov-March) periods. Habitat factors include cavity abundance (%), riparian vegetation structure (principal component correlated with vegetation height, volume, and woodland cover), width of riparian vegetation zone (log m), upland vegetation structure (principal component correlated with vegetation height and volume), and land-use intensity (sum of ranks; 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, σ^2_i}	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^2_j}	10	175.95	17.45	0.00

Fig. 1. Temporal variation and trends in abundance of Ferruginous Pygmy-Owls in northwest Mexico, 2000-2011. Top figure shows standardized annual estimates of 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). Inset figure shows trends based on each modeling approach. Bottom figure shows temporal variation in abundance in each of four regions based on estimates from a multivariate state-space that considered spatial population structure.

Fig. 2. Associations between weather and abundance of Ferruginous Pygmy-Owls in northwest Mexico, 2000-2011. Left panel shows how annual estimates of total abundance tracked different weather factors across time on a standardized scale. Right panel shows associations between total annual estimates of abundance and the weather factor depicted in the adjacent figure on the left panel on the observed scale. Lines are based on linear models.

Fig. 3. Associations between habitat factors and abundance of Ferruginous Pygmy-Owls along 18 transects in northwest Mexico, 2000-2011. Top figures show average predicted abundances for each transect from a linear mixed-effect model that included the effects of all five habitat factors, two weather factors included in the top-ranked model described in Table 3, and a linear time effect. Bottom figures show coefficients of variation in abundance for each transect across time versus the same five habitat factors. Riparian vegetation structure was quantified based on a principal component that was positively correlated with vegetation height, vegetation volume, and woodland cover in riparian areas and upland vegetation structure was quantified based on a principal component that was positively correlated with vegetation height and vegetation volume in upland areas. Lines are based on linear models.

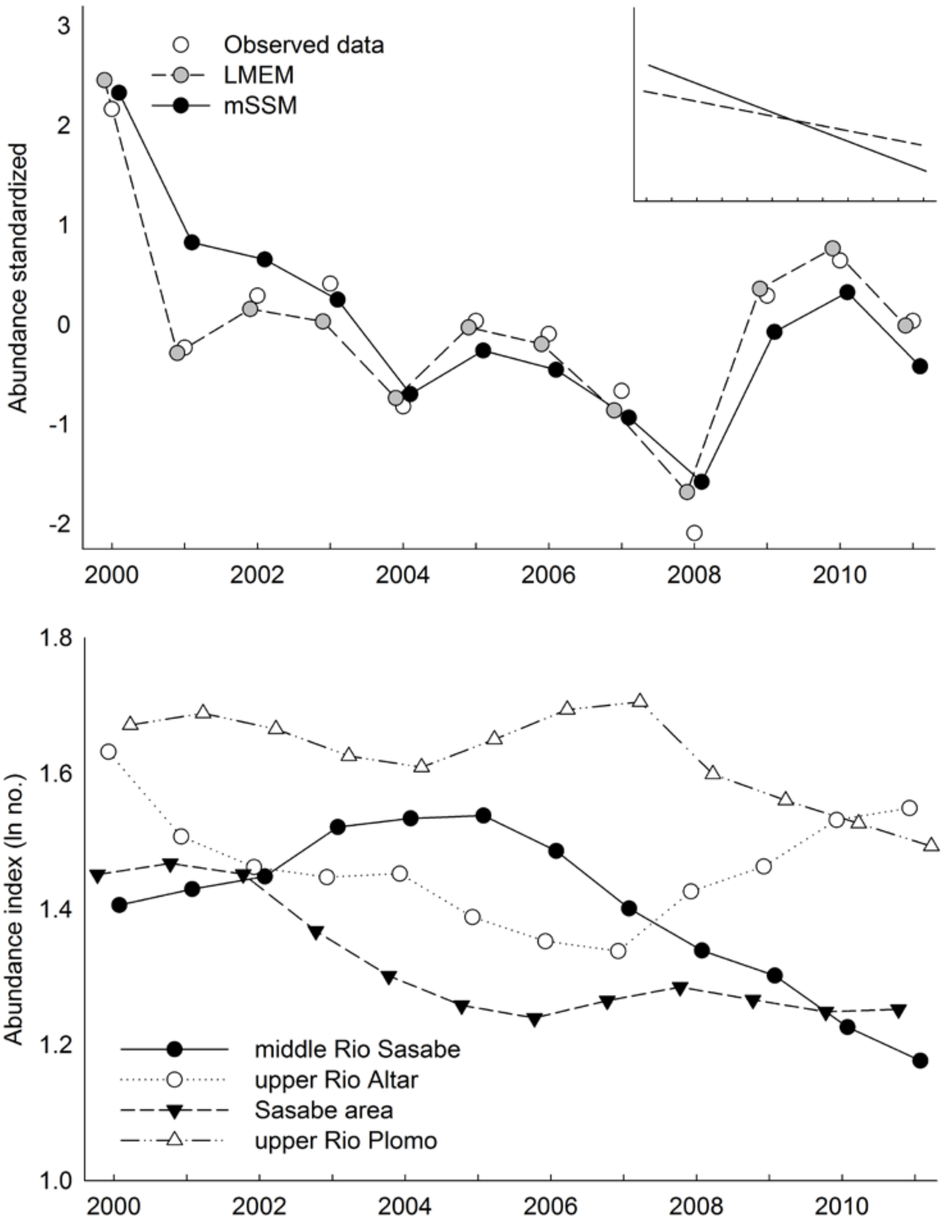

Abundance standardized
3
2
1
0
-1
-2
Observed data
LMEM
mSSM
2000
2002
2004
2006
2008
2010
Abundance index (ln no.)
1.8
1.6
1.4
1.2
1.0
middle Rio Sasabe
upper Rio Altar
Sasabe area
upper Rio Plomo
2000
2002
2004
2006
2008
2010

Fig. 1

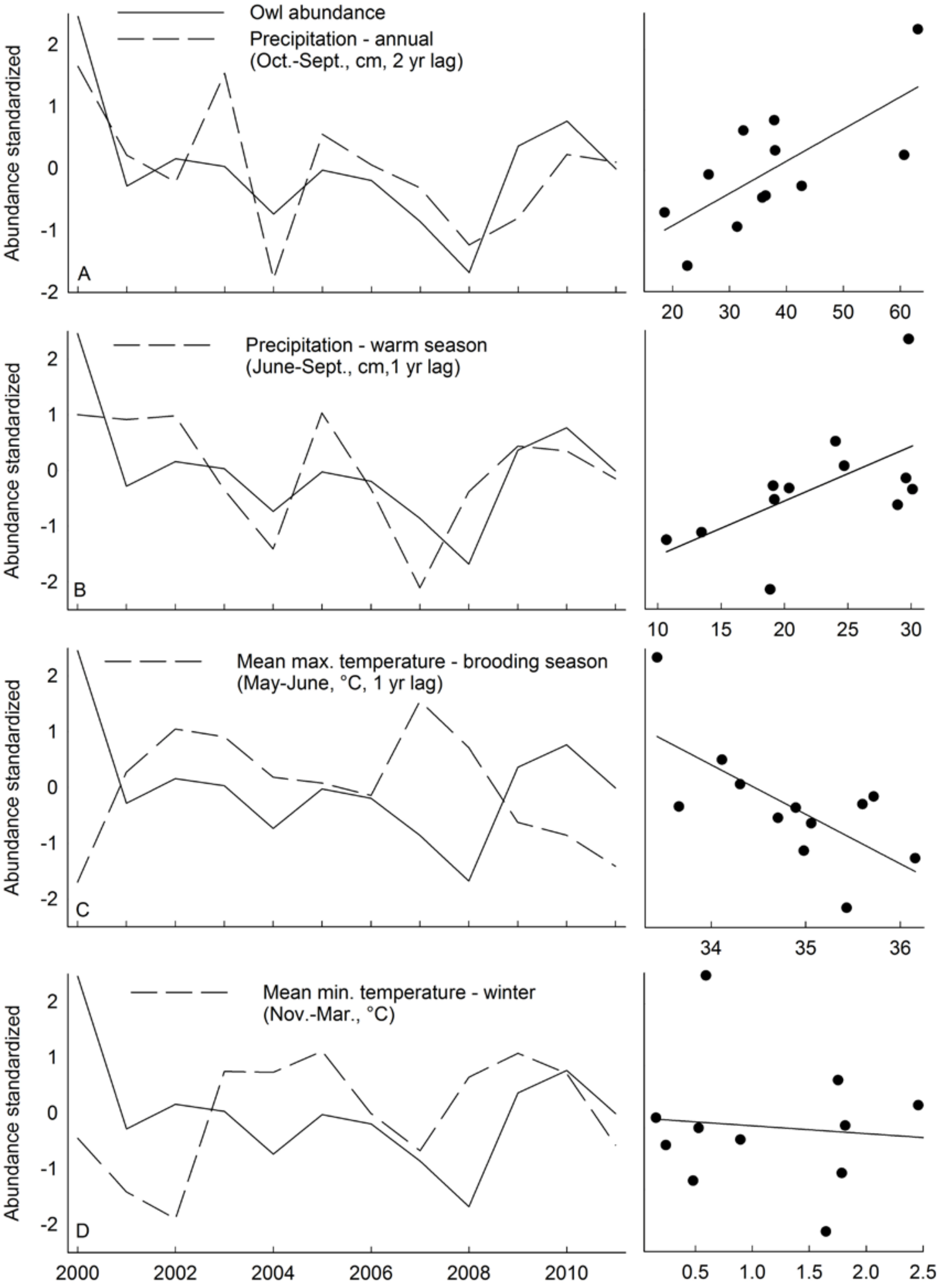
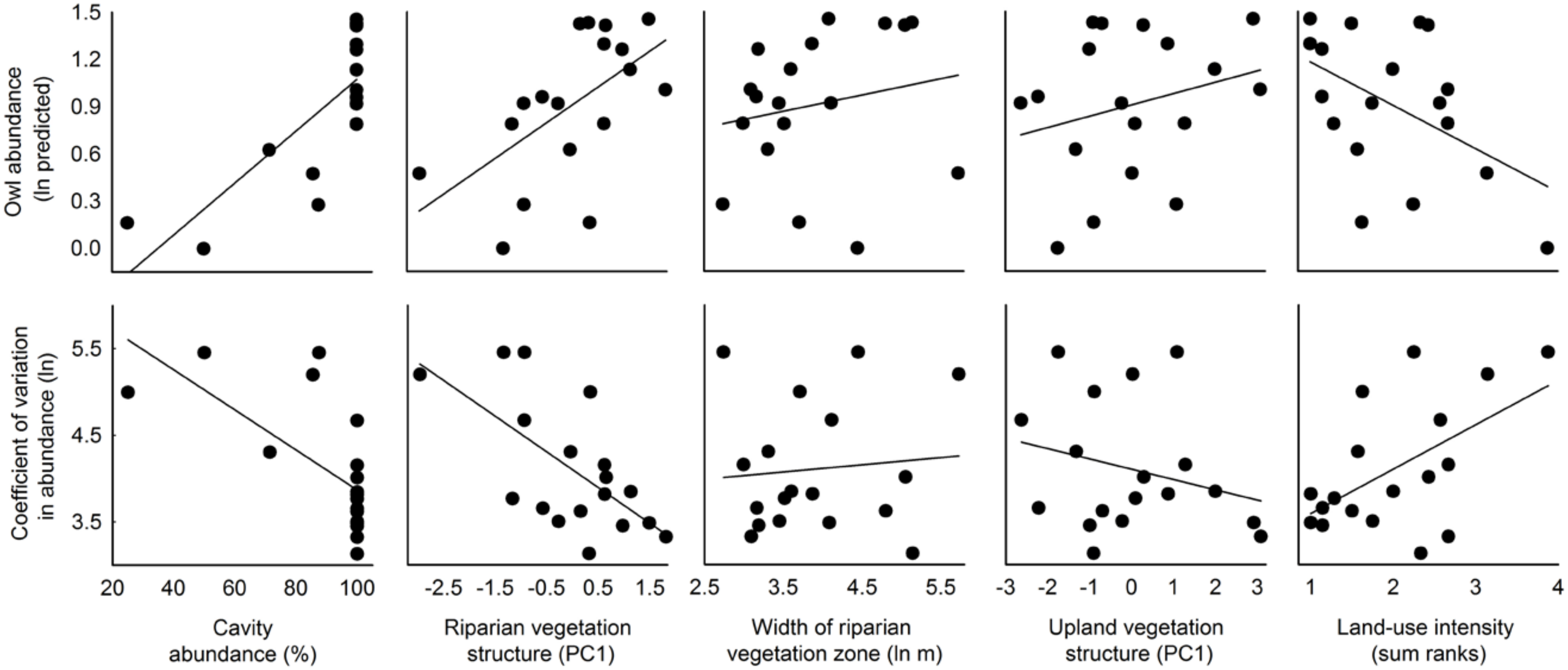

Owl abundance
Precipitation - annual
(Oct.-Sept., cm, 2 yr lag)
Precipitation - warm season
(June-Sept., cm,1 yr lag)
Mean max. temperature - brooding season
(May-June, °C, 1 yr lag)
Mean min. temperature - winter
(Nov.-Mar., °C)
Abundance standardized
A
B
C
D
2
1
0
-1
-2
2000
2002
2004
2006
2008
2010
20
30
40
50
60
10
15
20
25
30
34
35
36
0.5
1.0
1.5
2.0
2.5

Fig. 2

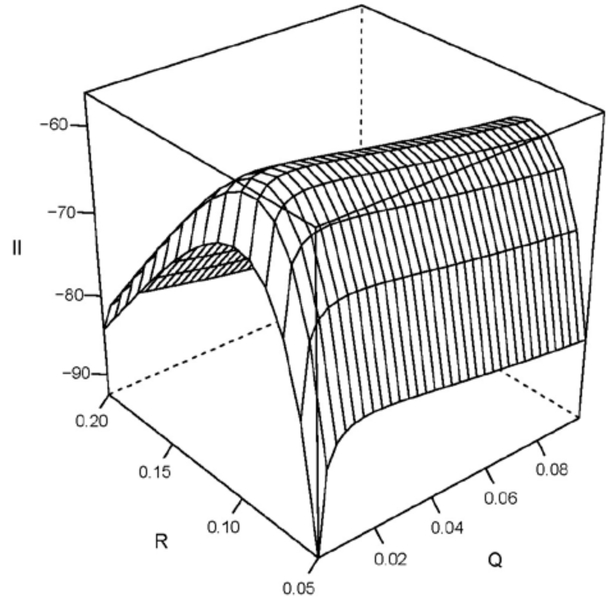


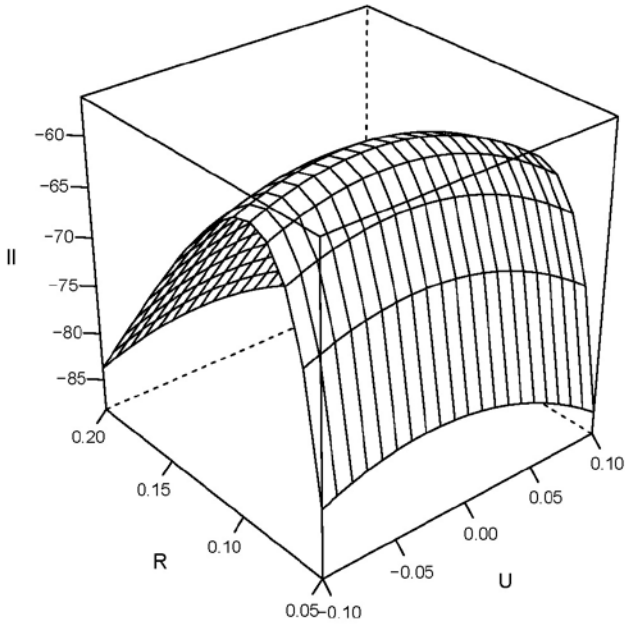
Owl abundance (ln predicted)
1.5
1.2
0.9
0.6
0.3
0.0
Coefficient of variation in abundance (ln)
5.5
4.5
3.5
20
40
60
80
100
Cavity abundance (%)
-2.5
-1.5
-0.5
0.5
1.5
Riparian vegetation structure (PC1)
2.5
3.5
4.5
5.5
Width of riparian vegetation zone (ln m)
-3
-2
-1
0
1
2
3
Upland vegetation structure (PC1)
1
2
3
4
Land-use intensity (sum ranks)

Fig. 3

APPENDIX A

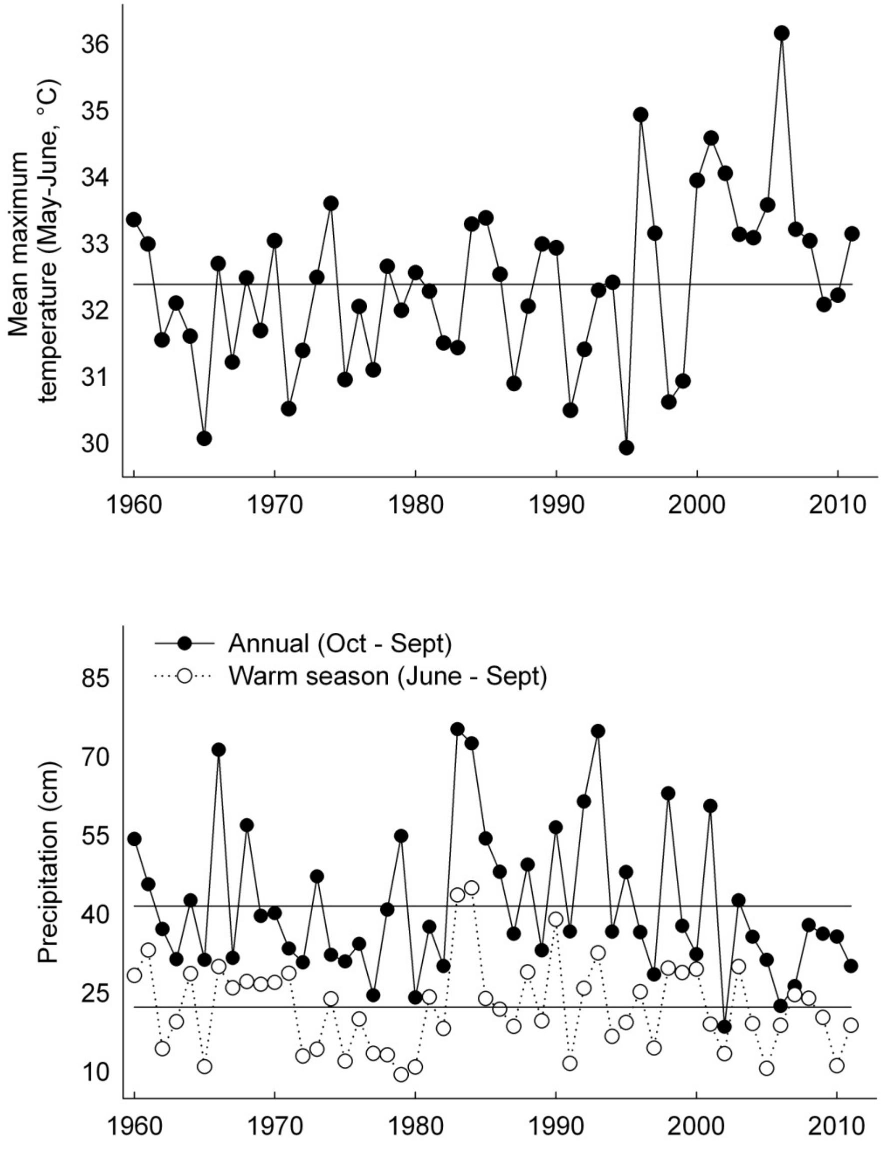
FIG. A1. Profile log-likelihoods (ll) of parameter estimates for population growth rate (U), observation error (R), and process error (Q) based on a top-ranked multivariate state-space model of population dynamics of Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2000 and 2011.





APPENDIX B

FIG. B1. Variation in mean maximum temperature during May and June and in annual and warm-season precipitation at Sasabe, Arizona 1960-2011, which is immediately adjacent to the study area in Sonora. Occasional missing values are from a weather station located 15 km north (WRCC 2011). Horizontal lines are averages. During the study period, temperature was typically much hotter and precipitation was often lower than long-term averages.



CHAPTER 2

SPATIAL, TEMPORAL, AND DENSITY-DEPENDENT COMPONENTS OF HABITAT QUALITY FOR FERRUGINOUS PYGMY-OWLS

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Abstract. Understanding processes that drive habitat quality is essential for explaining variation in individual performance and for developing effective conservation strategies. Spatial variation in resources is a fundamental driver of habitat quality but the realized value of resources at any point in space may depend on the effects of conspecifics and stochastic factors such as weather that also vary through time. We evaluated the relative and combined effects of habitat resources, weather, and conspecifics on habitat quality for Ferruginous Pygmy-Owls (*Glaucidium brasilianum*) in the Sonoran Desert of northwest Mexico by monitoring reproductive output over 10 years in 107 territory patches. Reproductive output varied much more across space than time and although habitat resources had greater effects than weather or conspecifics, evidence for interactions among factors associated with each of these components of the environment was strong. Relative to habitats that were persistently low in quality, high-quality habitat buffered the negative effects of conspecifics and amplified the benefits of favorable weather, but did not buffer the disadvantages of harsh weather. The positive effects of favorable weather at low conspecific densities were offset by intraspecific competition at high densities. Although realized habitat quality declined with increasing conspecific density suggesting interference mechanisms associated with an Ideal Free Distribution, broad spatial heterogeneity in habitat quality persisted. Factors associated with food and foraging space had positive effects on reproductive output but only when nest cavities were sufficiently abundant to mitigate predation and other risks. Annual precipitation and brooding-season temperature had strong multiplicative effects on reproductive output, which declined at increasing rates as drought and temperature increased, reflecting conditions that may become more frequent with climate change. Because the collective environment influences habitat quality in complex ways, integrative approaches that

consider resources, weather, and conspecifics are necessary to accurately assess habitat quality.

Key words: density dependence, environmental stochasticity, Ferruginous Pygmy-Owl, habitat quality, ideal despotic distribution, NDVI, Sonoran Desert, weather.

INTRODUCTION

A major goal in ecology is to understand how environmental variation affects the performance of individuals. Environmental factors that vary in both space and time drive habitat quality by affecting the fitness realized by occupants in a given habitat. Whereas fitness is often defined by an individual's contribution to population growth (DeJong 1994, McGraw and Caswell 1996, Coulson et al. 2006), habitat quality or habitat fitness potential (*sensu* Wiens 1989) is defined by the relative contribution of individuals in a specific habitat to population growth over periods that exceed the generation time of the focal species (Van Horne 1983, Franklin et al. 2000, Johnson 2007). Ultimately, habitat quality should drive settlement choices by individuals because those choices have important demographic consequences and are under natural selection (Jaenike and Holt 1991). Understanding factors that influence habitat quality can elucidate important selective pressures and help guide conservation and management.

Environmental factors that drive habitat quality can be organized into a spatial and temporal component and a component related to the endogenous effects of conspecifics. Spatial factors are those that vary across space at any given point in time and often vary in predictable ways from the perspective of a focal organism. Temporal factors in contrast, vary with time at any given point in space often in unpredictable ways. Presence and abundance of conspecifics varies both spatially and temporally but are considered separately because they affect the realized value of resources that may otherwise be of high fundamental quality. Although factors associated with each component vary to some extent in both space and time, a framework that considers these components can provide a useful context for assessing the environmental drivers of habitat quality.

Factors associated with the spatial component of habitat quality are often referred to collectively as habitat, which is a set of resources and conditions that foster occupancy and persistence of individuals of a given species through time (Morrison et al. 1992). This definition of habitat is conceptually similar to that of the niche (Holt et al. 2009) but represents an actual projection or mapping of the niche in space. While some definitions of habitat consider environments of similar structure and physiognomy to be the same habitat (Hutto 1985), our definition recognizes that different places even within similar environments (e.g., places traditionally considered a habitat type) can drive differences in performance due to variation in resources they provide. Regardless of specific resources that comprise habitat, their functional roles in providing food and reducing vulnerability to physiological stress and negative heterospecific interactions are fundamental (Newton 1998). Many studies have sought to identify factors that affect habitat quality, but until recently researchers have relied on indirect measures of habitat quality such as body condition, settlement patterns, or density rather than direct measures of vital rates (Johnson 2007, Gaillard et al. 2010). In systems where vital rates have been monitored over time, spatial variation in vegetation, landscape structure, and abiotic factors can have large and consistent effects on performance that persist longer than the generation time of the focal species (Blancher and Robertson 1985, Newton 1989, 1991, Dhondt et al. 1992, Franklin et al. 2000, McLoughlin et al. 2007). Thus, in some systems, good places tend to remain good for long periods.

Factors associated with the temporal component of habitat quality are related largely to stochastic fluctuations in environmental conditions that affect vital rates and thus population dynamics (Shaffer 1987, Tuljapurkar 1990, Doak et al. 2005). Temporal variation in weather for example, can have large effects on vital rates through either direct (physiological) or indirect (food web) pathways despite unpredictable timing (Rotenberry and Wiens 1991, Stenseth et al. 2002, Sæther et al. 2004, Mysterud et al. 2008). Although spatial factors such as vegetation structure are likely the primary cues used by animals to choose high-quality habitats (Hutto 1985), future conditions normally associated with those cues may not be realized due to unpredictable weather. Thus, realized habitat quality at a given point in time may be poor even at points in space that tend to be good on average over time. If temporal variation is high, good places may change through time and temporal factors may explain high levels of variation in performance, which can create moving targets for managers endeavoring to identify and preserve high-quality habitats. Moreover, weather can affect realized habitat quality in an additive or interactive manner. If weather effects are additive, they will be uniform across space and habitat may not attain its full potential until conditions are favorable. If weather effects are interactive, some resources may be able to buffer the negative effects of harsh weather or even amplify the benefits of favorable weather (Van Horne et al. 1997, Franklin et al. 2000), which has important implications for management in the face of climate change.

An important component of the environment that varies in both space and time and that can have marked effects on individual performance is the presence and abundance of conspecifics occupying a focal area (Svärdson 1949, MacArthur 1972). Individuals in habitats of high fundamental quality (e.g., basic suitability *sensu* Fretwell 1972, zero-density suitability *sensu* Bernstein et al. 1991, or intrinsic habitat value *sensu* McLoughlin et al. 2007), for example, may not realize the potential of those habitats due to intraspecific competition (Fretwell and Lucas 1969). At one extreme, under the Ideal Free Distribution (IFD), intraspecific competition equalizes realized habitat quality among individuals despite differences in the fundamental qualities of the habitat they occupy (Fretwell and Lucas 1969). Mounting antagonistic interactions and reductions in territory size are likely mechanisms for these patterns (Stamps 1990, Both and Visser 2000, Sillett et al. 2004). At the opposite extreme under the Ideal Dominance Distribution (IDD), individual competitive abilities vary, dominants relegate subordinates to habitat of lower quality, and thereby realize higher performance regardless of conspecifics (Brown 1969, Fretwell and Lucas 1969). Although often viewed as alternatives, processes that drive each distribution may operate simultaneously on the same or different vital rates (Both 1998, Nevoux et al. 2011) just as they often do on feeding rates (Parker and Sutherland 1986) and create a broader continuum of potential responses to conspecifics (López-Sepulcre et al. 2010). Moreover, although realized habitat quality may or may not decline with conspecific density, magnitudes of density dependence could depend on fundamental habitat quality (Morris 1987, McLoughlin et al. 2006). Thus, in systems that conform strictly to the IDD, spatial variation in resources alone will explain habitat quality whereas in systems with properties of both distributions, realized habitat quality will vary spatially and decline with conspecific density either uniformly in all habitat types or at rates that vary with fundamental habitat quality.

When the combined effects of each component are integrated, other potential explanations of habitat quality emerge. Although weather is often thought to act independent of conspecific density these effects may interact (Anderwartha and Birch

1954). Harsh winters for example, often have greater effects on performance when densities are high (Gaillard et al. 2000, Bonenfant et al. 2009) and the benefits of favorable weather could be offset by high competition. Finally, the combined effects of weather and conspecifics will be more complex if they also depend on habitat attributes.

Although the effects of factors associated with each component of habitat quality have been well-studied individually, few studies have assessed their integrated effects in wild animal populations. As a result, our understanding of how the collective environment influences habitat quality is incomplete, especially across continuous variation in important resources that drive fundamental habitat quality. The most problematic aspects with existing studies include the following: (1) they rarely consider how variation in resources and conspecific densities affect vital rates at individual vs. population scales (Sinclair 1989, Newton 1998), (2) they often treat habitats as discrete entities (Fretwell 1972, Morris 2003) that may not even exist in the eyes of the focal organisms, and (3) they consider time periods that are too short to capture sufficient variation in factors that vary across time. With respect to the latter issue, inferences on the effects of habitat resources could be misleading if they fail to consider the broader temporal context, which may include large effects of weather (e.g., crunches vs. bonanzas) and conspecifics (Van Horne et al. 1997, Morris 2011). With respect to the second issue, treating habitats as discrete entities is useful for developing elegant theory, but fails to incorporate the fact that habitats are intricate combinations of multiple resources that vary continuously in space and time (Southwood 1977, Newton 1998) and that variation in important resources at microhabitat or among-territory scales may be more important than that at larger macrohabitat scales (e.g., woodland vs. shrubland).

In addition to environmental components, intrinsic factors related to an individual's ability to cope with the environment can also affect performance. Age and experience, for example, can affect performance independent of resources (Sæther 1990, Newton 1991) and maternal effects due to genetics or the environment can affect individual quality and performance (Rossiter 1996, McLoughlin et al. 2008). Thus, habitat fitness potential may be driven by a combination of intrinsic and environmental factors, which could interact, or the fitness potential of an individual may be realized only when an optimal habitat is occupied. Nonetheless, individual effects are often found to be small relative to environmental ones (Alatalo et al. 1986, Franklin et al. 2000, Pärt 2001, Ferrer and Bisson 2003) and to dissipate over time (Sergio et al. 2009). Moreover, because the best individuals often have access to the best resources, intrinsic factors tend to be highly correlated with external factors that affect performance (Sherry and Holmes 1989, Holmes et al. 1996, Petit and Petit 1996, Sergio et al. 2007). Thus, while we acknowledge intrinsic differences among individuals exist, they are not considered further because our goal is to understand how the relative quality of different points in space varies across time for the average individual.

We assessed the effects of habitat resources, weather, and conspecifics on habitat quality of a Neotropical owl based on 10 years of monitoring across broad gradients in these factors. First, we assessed the extent to which performance varied across space and time. Second, we identified specific factors that explained habitat quality by evaluating hypothesized relationships between performance and factors associated with each component. Third, we assessed the relative importance of each component by estimating the quantity of variation in performance they explained. Finally, we assessed the combined effects of all three components by evaluating evidence for potential additive and interactive relationships among components.

STUDY SYSTEM

We studied Ferruginous Pygmy-Owls (*Glaucidium brasilianum*) in the Sonoran Desert of northwest Mexico immediately south of Arizona, U.S.A. (Fig. 1). Pygmy-owls are residents across much of the lowland Neotropics north to Arizona. Although once considered common in portions of southern Arizona, pygmy-owls were extirpated from much of their historic range likely due to habitat loss (Johnson et al. 2003). Consequently, they were listed as endangered in Arizona in 1997 but delisted for reasons unrelated to recovery in 2006; currently, the Arizona population is extremely small (USFWS 2011). In neighboring northwest Mexico, pygmy-owls are more common, use similar environments, but are declining (see Chapter 1). These populations are important for recovery in Arizona because natural or facilitated dispersal from Mexico can augment populations, especially when coupled with efforts to restore high-quality habitat.

Pygmy-owls are territorial, raise one brood per year, and exhibit high variation in clutch size (2-6) and annual reproductive output (0-6) in the region. Although generalists throughout their range, pygmy-owls' main prey in this region are diurnal lizards, and secondarily large invertebrates. In these arid environments, habitat is largely confined to riparian woodlands along drainages that are dominated by microphyllous trees such as mesquite (*Prosopis velutina*) and nearby uplands of desert-scrub and semi-desert grassland with giant saguaro cacti (*Carnegiea gigantea*) that provide nest cavities. Although historically pygmy-owls were often found in mesic riparian areas dominated by broadleaf trees, few recently occupied areas include these characteristics (USFWS 2011).

In Arizona, pygmy-owls were the focus of a major controversy between developers and conservationists in the late 1990s. At that time a large proportion of the Arizona population occupied lands with high economic and conservation values near Tucson. Although the controversy has subsided with the loss of regulations linked to endangered status and recent extirpation of pygmy-owls near Tucson, the owl remains a focal species in conservation plans in Arizona. Currently, unresolved questions with important conservation implications include whether pygmy-owls are associated with vegetation edges or woodland interiors, how anthropogenic disturbance and other factors affect habitat quality, and the relative importance of riparian vs. upland vegetation.

Two major vegetation communities occur in the study area. Desert-scrub is composed of woodland and scrub of short leguminous trees such as mesquite, shrubs such as creosote (*Larrea tridentata*) and bursage (*Ambrosia* sp.), and cacti. Semi-desert grassland is composed of savannah and open woodlands of mesquite, bunchgrasses, and sub-shrubs. Riparian areas in both communities are dominated by woodlands of mesquite. Climate in the region is arid to semi-arid with precipitation focused during a summer monsoon that originates in the Gulf of Mexico and during winter storms of Pacific origin that are most intense during the El Niño Southern Oscillation. Summers are typically hot with maximum temperatures >40°C and winters are cold with minimum temperatures near 0°C. Pygmy-owls establish breeding territories in Jan-Mar, lay eggs in Apr, and brood in mid-May and June.

METHODS

Study design and approach

Sampling strategy.—The basic units of our analyses are individual territory patches that can each be occupied by single territorial individuals or breeding pairs. This approach is advantageous because differences in resources and conditions at territory-specific scales should be more closely linked to variation in individual performance (Breininger and Oddy 2004, McLoughlin et al. 2007) and because variation in individual quality of different animals that occupy patches over time averages out (Sergio et al. 2009, Mosser et al. 2009). In 2001 and 2002, we used a stratified random sampling design to select survey transects across the study area, surveyed owls by broadcasting territorial calls, which yields nearly perfect detection probability, searched for nests along occupied transects and in other areas selected opportunistically, and located the nests of most individuals (Flesch and Steidl 2007). During subsequent years through 2010, we surveyed areas around nests from prior years (or locations where owls were detected but nests were not initially found) and located the nests of most individuals. Effort was focused early in the nesting season.

We defined territory patches based on observed and recurring patterns of use by owls. To identify patches, we plotted nest coordinates across time and identified clusters of use in space. Although owls often nested in different cavities each year, mean within-patch distances between nests in successive years (mean ± SE = 226 ± 13 m) was 5.5 times lower than that between nests in neighboring patches. Thus, because we located nests of most owls each year and because distribution of potential nests was clumped, this approach allowed easy identification of territory patches. To represent patches, we placed 50-ha circles around average nest locations for each patch, which maximized inclusion of all nests within patches, minimized overlap with neighboring patches, and is similar to average home-range area during the breeding season (Flesch, *unpubl. data*).

Fitness components.—Because habitat quality represents contributions to population growth of individuals in a specific habitat, it is a function of both reproduction and survival. At the individual scale, however, challenges in gathering sufficient demographic data have precluded estimating territory-specific population growth rates (λ_h) in all but a few cases (e.g., Franklin et al. 2000, Dugger et al. 2005). We used territory-specific estimates of reproductive output (R) to index habitat quality. This approach is plausible because in many vertebrates spatiotemporal variation in adult survival (S_a) is often very low compared to R, even across broad gradients in habitat quality, and because R is often highly correlated with λ_h ($r = 0.57$-0.71) and with S_a and juvenile survival ($r = 0.69$-0.83; Franklin et al. 2000, Gaillard et al. 2000, Eberhardt 2002, Dugger et al. 2005, Ozgul et al. 2007, Arlt et al. 2008). In a Spotted Owl (*Strix occidentalis*) population for example, territory-specific S_a was nearly constant except at very low λ_h whereas R declined proportionally with λ_h across the full range of variation in habitat quality (Franklin et al. 2000). Moreover, in a subset of patches where we monitored survival, R was correlated with juvenile survival before dispersal ($r = 0.49$, $n = 32$) and was 2.5 ± 0.5 times lower or zero in 69% of cases where adult mortality occurred (Flesch, *unpubl. data*).

Reproduction consists of two components: the probability territory holders attempt to breed and the number of offspring produced by breeders (Lebreton et al. 1990). Because annual breeding probabilities were high, we pooled both components when estimating R. We located nests by observing owls, searching for sign, and with a small pole-mounted video camera that we also used to monitor nests, estimate nestling age, and time final nest visits immediately before fledging. We defined R as the number of nestlings that survived to within one week of fledging, which is highly correlated with young that actually fledge ($r = 0.93$, $n = 35$, Flesch, *unpubl. data*). We considered R to be zero if patches were occupied at the start of the breeding season but no nest was found so long as (1) we adequately checked all potential nest sites, (2) time between visits was not sufficient to complete nesting, and (3) adults were undetected during successive surveys. We considered nests to have failed if they were empty before young could have reached an age of 26 days, which is the earliest we observed successful fledging; young typically fledge 28-30 days after hatching. If nests failed early and owls re-nested, we considered last nest attempts.

Hypotheses

We developed *a-priori* hypotheses to explain the effects of factors associated with each component on R. To develop hypotheses and translate them into statistical models we used information on this and related systems and considered three forms of most effects (linear, pseudo-threshold, and quadratic). Linear forms predicted hypothesized effects changed at a constant rate, pseudo-threshold forms (ln + 1) predicted effects changed at a constant rate then approached an asymptote, and quadratic forms predicted some maximal or minimal effect at intermediate values.

Temporal Hypotheses.—We developed 5 hypotheses to explain the effects of temporal factors on R. Temperature (T) could have direct physiological effects or indirect effects on food resources and explain R in two general ways. If severe winters affect body condition or food resources, we predicted R would decline with lower average minimum winter T. If high T during nesting causes direct mortality of nestlings, limits hunting activity by adults, or reduces prey activity or abundance, we predicted R would decline with increasing average maximum T during nesting. If precipitation (P) augments plant productivity and prey abundance, we predicted R would increase with increasing P. If increasing net primary productivity (PP) augments food or other resources, we predicted R would increase during periods of high normalized difference vegetation index (NDVI), which is highly correlated with PP (Pettorelli et al. 2005a, 2011). If owls time breeding to coincide with favorable conditions, we predicted timing of peak NDVI would explain R (Appendix A).

In addition to these 5 basic hypotheses, we considered 10 additional models representing the combined effects of multiple hypotheses (Appendix A). Because the effects of temporal factors may vary seasonally, we considered average maximum T during the incubation and brooding seasons, and cool-season, warm-season, and annual P and PP (Table 1). Because the effects of some factors may interact, we considered interactions between T and P and between T and PP.

Spatial Hypotheses.—We developed 6 general hypotheses to explain the effects of spatial factors on R that we based on the following themes: safe nesting sites, environmental harshness, habitat amount, type, and configuration, energy, topographic complexity, and anthropogenic disturbance (Appendix B). Because safe sites are critical for nesting (Martin 1993), we predicted R would increase (e.g., linear or pseudo-threshold forms) with abundance of potential nest sites. Because environmental harshness can affect productivity, we predicted R would be greater at higher elevations or in semi-desert grasslands than in more arid lowland desert-scrub or be greatest at moderate elevations (e.g., quadratic form). Because foraging space and cover are critical for reproduction, we predicted R would increase with habitat amounts within territory patches or be greatest at some moderate habitat amounts. Because we were unsure how best to represent habitat, we considered three potential definitions of habitat: woodland, woodland core area, and edge. Because habitat configuration can affect foraging opportunities, edge effects, and predation risk independent of habitat amount (Fahrig 2003), we predicted R would decline as woodland habitat became increasingly fragmented. Alternatively, because energy is a fundamental resource, we hypothesized spatial variation in PP explained R, and predicted R would increase with mean NDVI. Finally, because the benefits of foraging space may not be realized unless safe nest sites are present, we predicted effects of factors associated with food and foraging space (e.g., habitat amount, PP) depended on nest-site abundance.

Topographic complexity and anthropogenic disturbance could also drive R by affecting important resources. In the Sonoran Desert, pygmy-owl's main prey consists of various species of diurnal lizards, which partition their use of the environment across a range of soil substrates and habitat types (González-Romero et al. 1989). Thus, we hypothesized that patches with higher substrate diversity and hence more species of prey would affect reproduction, and predicted R would increase with increasing average slope or be greatest at moderate slopes. Because anthropogenic disturbance can degrade resources, we predicted R would decline as disturbance within patches increased or be greatest at moderate disturbance.

In developing models to represent hypotheses, we considered each potential definition of habitat (e.g., woodland, edge), then the effects of topographic complexity and disturbance. Because an effect of habitat configuration is implicit when considering edge and core-area effects, we considered fragmentation only when assessing the effect of woodland amount. Because we suspected safe nest sites and environmental harshness were important regardless of other processes, we considered them in all models.

Conspecifics.—We hypothesized conspecifics had negative effect on R driven by intraspecific competition, and predicted R would decline with the presence or abundance of conspecifics. Although conspecifics can have positive effects (Courchamp et al. 2008) they were not considered.

Environmental measurements

Temporal factors.—We used satellite and weather-station data to quantify factors associated with temporal hypotheses (Table 1). To quantify weather, we used data on monthly P and monthly average minimum and maximum T from one of five weather stations closest to each territory patch (WRCC 2011; Fig. 1). To quantify NDVI, we compiled time series data (250-m resolution; available at http://modis.gsfc.nasa.gov) at 16-day intervals between 9 June 2000 and 25 May 2010 (n = 23 samples/yr) and extracted estimates as area-weighted averages for each patch; NDVI ranged from 0.133 to 0.725 and cloud contamination was low (1.4%). NDVI measures the normalized ratio of near-infrared (NIR) and red (RED) reflectance. Because green leaves have high NIR reflectance and high RED absorption they produce positive NDVI values (0.9 for dense green vegetation) whereas bare ground has values close to 0.1. To quantify temporal variation in PP independent of spatial variation, we calculated proportional deviations from mean NDVI where NDVI deviation = (mean NDVI for the period – mean of NDVI for the period in all years)/mean of NDVI for the period in all years. To estimate temporal variation in timing of peak NDVI, we calculated the number of days between peak NDVI and the start of the warm and cool seasons each year. Because we were unsure how best to represent some predicted effects, we quantified temporal factors during different seasonal periods (Table 1).

Spatial factors.—We used remote sensing and on-the-ground measurements to quantify explanatory factors associated with spatial hypotheses (Table 2). Because saguaros were the only substrate used for nesting, we quantified abundance of potential nest sites by counting the number of saguaros with at least one potential nest cavity in patches on a logarithmic scale. To quantify mean elevation, slope, and coefficients of variation in elevation, we used 30-m digital elevation models. To quantify average NDVI within patches, we used all area-weighted averages for each patch across time (Table 2).

We used a variety of methods to classify land cover into five classes (woodland, non-woodland, agriculture or other clearing, housing or development, and roadway corridor) and estimate cover of each class (see Appendix C). We extracted spectral vegetation and soil abundance data from 30-m-resolution Landsat5 Thematic Mapper (TM) images and other data sources to quantify woody vegetation cover (see Appendix C). We classified pixels with ≥20% woody vegetation cover as woodland, which given typical tree spacing in the study area distinguished open woodland and savannah from more closed-canopy woodland. To classify land cover classes that represented disturbance, we used Google Earth imagery (GE) and digitized polygons around these features.

We used the TM- and GE-derived land cover data and program FRAGSTATS (McGarigal et al. 2012) to estimate coverage of each land cover class within patches, woodland fragmentation, and amount of woodland core-area and edge within patches. To quantify woodland fragmentation independent of woodland amount, we scaled density of woodland patches by average woody vegetation cover (Table 2). To quantity amount of edge, we estimated edge length between all land cover class and between woodland and other land cover classes. To quantify amount of core-area habitat, we subtracted an edge width of 30 m from all woodland patches and computed remaining woodland areas. Because landscape structure around home ranges can affect performance, we also estimated area of land cover classes that represented disturbance within 500 m of patches.

Data of negative heterospecific interactions are useful for evaluating the functional roles of important resources. Thus, we recorded evidence of these interactions with two species of cavity nesters (Western Screech-Owl, *Megascops kennicottii*; American

Kestrel, *Falco sparverius*) that exhibited heterospecific aggression toward pygmy-owls by noting evidence where these species appropriated nests from owls or killed owls.

Conspecifics.—To describe the presence and abundance of conspecifics, we estimated five explanatory factors at three spatial scales (Appendix D). At large scales, we used survey data to calculate the proportion of territory patches occupied each year across the study area and within each of 11 watershed regions (Fig. 1). At local scales, we estimated the presence, number, and density of nearest-neighbor nests around each focal patch. We estimated local density (territories/km^2) as

$$\frac{1{,}000{,}000 \text{ m}^2}{\left((\bar{D}^2)\times\left(\frac{1}{n}\right)\right)} \quad \text{(eq. 1)}$$

where $\bar{D}$ is the mean distance to nests in m, n is the number of nests, and 1,000,000 m^2 is the number of m^2 in a km^2. Thus, estimates of local density (*sensu* Coulson et al. 1997) were based on the number of neighbors and exact distances to their nests, which was easy to measure in this system because most nests had zero, one, or two nearest neighbors given the linear arrangement of habitat along drainages.

Modeling approach

We used linear mixed-effects (LME) models of the following general form to estimate parameters

$$Y_{ij} = X_{ij} \times \beta + Z_i \times b_i + \varepsilon_{ij} \quad \text{(eq. 2)}$$

where Y_{ij} is a vector of observed R in the i^{th} patch and j^{th} year; the fixed effects X_{ij} is a design matrix of dimension $n \times p$ where n is the number of observations in each patch and p is the number of explanatory variables in X_{ij}, and β is a vector of regression parameters and p slope parameters for the overall population; the random effects Z_i is a design matrix of dimension $n \times q$ where q is the number of explanatory variables in Z_i, and b_i are vectors of random effects that are normally distributed with a mean of zero and a variance-covariance matrix D with diagonal elements $\sigma^2_{\text{process}}$ that measure process variance; and ε_{ij} is a vector of residual errors that are normally distributed with a mean of zero and a variance-covariance matrix E with diagonal elements σ^2_{ε} that measure random noise (Pinheiro and Bates 2000).

We considered different forms of the random effects and variance-covariance matrices D and E. First, we fit territory patch as a random intercept, which ensured standard errors of fixed effects were based on the number of patches not the number of observations. Second, we considered crossed (factorial) random effects for patch and year. To model potential heterogeneity in σ^2_{ε}, we considered models with one variance, variances for each year, and the variance covariates annual P and annual rate of patch occupancy, which could explain heterogeneity by affecting variation in patch qualities occupied over time. To assess models with different random effects and variance-covariance structures, we used an over-fitted model, restricted maximum likelihood (REML), and model the selection procedures described below. Temporal autocorrelation was low and spatial autocorrelation was undetectable and thus no spatial or temporal correlation structures we used to model E. We fit models with the nlme library in R (R Core Development Team 2012); estimates of fixed effects were based on maximum likelihood (ML) methods.

We used a Gaussian-based approach because (1) ANOVA techniques are highly robust to departures from normality even when response data are distributed as Poisson or negative binomial, (2) are more robust than generalized linear models when data do not conform to those distributions, and because (3) R was not distributed as Poisson or negative binomial given few broods of 1 or 2 young (White and Bennetts 1996, McDonald and White 2010). Regardless, zero-inflation was low (22%), diagnostic tools indicated all models met all assumptions, and all predictions were positive.

We used an information-theoretic approach and Akaike's Information Criteria for small sample sizes (AIC_c) to evaluate support among models (Burnham and Anderson 2002). To compare models, we computed differences in AIC_c between each model and the best approximating model in each set and used AIC_c weights (w_i) to quantify model likelihoods. We considered models within approximately 2 ΔAIC_c units as competitive except in cases where models included uninformative parameters.

Our model selection approach involved three steps. First, we selected the best model to represent each hypothesis by comparing suites of models that each considered related factors (e.g., seasonal vs. annual P), hypothesized interactions, and linear, pseudo-threshold, and quadratic forms of some factors associated with each hypothesis. Although most related factors were correlated, we avoided subjective bias by evaluating factors separately and choosing the best model to represent each hypothesis. Second, we used AIC_c to rank models representing each hypothesis. Finally, we refined the best models by assessing the effects of including or excluding some factors and interactions. When refining models, we considered correlations between factors; correlation coefficients (r) between factors in models representing hypotheses were ≤ 0.41.

Components of variance analysis

In addition to identifying important fixed effects, we estimated the magnitude of variances of the random effects across space (patch) and time (year). We used components of variance analyses (Searle et al. 1992) to decompose process variance into spatial and temporal components and estimate the proportion of variance in R explained by factors in the best approximating models for each component of habitat quality. Spatial and temporal process variation in a population parameter can be decomposed as

$$\sigma^2_{process} = \sigma^2_{temporal} + \sigma^2_{spatial}. \quad \text{(eq. 3)}$$

To estimate $\sigma^2_{spatial}$, we used an intercepts-only model with a random intercept for territory patch, the best variance-covariance structure for *E*, and REML. To estimate $\sigma^2_{temporal}$, we used the same approach with year as a random intercept. Magnitudes of spatial vs. temporal process variance were expressed as ratios and proportions (e.g., $\sigma^2_{spatial}/\sigma^2_{process}$).

To describe the amount of temporal and spatial process variation explained by important factors, we used the best approximating models for spatial and temporal factors to partition process variance as

$$\sigma^2_{process} = \sigma^2_{model} + \sigma^2_{residual} \quad \text{(eq. 4)}$$

where $\sigma^2_{process}$ is either total spatial or temporal variation in R, σ^2_{model} is the amount of that variation explained by the best model for either habitat or weather factors, which thus estimates $\sigma^2_{habitat}$ and $\sigma^2_{weather}$, and $\sigma^2_{residual}$ is unexplained variance. Total process variation explained by models for the effects of habitat or weather was estimated as

$$\sigma^2_{model} = \sigma^2_{process} - \sigma^2_{residual}. \quad \text{(eq. 5)}$$

In the LME approach used here, we estimated $\sigma^2_{process}$ using an intercepts-only model, REML, and the most parsimonious structure of *E*. To estimate $\sigma^2_{residual}$, we fit the best model for either spatial or temporal factors using REML, which provides unbiased estimates of variance not explained by the fixed effects (Searle et al. 1992). Because conspecifics affect R across both space and time, we further decomposed $\sigma^2_{process}$ to estimate the magnitude of those effects. To assess the proportion of additional spatial and temporal variation explained by conspecifics we combined our best model for the effect of conspecifics with that for habitat and weather into two models and repeated the variance decomposition procedure described above. To estimate the degree to which R varied across space and time, we computed coefficients of process variation (CV) as

$$\frac{\sqrt{\sigma^2_{\text{process}}}}{\bar{R}} \quad \text{(eq. 6)}$$

where $\bar{R}$ is average R among years or patches and $\sigma^2_{\text{process}}$ is either spatial or temporal process variance based on eq. 3.

Relative contribution of each environmental component

We used several approaches to evaluate the combined effects of multiple components of habitat quality and to assess the relative and combined effects of each component. In a model selection framework, we combined the best models for the effects of habitat, weather, and conspecifics into all possible combinations of additive models, which produced seven models (e.g., Space only, Space + Time, etc.). Additionally, we considered models with all possible combinations of interactions among components, which produced another seven models (e.g., Space × Time, Space × Conspecifics + Time, etc.). For hypotheses with interactions, we considered all possible combinations of interactions between factors for each component and used AIC_c to select the best models to represent hypotheses. If a model that included the effects of habitat only was selected, it suggested only habitat resources drove habitat quality. In contrast, if a model that included interactions between habitat and weather was selected, it suggested that high-quality habitats buffered or amplified the effects of weather more than low-quality habitats. If a model that included interactions between habitat and conspecifics was selected, it suggested rates of density dependence varied among habitats.

We used components of variance analysis to compare the relative contribution of each component in explaining R. Total variation in a vital rate explained by the environment can be expressed as

$$\sigma^2_{\text{total}} = \sigma^2_{\text{temporal}} + \sigma^2_{\text{spatial}} + \sigma^2_{\text{conspecifics}} = \sigma^2_{\text{model}} + \sigma^2_{\text{residual}} \qquad \text{(eq. 7)}$$

where $\sigma^2_{\text{temporal}}$, $\sigma^2_{\text{spatial}}$, and $\sigma^2_{\text{conspecifics}}$ are estimates of variation due to temporal, spatial, and conspecific factors, σ^2_{model} is the amount of that variation explained by the best model describing those effects, and $\sigma^2_{\text{residual}}$ is unexplained variation. Estimates of σ^2_{model} can be further decomposed as

$$\sigma^2_{\text{model}} = \sigma^2_{\text{weather}} + \sigma^2_{\text{habitat}} + \sigma^2_{\text{conspecifics}} \qquad \text{(eq. 8)}$$

where $\sigma^2_{\text{weather}}$ and $\sigma^2_{\text{habitat}}$ were estimated based on the best models for each component and procedures described above. Because conspecifics affect habitat quality in both space and time, we estimated $\sigma^2_{\text{conspecifics}}$ using eq. 5 and computed σ^2_{model} by summing estimates from both temporal and spatial models that included the effect of conspecifics. To estimate relative contributions of each environmental component, we expressed the proportion of σ^2_{model} attributable to each component as $\sigma^2_x/\sigma^2_{\text{model}}$, where x is weather, habitat, or conspecifics. Because the effects of conspecifics may depend on the spatial arrangement of habitat, we preformed analyses for the entire population and for only those patches with conspecific neighbors.

RESULTS

We identified 107 territory patches over 10 years; 56% were in desert-scrub (vs. semi-desert grassland) and 89% were monitored for ≥7 years. We obtained a total of 468 estimates of R and an average of 4.4 ± 0.2 (± SE) estimates per patch across time. We obtained ≥3 estimates of R in 73% of patches and only single estimates in 14% of patches that were rarely occupied. Among years, we obtained 46.8 ± 4.3 estimates per year and ≥43 estimates per year except during 2001 (*n* = 32) and 2003 (*n* = 18).

Time

Temporal variation.—Annual estimates of R averaged 2.77 ± 0.11 young per occupied patch and varied somewhat across time with estimates that ranged from 2.16 ± 0.25 in 2006 to 3.18 ± 0.25 in 2007 ($F_{9,\,458} = 1.59$, $P = 0.116$, ANOVA; Fig. 2). Temporal process variance ($\sigma^2_{\text{temporal}}$) was relatively low (0.0380; 95% CI = 0.0031–0.472). A coefficient of temporal process variation in R (0.0703) was also relatively low.

Temporal factors.—A model with territory patch fit as a random intercept and a single residual variance were the best approximating structures when compared to models with both territory patch and year fit as crossed random effects ($\Delta\text{AIC}_c = 2.20$) and models with residual variances estimated for each year ($\Delta\text{AIC}_c = 7.41$) or variance covariates ($\Delta\text{AIC}_c \geq 9.25$). Assessment of all final models indicated these structures were optimal.

The best approximating model for the hypothesized effects of temporal factors on R was model $\{\ln T_{\text{brood}} + \ln P_{\text{yr}} + \ln T_{\text{brood}} * \ln P_{\text{yr}} + \text{NDVI}_{\text{yr}}^2\}$ (model 8 in Table 3). This model represented the hypotheses that high temperatures (T) during nesting, and both annual precipitation (P) and primary productivity (NDVI) before nesting, explained R through either direct or indirect pathways.

When considered in the best model, timing of peak productivity had no effect on R (Table 3). Moreover, likelihood of a simpler model without the effect of T, and thus an interaction between T and P, was 3-times lower than that for the best model (Table 3). There was no evidence of a linear or non-linear temporal trend in R (Table 4) or for the intercepts-only model ($\Delta\text{AIC}_c = 7.76$).

The best model included a quadratic effect of annual NDVI deviation (e.g., annual proportional difference from average NDVI) and an interaction between annual P and brooding-season T. R was low or moderate during periods of low or moderate NDVI and increased rapidly as NDVI increased (Fig. 2). Although when considered alone, annual P had marked effects on R equaled to a 0.30 ± 0.13 young increase with each doubling of P (Table 3), the effect of P was best described by its interaction with brooding-season T. R increased markedly with increasing P but only during periods of high to moderate T and P had little effect on R during periods of low T. Importantly, R decreased to extremely low levels during periods of low P and high T (Fig. 2). R was particularly low during 2002 and especially 2006 when annual P averaged only 28.7 ± 5.8 and 19.0 ± 3.3 cm, respectively, or 19 to 46% lower than the decadal average. In 2006, the hottest year on record in the region, brooding-season T averaged 38.9 ± 1.1°C or 4.7% higher than the decadal average. Despite a combination of hot dry conditions in 2006, annual P and brooding-season T were uncorrelated ($r = -0.10$, $P = 0.49$, $n = 50$). Parameter estimates for the interaction between P and T were relatively precise (95% CI = 1.45-15.92).

Seasonal periods used to describe the effects of important temporal factors on R were strongly supported by the data. Substituting cool-season P for annual P in the best model for example, increased AIC_c by 8.41, with more support for an effect of warm-season P ($AIC_c = 1.96$). Substituting incubation-season T for brooding-season T increased AIC_c by 4.65.

Space

Spatial variation.—R averaged 2.65 ± 0.11 young per occupied patch and varied markedly across space ($F_{106, 361} = 1.32$, $P = 0.032$, ANOVA). Spatial process variance ($\sigma^2_{spatial}$) in R was relatively high (0.216; 95% CI = 0.070 – 0.661). Coefficients of spatial process variation in R (0.176) and fecundity (0.0878) were relatively high. Moreover, when the effects of important habitat factors were considered (see below), patch-specific predictions of R varied over 4 fold (0.91 ± 0.37 to 3.97 ± 0.18).

Spatial factors.—The best approximating model for the hypothesized effects of spatial factors on R was model {lnCav + Comm + Hab_f + lnCav*Hab_f + Frag_hab} (model 3 in Table 5). This model represented the hypotheses that abundance of potential nest sites, environmental harshness, and amount and configuration of woodland habitat explained R by affecting food, foraging space, predation risk, and other processes. This model included a positive effect of presence of semi-desert grassland, a negative effect of woodland fragmentation, and an interaction between amount of woodland habitat and abundance of potential nest sites.

Two others models received some support ($\Delta\text{AIC}_\text{c}$ = 0.01-1.47; Table 5). One model (no. 4) included the same factors as the top-ranked model and an interaction between slope and abundance of potential nest sites. The second model (no. 11) hypothesized overall net primary productivity explained R and included a positive effect of presence of semi-desert grassland and an interaction between mean NDVI and abundance of potential nest sites (Table 5).

Evidence for an effect of woodland habitat was much stronger than that for edge or woodland core-area habitat. Relative to the best model, likelihoods of models that included edge habitat or woodland core-area habitat were ≥4.8 times lower (Table 5). Although R increased somewhat with increasing edge, there was little evidence for the effect when included in the best model (Table 4). Amount of woodland habitat was best represented by mean proportional woody vegetation cover (Hab_f) vs. proportion of patches classified as woodland (Hab_w; $\Delta\text{AIC}_\text{c}$ = 1.46). Although evidence for an effect of woodland habitat was strongest overall, it was highly correlated with woodland core-area (*r* = 0.85) and somewhat less so with edge (*r* = 0.44) and mean NDVI (*r* = 0.57).

The effects of factors related to food and foraging space depended largely on abundance of potential nest sites, which had an overwhelming effect on R. Excluding abundance of potential nest sites from the best model increased AIC_c by 38.17, whereas retaining this factor and excluding the interaction with amount of woodland habitat increased AIC_c by 2.88 (Table 4). Although R increased markedly with nest-site abundance (e.g., main effects = 2.2 ± 0.4/young increase across the full range of variation; Fig. 3), its effect was best represented by an interaction with amount of woodland habitat. R increased markedly with nest-site abundance but only in patches with moderate to high amounts of woodland and much less otherwise. Moreover, the same general pattern applied to most other factors related to food and foraging space (Fig. 4). Once nest-site abundance reached moderate levels, R increased with increasing amount of woodland habitat, NDVI, and slope, with much weaker effects of woodland core-area habitat (Fig. 4). Where nest-site abundance was low, however, amount of woodland habitat had negative effects on R (Fig. 4). Parameter estimates for interactions between nest-site abundance and woodland amount and NDVI were precise (95% CI= 0.0034-0.043 and 0.038-0.78, respectively) but less so for that with slope (-0.024-0.56).

Woodland fragmentation but not anthropogenic disturbance had important effects on R (Table 4). On average, R decreased with increasing woodland fragmentation (Figs. 3 and 5), which was only moderately correlated with woodland amount (*r* = 0.41)

Differences between macrohabitats (e.g., vegetation communities) had important effects on R (Fig. 3). For example, R averaged 0.38-0.50 ± 0.16-0.18 young higher in semi-desert grasslands than in desert-scrub, after considering other factors (Table 5).

Although R was higher on average at moderate elevations (Fig. 3), macrohabitat effects provided a much better explanation of the data than the continuous, nonlinear effect of elevation or both factors combined (Table 4). Differences in R between macrohabitats were likely not driven by other important factors because they either did not vary between macrohabitats ($p \geq 0.77$, *t*-tests for $\mathrm{NDVI}_{\mathrm{mean}}$ and $\mathrm{Frag}_{\mathrm{hab}}$) or were greater in desert-scrub ($p \leq 0.051$, lnCav and $\mathrm{Hab}_{\mathrm{f}}$). Although magnitudes of slope parameters for other important effects were similar in both macrohabitats, R declined with increasing woodland fragmentation at a much greater rate in grassland ($\beta \pm \mathrm{SE} = -0.35 \pm 0.088$) than in desert-scrub ($-0.10 \pm 0.085$). Instead, macrohabitat effects seemed to be driven by environmental harshness as decadal differences in annual P and brooding-season T averaged 44.8 ± 6.0% higher and 3.1 ± 1.0% lower in grassland, respectively.

We observed evidence of negative heterospecific interactions in 7.5% of patches, 92% of which were with Western Screech-Owls. Prevalence of these interactions decreased as abundance of potential nest sites increased (Fig. 3). Where nest substrates were rare, woodland cover averaged 51.7 ± 26.3% higher in patches where we observed negative heterospecific interactions.

Conspecifics

Variation in conspecifics.—Presence and abundance of conspecifics varied across time and space. Although most patches (73.8%) were in areas where conspecifics were present at least one year, conspecifics occupied adjacent patches during only 55.8% of observations ($n = 261$) and nested within 1.5 km of focal nests during only 43.6%. Both the number and density of conspecific neighbors around focal patches varied widely among patches ($F_{106, 361} \geq 5.14$, $P < 0.001$, ANOVA). Conspecific densities ranged from 0 to 5.5 territories/km^2 (mean = 0.68 ± 0.04) and distances between nearest neighbors ranged from 425 to 2,619 m (mean = 1,251 ± 33, $n = 287$). Conspecific density varied also varied across time ($F_{9,\,458} = 2.36$, $P < 0.001$, ANOVA) with annual means that varied >2.5 fold (range = 0.38-1.01).

Conspecific effects.—Effects of conspecifics were best described by factors measured at a local patch-specific scale, and more specifically, by local conspecific density (Appendix D). R declined by 0.18 ± 0.084 young with each 1-territory/km^2 increase in local density (95% CI = 0.015-0.34). Although R also declined with increasing number and presence of conspecific neighbors, estimates were less precise (95% CI = -0.015-0.49 and -0.023-0.64, respectively; Fig. 6). After adjusting for local density, R increased by 0.070 ± 0.042 young with each 10% increase in regional occupancy (Fig. 6) but considering both effects together reduced AIC_c by only 0.69.

Relative contribution of each component

Spatial process variance in R (0.216) was 5.7 times greater than temporal process variance (0.0380) and thus 85.0% of total process variance was attributable to space. Habitat factors in the best model explained >99.9% of spatial process variance (among-group variance) but only 3.7% of residual variance (within-group variance), and $\sigma^2_{\text{habitat}}$ equaled 0.321. Weather factors in the best model explained >99.9% of temporal process variance but only 1.3% of residual variance, and $\sigma^2_{\text{weather}}$ equaled 0.0779. An estimate of $\sigma^2_{\text{conspecifics}}$ equaled 0.0597. Thus, σ^2_{model} equaled 0.459 and the relative contribution of habitat, weather, and conspecifics in explaining R was 0.70, 0.17, and 0.13, respectively.

When the relative effects of conspecifics vs. habitat or weather were evaluated further, habitat effects were consistently strong but the relative effects of conspecifics vs. temporal factors varied. When modeled with habitat factors, conspecifics explained little additional spatial variance (4.0 vs. 3.7%) and $\sigma^2_{\text{habitat}}$ (0.328) increased by only 2.2%.

When modeled with temporal factors, conspecifics explained much more temporal variance (3.6 vs. 1.3%) and $\sigma^2_{weather}$ (0.146) increased by 87.4%. When contributions of each component were considered in only those patches where conspecifics were present, σ^2_{model} increased to 0.555 and relatively more variation was explained by habitat (0.82) than by weather (0.09) or conspecifics (0.09).

When assessed in a model-selection framework, evidence for effects of habitat was much greater than that for weather or conspecifics. When the best models for each component were compared, ΔAIC_c for a model with only habitat factors was 4.2-4.6 times lower than that for models with only weather or conspecifics (Table 6). Regardless, likelihood of a model that included the additive effects of all factors in the best models for each component was 125-times higher than that for the habitat-only model (Table 6). Although support for an effect of conspecifics was lowest overall, a model that included conspecifics was 4.8 times more likely than a model that considered only habitat and weather.

When the effects of important habitat factors were considered, patch-specific predictions of R varied widely across space and increased rapidly at low R but more gradually thereafter (Fig. 7). When the additive effects of habitat and weather were considered together, this same general pattern remained but weather effects re-ordered the relative quality of patches somewhat (Fig. 7). Weather effects amplified R by up to 56% or depressed it by up to 49% in some years but changes of these magnitudes were limited to few patches and the absolute value of weather effects averaged 10.5 ± 0.4% overall. In contrast, when the additive effects of habitat and conspecifics were considered together, differences in patch-specific predictions of R were much lower (Fig. 7). Changes in conspecific density amplified R by up to 13% or depressed it by up to 27%

but changes of these magnitudes were limited to few patches and the absolute value of conspecific effects averaged only 3.3 ± 0.2% overall.

Interactions among components

Evidence for interactions between components was strong. Models with interactions between habitat and weather, weather and conspecifics, and habitat and conspecifics all had greater support than corresponding additive models, with similar results when all three components were considered together (Table 6). Although support for interactions was high, relative support among different models that included them was similar (Table 6). The best model included interactions between brooding-season T, annual P, and amount of woodland habitat (Table 6, Appendix E). When this effect was evaluated across a hypothetical weather gradient ranging from favorable cool wet conditions to harsh hot dry conditions, patches with more habitat amplified the positive effects of favorable weather more than those with less habitat (e.g., slopes varied; Fig. 8). Patches with more habitat, however, did not buffer the negative effects of harsh weather more than those with less habitat (e.g., intercepts did not vary). A highly competitive second-ranked model included an interaction between annual P and conspecific density (Table 6). When this effect was evaluated across variation in annual P, R increased steadily with P when conspecifics were absent or present at low densities but less so at moderate densities (Fig. 8). When densities were high, however, R declined with increasing annual P, suggesting intraspecific competition offset the benefits of favorable weather.

Models with interactions between habitat and conspecifics included interactions between density and three habitat factors (Table 6). When the effect of woodland fragmentation was evaluated across variation in density, conspecifics had no effect on R when fragmentation was low but R declined at increasingly higher rates as fragmentation increased (Fig. 8). The effects of conspecifics also varied between vegetation communities; although fundamental habitat quality was higher on average in grasslands (e.g., greater intercept), R declined with increasing density at a rate 2.4 times greater in grasslands than in desert-scrub (Fig. 9). When the effects of all important habitat factors were considered together, magnitudes of density-dependence varied with fundamental habitat quality; although R declined with density in all habitats, high-quality habitats buffered the negative effects of conspecifics more that low-quality habitats (Fig. 9).

DISCUSSION

We assessed habitat quality for Ferruginous Pygmy-Owls during the breeding season at the scale of individual territory patches by estimating magnitudes of spatial and temporal variation in reproductive output (R) over 10 years, and by evaluating the relative contribution and specific effects of factors associated with three general components of the environment that drive habitat quality. Although factors associated with each component had important effects, spatial factors (e.g., habitat resources) were more influential than temporal factors such as weather or conspecifics. Nonetheless, weather and conspecifics had large effects during some years and the effects of important factors associated with each component often interacted indicating that the collective environment influences habitat quality in complex ways and that considering only one component in isolation of others may produce misleading results.

Habitat

Habitat determines the availability of resources such as food and nest sites, abundance of conspecific and heterospecific competitors, and vulnerability to predation, parasitism, and physiological stress (Southwood 1977, Cody 1985, Block and Brennan 1993). Vegetation structure is a fundamental attribute of habitat because it simultaneously affects food availability, predation risk, and susceptibility to physiological stress (Cody 1981, Newton 1998). In this system, attributes of vegetation structure seemed to reduce vulnerability to heterospecific enemies, promote foraging opportunities, and mitigate exposure to environmental harshness. With regard to general vegetation structure, the overall quantity of woody vegetation had greater effects on R than the amounts of edge or woodland interior. These patterns largely conform to general descriptions of habitat use by pygmy-owls across their range, which occur in a diversity of vegetation types that often include scattered patches of dense vegetation interspersed with openings (Cartron et al. 2000, Flesch 2003). In our region, areas used by breeding pygmy-owls include areas of desert-scrub, thorn-scrub, and tree-invaded grasslands associated with riparian woodlands and at least one saguaro cactus with a suitable nest cavity.

Because energy is the ultimate resource, differences in habitat quality should be linked to spatial variation in trophic energy (Van Valen 1976, Lomnicki 1980). Although woody vegetation cover best described spatial variation in R, differences in net primary productivity as indexed by normalized difference vegetation index (NDVI), provided a highly competitive explanation of the data. In fact, when the effects of both factors were compared, R actually increased more at high levels of NDVI but decreased more at low levels of vegetation cover (Fig. 4). These differences are likely because NDVI responds to productivity of both woody and non-woody vegetation, which is rarely used by owls but provides important resources for their prey. Nonetheless, greater effects of woody vegetation were likely due to its more direct effect on foraging space and abundance of heterospecific enemies. Because NDVI is closely associated with the concept of trophic energy, it has proved useful in explaining patterns of distribution, abundance, growth, and phenology in a variety of animal systems (Pettorelli et al. 2005a, 2011). Associations between NDVI and vital rates (e.g., Saino et al. 2004, Schaub et al. 2005, Pettorelli et al. 2007, Tafani et al. 2013, this study), however, are less common.

Nest-site availability and specific nest-cavity features can have large effects on abundance and demography of cavity-nesting birds due to a broad range of processes (Nilsson 1984, Sonerud 1985, Newton 1994). In this system, important nest-cavity features include cavity height, entrance area, and orientation, which by affecting thermal conditions or predation risk affect both nest-site selection and its demographic consequences (Flesch and Steidl 2010). Because availability of these cavity features increases with saguaro abundance and because higher abundance of potential nest sites augments predator search times and reduces predator efficiency (Martin and Roper 1988), patches with more saguaros provide higher quality habitat. Moreover, in the Sonoran Desert, pygmy-owls coexist with numerous other cavity nesters such as Western Screech-Owl, American Kestrel, Elf Owl (*Micrathene whitneyi*), Gilded Flicker (*Colaptes chrysoides),* Gila Woodpecker (*Melanerpes uropygialis*), flycatchers (*Myarchis* sp.), and Purple Martin (*Progne subis*). Thus, when nest sites are rare, space use by these species becomes more concentrated, which likely increases cues to predators and promotes negative interactions with heterospecific (Fig. 3). Due to these and other processes (e.g., Brown and Brown 1986), territories with few potential nests provide lower-quality habitat.

In arid environments, tree cover is often limited by soil moisture and woodlands are restricted to riparian areas that provide essential foraging space and cover (Knopf et al. 1988). Although riparian areas used by owls rarely supported broadleaf trees, microphyllous species such as mesquite provide important habitat for owls and prey (Szaro and Jakle 1985, Szaro and Belfit 1986). In the Sonoran Desert, abundance or diversity of common prey increases with vegetation cover, heterogeneity, and mesquite abundance, which are all associated with riparian areas and their ecotones (Rosenzweig and Winakur 1969, Price 1978, Germano and Hungerford 1981, Jones and Glinski 1985, Lloyd et al. 1998). Moreover, independent of the amount of woody vegetation, R declined with increasing woodland fragmentation, especially in grasslands where vegetation physiognomy and composition are less diverse and edge effects are likely higher. Thus, larger patches of riparian woodland provide higher quality habitat, which also promotes local persistence over time (Chapter 1).

Factors associated with prey habitat in uplands were also important but much less so than riparian vegetation. Although most patches were dominated by fine bottomland soils, R increased somewhat in patches with higher average slope and thus a greater range of soil substrates. Because lizards partition their use of the environment among different substrates types and may depend on rocky substrates to maintain preferred body temperatures, territories with rocky uplands likely promote lizard diversity and body size (Jones and Glinski 1985, Szaro and Belfit 1986, González-Romero et al. 1989, Sinervo and Adolph 1994), which enhances resources for owls that rely heavily on lizard prey.

Food availability and predation risk are often considered the main drivers of reproduction in birds but their relative importance has been debated for decades (Lack 1954, Ricklefs 1969, Martin 1987, Newton 1998). Behavioral studies show that individuals balance the benefits of foraging with the predation risk incurred while doing so (Lima 1998), whereas experimental studies show that augmenting food and reducing predation risk may have multiplicative benefits (Krebs et al. 1995, Zanette et al. 2003, but see Preston and Rotenberry 2006). We found that the effects of a resource that mediates predation risk and vulnerability to heterospecific enemies (nest-site abundance) interacted with factors associated with food and foraging space (e.g., woody vegetation cover). R increased markedly with increasing nest-site abundance but only in patches where vegetation cover was at moderate to high levels (Fig. 4). Thus, once nest sites became sufficiently abundant to mitigate predation and other risks, the benefits of food and foraging space were realized. Where nests were rare, however, increasing vegetation cover actually had negative effects on R, likely because abundance of heterospecific enemies such as Western Screech-Owls increases with woody vegetation cover (Hardy et al. 1999), which in fact, was much higher in patches where nest sites were rare and evidence of these interactions was observed. Although our results suggest the effect of heterospecific interactions is greater than food, these effects can be challenging to separate because vegetation complexity often affects both foraging and nesting resources (Bowman and Harris 1980, Chalfoun and Martin 2009). Because cavity abundance likely has little effect on food in this system, such confounding was likely low. Thus our results suggest strong evidence of interactive effects between predation and food availability on reproduction.

The ability of macrohabitat (e.g., vegetation community) vs. microhabitat (e.g., small-scale features such as nest sites) factors to explain variation in animal abundance and demography is rarely assessed (Morris 1985, McClure et al. 2012). With regard to habitat quality, most studies consider variation due only to macrohabitats (e.g., Korpimäki 1988, Holmes et al. 1996, Van Horne et al. 1997, Pettorelli et al. 2003, Breininger and Oddy 2004, Nilsen et al. 2004, McLoughlin et al. 2007, Arlt et al. 2008), whereas those that consider both types of factors are less common (e.g., Franklin et al. 2000, Pettorelli et al. 2001, 2005b, Mosser et al. 2009). Because the spatial extent of macrohabitats are typically broad, studies that focus on them often pool observations of individuals within each macrohabitat rather than assessing the effects of microhabitat factors on performance at home-range scales (but see Franklin et al. 2000, Pettorelli et al. 2005b, McLoughlin et al. 2007). Thus, in evaluating patterns and drivers of spatial variation in demography, studies focused on macrohabitats often assume populations in these areas are single demographic units with little internal structure and that macrohabitat factors drive variation in demography. We found that macrohabitat, microhabitat, and landscape (e.g., woodland fragmentation) factors all explained variation in R among home ranges. Moreover, spatial autocorrelation was undetectable because abundance of important resources often varied markedly in adjacent patches in the same macrohabitats. Thus, had we considered only macrohabitat factors, important insights on processes that drove habitat quality would have been lost. Although habitat quality was greater on average in semi-desert grasslands, differences in important microhabitat and landscape factors did not explain these differences, and macrohabitats effects seemed to be driven by less extreme climates in grasslands. Assessments of habitat quality should consider macrohabitat, microhabitat, and potentially landscape factors because they may all be important and because macrohabitat effects could be driven by underlying variation in microhabitat resources. Because habitat quality is driven by differences in vital rates among individuals in specific habitats and depends on environmental variation at home-range scales, evaluating habitat quality at this scale can provide more process-oriented insights.

Weather

Temporal variation in weather can have indirect effects on vital rates by affecting resources and direct physiological effects (Stenseth et al. 2002, Mysterud et al. 2008). In arid environments where climates are already harsh, extreme events can have major effects on populations and may be increasing due to climate change (Taylor 1934, Easterling et al. 2000, Holmgren et al. 2006). Extreme events and the ecological crunches they can create are characterized by major perturbations in vital rates that affect population dynamics (Van Horne et al. 1997, Holmgren et al. 2006) and potentially microevolution (Grant 1986). In the Sonoran Desert, precipitation largely had positive effects on R, high brooding-season temperature largely had negative effects, and a combination of hot dry conditions contributed to an apparent ecological crunch characterized by very low R (Fig. 2), which also affected population dynamics (Chapter 1). During extreme times, however, most owls still attempted to breed despite realizing lower performance. Thus, pygmy-owls seem largely adapted to extreme events likely as a result of evolving to cope with a seasonal and highly stochastic environment.

In arid environments, precipitation often drives rapid increases in plant and insect biomass (Beatley 1969, Jaksic 2001), which augments food and productivity of small vertebrates, and subsequently promotes higher productivity and abundance of predators (Jaksic et al. 1992, Lima et al. 2002, Letnic et al. 2005, Previtali et al. 2009). Because in the Sonoran Desert owls are generalists that often consume large numbers of lizards, which are affected more by summer vs. winter precipitation (Rosen 2000), our findings that warm-season precipitation was more important than cool-season precipitation and that annual precipitation was most influential overall, are consistent with the natural history of this system.

Despite the importance of precipitation, its effects were largely limited to periods of moderate to high temperatures during the brooding season (Fig. 2). This pattern is likely due to effects of precipitation on prey abundance and the effects of temperature on prey activity during periods of rapid nestling growth and thus high energy demands. Activity levels of lizards depend on their thermoregulatory requirements that vary with the physiology and behavior of individual species (Dunham et al. 1989). Because activity levels of common prey species decline at high temperatures (Flesch, *unpubl. data*), temperature likely has important effects on prey availability. When precipitation is sufficient to promote high prey abundance, however, the effect of temperature on prey availability is likely less important, especially in patches with high prey diversity. When temperatures are low and thermal conditions are favorable, however, lizards likely remain active for longer periods, which bolsters prey availability and compensates for lower prey abundance. Because temperature had no effect when precipitation was high, our results suggest weather had largely indirect effects on owls. Interactive effects of temperature and precipitation on animals (e.g., Alto and Juliano 2001) are rarely observed likely because they are rarely considered. When precipitation affects food supply and temperature affects prey activity, however, these relationships could be common and have important implications given regional predictions for increasing drought and higher temperature due to climate change (Seager et al. 2007, Overpeck and Udall 2010).

Conspecifics

Reproductive output within territory patches declined with the presence and abundance of conspecific neighbors. Thus, although pygmy-owls are highly territorial, conspecifics affect individual performance in this system, which does not conform strictly to an Ideal Dominance Distribution (IDD) where performance is maintained despite increasing conspecific density. Despite these effects, broad spatial heterogeneity in R among territories remained (Fig. 7) indicating general conformance to an IDD. Density-dependent declines in performance at individual scales are indicative of interference mechanisms of an Ideal Free Distribution (IFD), yet because R clearly did not equilibrate among territories in response to conspecifics, this system does not conform to an IFD. Although interference and scramble competition are fundamental mechanisms in models of the IFD (Sutherland and Parker 1992, Parker and Sutherland 1986), our results add to a small but growing literature indicating they may also operate in despotic systems (Wauters and Lens 1995, Armstrong et al. 2005, Carrete et al. 2006a, López-Sepulcre et al. 2010, Nevoux et al. 2011). Because ideal distributions were developed to represent theoretical extremes, such mixed models may be more common in nature and suggest a model of the IDD that includes interference should be developed.

Levels of negative density dependence were moderate in magnitude and on average resulted in a decline of approximately one young per occupied patch across a full range of variation in density. Although magnitudes of density dependence in this system may be limited by the linear arrangement of habitat and high levels of territoriality, this estimate is difficult to compare with those from the literature because (1) most studies of density-dependent reproduction focus on average performance at population scales in a given year (Newton 1998), (2) reports of significant results often include interactions (Carrete et al. 2006a, 2006b), and because (3) studies that manipulate local densities consider high- vs. low-density treatments rather than continuous effects (Alatalo and Lundberg 1984, Sillett et al. 2004). Regardless, magnitudes of density dependence we observed did not eliminate differences in realized quality among territories as has been reported in other despotic systems (López-Sepulcre et al. 2010).

Studies of density-dependent reproduction and survival typically focus on population regulation or population dynamics rather than habitat quality, and thus are framed at population vs. individual scales (Sinclair 1989, Newton 1998). Nonetheless, processes that create density dependence are not driven by the abundance of animals *per se* but rather by their effects on resources and social conditions. We observed negative density dependence at local territory-specific scales but not at larger scales. Moreover, when different local metrics were considered, estimates of conspecific density based on the number of neighbors and exact distances to their nests best described the effect (Appendix D). Despite these local effects, during an overlapping period in this system, models of population dynamics failed to detect significant levels of density dependence (Chapter 1). Thus, the spatial scale at which density dependence is assessed can affect whether it is detected, which is why studies framed at scales larger than the spatial use of individual animals often fail to detect density dependence (Hails and Crawley 1992, Ray and Hastings 1996, Coulson et al. 1997, Williams and Leibhold 2000). In this system, areas between some patches were occasionally occupied by intervening pairs, which augmented local densities. As distances between neighbors contract, territory sizes and resource availability likely also contract and antagonistic interactions and costs of territorial defense increase, which are the mechanisms that drive density dependence (Huxley 1934, Stamps 1990, Both and Visser 2000, Sillett et al. 2004). When density dependence is driven by interference or scramble competition, territory- or individual-specific metrics such as local density (Coulson et al. 1997, this study) or other distances-based metrics (Newton et al. 1977, Carette et al. 2006a) are best suited for detecting it.

In addition to interference, density dependence may also be driven by the effects of local interactions manifested at much larger scales. This is because when habitat quality varies spatially and despots relegate subordinates to patches of lower quality through contest competition, increased variation in resource holding potential among individuals can cause average per capita performance to decline with population size (Kluyver and Tinbergen 1953, Andrewartha and Birch 1954, Brown 1969). After the negative effects of conspecifics at local scales were considered, however, R actually increased somewhat with regional population size (Fig. 6). Thus, owls actually performed better on average as regional abundance increased likely because favorable weather augmented food supply and carrying capacity that benefits all individuals. Because different density-dependent processes may operate simultaneously at different scales, identifying them can elucidate how conspecifics affect individual performance and population dynamics. Nonetheless, when assessing density-dependent habitat quality, estimating the effects of conspecifics at scales relevant to individuals is essential.

Relative contribution of each component

Few studies compare variation in vital or population growth rates across both space and time, especially at small spatial scales (Sæther et al. 1999, Franklin et al. 2000, Reid et al. 2006, Ozgul et al. 2007). We found that spatial process variation in R among territory patches was nearly 6 times greater than that across time and that coefficients of process variation were 2.5 times greater across space than time, suggesting large effects of habitat. In comparison, magnitudes of spatial vs. temporal process variation in reproductive output among territories occupied by Spotted Owl were nearly equal, a coefficient of spatial process variation was similar, but that for temporal process variation was much greater than in our system (Franklin et al. 2000). Thus, whereas habitat effects were also large, R was much more resilient to extreme events in this system. Coefficients of temporal variation in R of Barn Owls (*Tyto alba*, 0.081; Altwegg et al. 2007) is similar to that reported here (0.0703), whereas that for multiparous ungulates (0.091-0.098; Gaillard et al. 2000) are also similar despite differences in life history.

Spatial variation in habitat can have large and persistent effects on animal performance (Blancher and Robertson 1985, Newton 1989, 1991, Franklin et al. 2000, McLoughlin et al. 2007), but few studies have estimated these effects in wild populations while also considering stochastic temporal factors and conspecifics. Although habitat resources explained much greater proportions of variation in R than stochastic factors or conspecifics (0.70 vs. ≤0.17), R varied by up to 56% due to stochastic effects and by up to 27% due to conspecifics in some patches during some years (Fig. 7). Thus, while good territory patches tended to remain good over time, the effects of stochastic factors and conspecifics can reorder the realized quality of different points in space across time. Although habitat effects should be strong in systems where individuals maintain exclusive use of space and depend on largely static resources linked to gross vegetation structure, stochastic processes can have large effects on vital rates and population dynamics that should be considered when estimating the fitness potential of habitat (Tuljapurkar 1990, Boyce et al. 2006, Ezard et al. 2008).

Interactions among components

Processes that drive ecological patterns can involve complex multi-factorial explanations that include interactions (Hilborn and Stearns 1992, Holmes 1995). In evaluating how the collective environment affected performance, we found that spatial and temporal factors interacted in complex and often novel ways and that some habitat and weather effects depended on conspecific density. When evaluated in a model selection framework, evidence for interactions among components was much stronger than that for additive relationships but relative support for different interactions was similar suggesting a broad range of processes drove habitat quality simultaneously.

Habitat × *weather*.—Van Horne et al. (1997) suggested that when weather affects food supply, habitat quality is likely driven by interactions between habitat and weather. Franklin et al. (2000) found that high-quality habitat buffered the effects of harsh weather on survival but not on reproduction of Spotted Owls. Here, we found that territories with greater woody vegetation cover magnified the benefits of favorable weather characterized by high precipitation and low temperature. However, high-quality habitat failed to buffer the negative effects of harsh weather suggesting adverse conditions affect all individuals equally. Because in our system precipitation augments prey abundance, which is likely already higher on average in territories with more vegetation cover, owls occupying these areas attain multiplicative benefits when conditions improve, which further suggests interactions between habitat and weather are widespread. Such relationships indicate the importance of considering broad temporal contexts when evaluating habitat quality and suggest caution when inferring differences in habitat quality based on short-term studies (Van Horne et al. 1997). If some habitats are capable of buffering the negative effects of harsh weather, habitat quality could be higher where animals are more resilient to weather effects than in areas that occasionally support very high performance. Moreover, if some habitats magnify the benefits of favorable weather, then relative differences in habitat quality may not be detectable until those conditions are present. Assessing the extent to which habitat resources can mediate weather effects has important implications for management and conservation responses to climate change.

Weather × density.—The relative importance of density-dependent vs. density-independent processes in population biology is a question of great debate (Anderwartha and Birch 1954, Turchin 1995). In recent decades, recognition that the effects of extrinsic factors may depend on conspecific densities has become widespread (Fowler 1987, Sinclair et al. 1989, Turchin 1995, Coulson et al. 2004). Perhaps the most frequently reported examples of these interactions involve increasing negative effects of harsh winters as conspecific densities rise (Gaillard et al. 2000, Bonenfant et al. 2009). Here, we found that the positive effects of favorable weather on performance acted in a density-independent manner at low conspecific densities but much less so at moderate densities (Fig. 8). When densities were high, however, performance decreased as weather conditions improved suggesting its positive effects on resources were offset by high intraspecific competition. Interactions between weather and conspecific density are typically found during periods of resource scarcity (Fowler 1987, Bonenfant et al. 2009) vs. resource abundance (e.g. Owen-Smith 1990, this study). This tendency is likely because key factors that drive vital rates vary geographically and because studies in temperate vs. tropical systems are much more common (Sinclair 1989, Gaillard et al. 2000, Newton 1998). While broad generalizations have yet to fully emerge, density-dependent mortality in the non-growing season may have greater effects on vital rates in temperate vs. tropical systems, where density-dependent reproduction or recruitment in the growing season seems more influential (Lack 1954, 1966, Fowler 1987, Sæther et al. 2004). Although we did not assess mortality in the non-growing season, winter severity has no effect on reproduction or temporal variation in abundance in this system and the same weather factors identified here also drove population dynamics (Chapter 1).

Habitat × density.—Understanding how conspecifics affect individual performance is an important aspect of behavioral ecology and population biology (Fretwell 1972, Morris 2003). Nonetheless, few studies have addressed if and how habitat resources mediate the effects of conspecifics on performance (Morris 1987, 1989, Knight and Morris 1996, Pettorelli et al. 2003, 2005b, McLoughlin et al. 2006). McLoughlin et al. (2006) found that high-quality habitats had positive effects on lifetime reproductive success at low but not at high conspecific densities. In another ungulate system, Pettorelli et al. (2005b) suggested similar patterns in juvenile survival but did not separate the effects of weather and conspecifics, and Pettorelli et al. (2003) found that juvenile survival was high regardless of habitat quality at low densities and that high-quality habitat buffered the negative effects of conspecifics at high densities. Here, we found that important habitat resources mediated the effects of conspecific density on R, albeit in different ways, and that habitat of greater fundamental quality typically buffered the negative effects of conspecifics more than low-quality habitat (Figs. 8-9). Our findings are novel because we considered continuous variation in habitat based on the estimated effects of macrohabitat, microhabitat, and landscape factors and because the effects of conspecifics varied depending on the habitat factors considered. With regard to landscape factors, conspecifics had no effect on R at low levels of woodland fragmentation but increasingly negative effects with increasing fragmentation (Fig. 8). With regard to macrohabitat factors, rates of negative density dependence were higher in grasslands despite the fact that fundamental quality was higher on average in grasslands (Fig. 9). Nonetheless, when the effects of all important habitat factors were considered together, high-quality habitats buffered the negative effects of conspecifics more than low-quality habitats. Consequently, had we considered only macrohabitat effects, insights regarding the effects of conspecifics would have varied. Although conspecifics can degrade realized quality in a general sense, high-quality resources can buffer these effects and provide greater rewards to occupants. While identifying mechanisms that drove these patterns was beyond the scope of our efforts, we suspect that territory sizes likely decline as patch quality increases, which makes individuals in high-quality habitats less susceptible to the effects of conspecifics.

Implications

Assessments of habitat quality often focus exclusively on habitat resources that vary spatially. However, we show that factors such as conspecific density and weather, which vary both spatially and temporally, can mediate habitat effects. Thus, more general understandings of how the collective environment affects performance may require consideration of multiple environmental components and their interactions. In our system, individuals that occupied habitats of high fundamental quality realized higher performance not only because resources were better, but also because these areas buffered the negative effects of conspecifics and amplified the benefits of favorable weather. Thus, nonrandom habitat use driven by cues associated with the perceived quality of spatial components such as vegetation structure should largely match differences in quality among locations through time. This means that organisms (and land managers) should be able to locate relatively good territory locations reliably at any single point in time. It follows directly that natural selection should promote the evolution of habitat selection based on spatially variable environmental characteristics in this system.

Conservation and management.—Information on factors that drive habitat quality is important for guiding management, especially for pygmy-owls that have declined to endangered levels in Arizona. Because habitat quality is measured at an individual scale whereas conservation focuses on populations, understanding how conspecifics affect individual performance and how resources and individuals are distributed is important for applying information on habitat quality to conservation. We found that conspecifics had only moderate effects on realized habitat quality that declined as fundamental quality increased. Thus, strategies focused on enhancing habitat quality should aid conservation, especially when they simultaneously augment habitat area. Because the negative effects of conspecifics were limited at densities <0.5 territories/km^2, small-scale habitat-improvement efforts that match these scales will be most efficient. Although we did not assess how resources affected territory size or density at larger scales, high-quality patches were often immediately adjacent to low-quality patches and individuals were not distributed in an ideal free manner. Thus, strategies focused on resources that directly affect performance should be more efficient than those focused on density (Johnson 2007).

Our results suggest a variety of strategies to augment populations and recovery prospects. Abundance of potential nest cavities had overwhelmingly positive effects on performance, especially in areas where foraging space and other resources were abundant. Thus, management that promotes the survival and recruitment of saguaros will benefit owls. Although habitat manipulations aimed at single species should be approached with caution due to potential unintended consequences, erecting nest boxes or translocating saguaros in ways that increase nest-site abundance will enhance habitat quality, especially when guided by recommendations on specific nest-cavity features (see Flesch and Steidl 2010). Focusing such efforts in areas that support large, unfragmented woodlands and other important habitat features will be most efficient.

Most historical records of pygmy-owls in the Sonoran Desert were from large riparian areas in valley bottoms (Flesch 2003, Johnson et al. 2003) that have been lost or degraded in the last century (Webb et al. 2007, Flesch 2008). Restoring these once extensive desert riparian areas by fostering the establishment and growth of mesquite and other trees will enhance recovery prospects for pygmy-owls while also providing habitat for other species. Moreover, because increasing woodland cover amplified the positive effects of favorable weather, and decreasing woodland fragmentation reduced the negative effects of conspecifics, restoring large unfragmented woodlands such as those typically associated with riparian areas should have multiplicative benefits, especially in more arid regions where vegetation cover is more limited in uplands.

Intensity of hot dry conditions had negative effects on performance that were not buffered by high-quality resources. Thus, enhancing habitat quality may not be a realistic strategy for adapting to climate change unless resources can buffer the effects of harsh weather on survival (e.g., Franklin et al. 2000). Future research in this and other systems should assess the degree to which resources can mediate weather effects on survival and identify resources that promote high persistence and population growth despite unfavorable weather. More generally, because the collective environment affects habitat quality in complex ways, integrative approaches that consider the effects of resources, stochastic factors, and conspecifics are needed to guide management.

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SUPPLEMENTAL MATERIAL

Appendix A

Models representing the hypothesized effects of temporal factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010 (Ecological Archives XXX-XXX-XX).

Appendix B

Models representing the hypothesized effects of spatial factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010 (Ecological Archives XXX-XXX-XX).

Appendix C

Description of remote sensing methods used to quantify woody vegetation cover and other land-cover classifications within territory patches of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010 (Ecological Archives XXX-XXX-XX).

Appendix D

Factors, spatial scales, and models that described the effects of presence and abundance of conspecifics on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010 (Ecological Archives XXX-XXX-XX).

Appendix E

Parameter estimates and standard errors for the effects of spatial, temporal, and conspecific factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010 (Ecological Archives XXX-XXX-XX).

Table 1. Temporal factors considered when modeling the effects of weather, primary productivity, and seasonal timing of peak primary productivity on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Primary productivity was quantified based on normalized difference vegetation index (NDVI) at the scale of individual territory patches (50 ha) whereas weather was quantified at the closest of five weather stations to each patch.

Variable	Period	Code	Definition	Units
Temperature	Winter - recent	T_{winter}	Mean daily minimum temperature Nov. - March	^{0}C
	Incubation – current	T_{incub}	Mean daily maximum temperature April	^{0}C
	Brooding - current	T_{brood}	Mean daily maximum temperature May and June	^{0}C
Precipitation	Warm season - 1 yr lag	P_{ws}	Total precipitation June - Sept of prior year	cm
	Cool season - 0.5 yr lag	P_{cs}	Total precipitation Oct. - May, recent cool season	cm
	Annual - 0-1 yr lag	P_{yr}	Total precipitation recent cool season and prior warm season	cm
Primary Productivity	Warm season - 1 yr lag	$NDVI_{ws}$	Deviation from mean NDVI June – Sept of prior year	Proportion
	Cool season - 0.5 yr lag	$NDVI_{cs}$	Deviation from mean NDVI Oct. – May, recent cool season	Proportion
	Annual - 0-1 yr lag	$NDVI_{yr}$	Deviation from mean NDVI recent cool season and prior warm season	Proportion
Timing of Primary Productivity	Warm season - 1 yr lag	S_{NDVIws}	Days since June 1 of maximum NDVI June - Sept of prior year	Day no.
	Cool season - 0.5 yr lag	S_{NDVIcs}	Days since Oct 1 of maximum NDVI Oct. - May, recent cool season	Day no.

Table 2. Spatial factors considered when modeling the effects of habitat variation on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Factors where quantified at the scale of individual territory patches (50 ha)

Variable	Abbreviation	Definition	Units
Cavities	Cav	No. of saguaros with at least one suitable nesting cavity	no., log scale
Vegetation Community	Comm	Dominant community type in patch (desert-scrub or semi-desert grassland).	categorical
Elevation	Elev	Mean elevation from digital elevation model	m
Woodland Habitat	Hab_f	Mean fractional woody vegetation cover among all 30 × 30 m grid cells across patch	%
	Hab_w	Proportion of patch classified as woodland (e.g. 30 × 30 m grid cells with ≥20% fractional woody cover)	%
Core-Area Habitat	$Core_{hab}$	Proportion of patch classified as woody vegetation minus 30 m edge width	%
Edge Habitat	$Edge_{total}$	Length of edge between all 5 total land-cover classes	m
	$Edge_{hab}$	Length of edge between woodland and other land-cover classes	m
Mean Productivity	$NDVI_{mean}$	Mean normalized-difference vegetation index measured every 16 days over 10 years	ratio × 1000
Substrate	$Elev_{cv}$	Coefficient of variation in elevation among all 30 × 30 m grid cells	m
	Slope	Mean slope among all 30 × 30 m grid cells in patch	%
Disturbance	Disturb	Proportion of patch classified as agriculture, development, or road land-cover classes	%
Woodland Fragmentation	$Frag_{hab}$	No. of patches of woodland per ha divided by Hab_f	no./ha/%

Table 3. Rankings and estimated slope parameters for 15 hypothesized models that explained the effects of temporal factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Factor names and definitions are in Table 1 and descriptions of hypotheses and model numbers are in Appendix A.

Model	K	LL	ΔAICc	w_i	Slope ± SE
8) $lnT_{brood} + lnP_{yr} + lnT_{brood}*lnP_{yr} + NDVI_{yr}^2$	7	-915.10	0.00	0.318	$\beta_1 = -33.6 \pm 14.0$ $\beta_2 = -31.0 \pm 13.6$ $\beta_3 = 8.7 \pm 3.7$ $\beta_4 = 20.3 \pm 9.2$
11) $lnT_{brood} + lnP_{yr} + lnT_{brood}*lnP_{yr} + NDVI_{yr}^2 + S_{NDVIws}^2$	8	-914.43	0.72	0.222	$\beta_1 = -33.5 \pm 14.0$ $\beta_2 = -31.0 \pm 13.6$ $\beta_3 = 8.6 \pm 3.7$ $\beta_4 = 20.6 \pm 9.2$ $\beta_5 = 0.30 \pm 0.30$
12) $lnP_{yr} + NDVI_{yr}^2$	5	-918.26	2.19	0.106	$\beta_1 = 0.44 \pm 0.19$ $\beta_2 = 18.6 \pm 9.2$
14) $lnP_{yr} + NDVI_{yr}^2 + S_{NDVIws}^2$	6	-917.53	2.80	0.078	$\beta_1 = 0.42 \pm 0.19$ $\beta_2 = 19.0 \pm 9.2$ $\beta_3 = 0.30 \pm 0.30$
6) $lnT_{brood} + lnP_{yr} + lnT_{brood}*lnP_{yr}$	6	-917.54	2.81	0.078	$\beta_1 = -31.6 \pm 14.0$ $\beta_2 = -29.2 \pm 13.6$ $\beta_3 = 8.2 \pm 3.7$
9) $lnT_{brood} + lnP_{yr} + lnT_{brood}*lnP_{yr} + S_{NDVIws}^2$	7	-916.95	3.69	0.050	$\beta_1 = -31.5 \pm 14.0$ $\beta_2 = -29.2 \pm 13.6$ $\beta_3 = 8.1 \pm 3.7$ $\beta_4 = 0.30 \pm 0.30$
3) lnP_{yr}	4	-920.30	4.23	0.038	$\beta_1 = 0.44 \pm 0.19$
13) $lnP_{yr} + S_{NDVIws}^2$	5	-919.67	5.01	0.026	$\beta_1 = 0.43 \pm 0.19$ $\beta_2 = 0.29 \pm 0.26$
4) $NDVI_{yr}^2$	4	-920.99	5.62	0.019	$\beta_1 = 19.9 \pm 9.3$
15) $NDVI_{yr}^2 + S_{NDVIws}^2$	5	-920.11	5.90	0.017	$\beta_1 = 19.4 \pm 9.3$ $\beta_2 = 0.34 \pm 0.25$
7) $lnT_{brood} + NDVI_{yr}^2$	5	-920.21	6.10	0.015	$\beta_1 = -1.8 \pm 1.4$ $\beta_2 = 19.5 \pm 9.3$
10) $lnT_{brood} + NDVIyr^2 + S_{NDVIws}^2$	6	-919.40	6.54	0.012	$\beta_1 = -1.7 \pm 1.4$ $\beta_2 = 19.9 \pm 9.3$

						$\beta_3 = 0.32 \pm 0.25$
	$\beta_0 + b_{0i}$	3	-923.08	7.76	0.007	
5)	S_{NDVIws}^2	4	-922.30	8.24	0.005	$\beta_1 = 0.32 \pm 0.26$
2)	$\ln T_{brood}$	4	-922.41	8.46	0.005	$\beta_1 = -1.7 \pm 1.4$
1)	T_{winter}	4	-923.06	9.76	0.002	$\beta_1 = -0.0057 \pm 0.029$

Notes: The intercepts-only model ($\beta_0 + b_{0i}$) is included for comparison. Slope estimates and SE for S_{NDVIws} were multiplied by 1000

Table 4. Rankings of best approximating models of the effects of temporal and spatial factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010 compared to other models where some effects were included, excluded, or changed.

Change in effects	Model	ΔAICc	w_i
Time			
Best approximating model	lnT$_{brood}$ + lnP$_{yr}$ + lnT$_{brood}$*lnP$_{yr}$ + NDVI$_{yr}^{2}$	0.00	0.436
Inclusion of quadratic time effect	Year^2 + lnPyr + lnTbrood*lnPyr + NDVI$_{yr}^{2}$	1.57	0.199
Inclusion of linear time effect	Year + lnP$_{yr}$ + lnTb$_{rood}$*lnP$_{y}$r + NDVI$_{yr}^{2}$	1.58	0.198
Exclusion of P*T interaction	lnT$_{brood}$ + lnP$_{yr}$ + NDVI$_{yr}^{2}$	3.33	0.083
Exclusion of NDVI effect	lnT$_{brood}$ + lnP$_{yr}$ + lnT$_{brood}$*lnP$_{yr}$	3.80	0.065
Intercepts only model	$\beta_0 + b_{0i}$	7.76	0.009
Quadratic time effect only	Year^2	8.92	0.005
Linear time effect only	Year	9.13	0.005
Space			
Best approximating model	lnCav + Comm + Hab$_f$ + lnCav*Hab$_f$ + Frag$_{hab}$	0.00	0.266
Inclusion of Disturb effect	lnCav + Comm + Hab$_f$ + lnCav*Hab$_f$ + Frag$_{hab}$ + Disturb	0.31	0.227
Exclusion of Hab effect	lnCav + Comm + Frag$_{hab}$	0.93	0.167
Inclusion of Edge effect	lnCav + Comm + Hab$_f$ + lnCav*Hab$_f$ + Frag$_{hab}$ + Edge$_{total}$	1.02	0.159
Inclusion of quadratic Elev effect	lnCav + Comm + Hab$_f$ + lnCav*Hab$_f$ + Frag$_{hab}$ + Elev^2	1.90	0.103
Exclusion of Hab*Cav interaction	lnCav + Comm + Hab$_f$ + Frag$_{hab}$	2.88	0.063
Exclusion of Comm effect	lnCav + Hab$_f$ + lnCav*Hab$_f$ + Frag$_{hab}$	5.72	0.015
Exclusion of lnCav effect	Comm + Hab$_f$ + Frag$_{hab}$	38.17	0.000

Table 5. Rankings and estimated slope parameters for hypothesized models that explained the effects of spatial factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Descriptions of hypotheses and model numbers are provided in Appendix B.

	Model	K	LL	ΔAICc	w_i	Slope ± SE
3)	$\ln Cav + Comm + Hab_f + \ln Cav * Hab_f + Frag_{hab}$	8	-896.87	0.00	0.237	$\beta_1 = 0.15 \pm 0.20$ $\beta_2 = 0.46 \pm 0.16$ $\beta_3 = -0.068 \pm 0.034$ $\beta_4 = 0.023 \pm 0.010$ $\beta_5 = -0.18 \pm 0.085$
4)	$\ln Cav + Comm + Hab_f + \ln Cav * Hab_f + Slope + \ln Cav * Slope + Frag_{hab}$	10	-894.79	0.01	0.235	$\beta_1 = -0.17 \pm 0.26$ $\beta_2 = 0.38 \pm 0.18$ $\beta_3 = -0.069 \pm 0.034$ $\beta_4 = 0.023 \pm 0.010$ $\beta_5 = -0.66 \pm 0.44$ $\beta_6 = 0.27 \pm 0.15$ $\beta_7 = -0.19 \pm 0.086$
11)	$\ln Cav + Comm + NDVI_{mean} + \ln Cav * NDVI_{mean}$	7	-898.63	1.47	0.114	$\beta_1 = -0.55 \pm 0.53$ $\beta_2 = 0.50 \pm 0.16$ $\beta_3 = -1.00 \pm 0.57$ $\beta_4 = 0.41 \pm 0.19$
B)	$\ln Cav + Comm$	5	-901.39	2.86	0.057	$\beta_1 = 0.57 \pm 0.085$ $\beta_2 = 0.54 \pm 0.16$
2)	$\ln Cav + Comm + Hab_f + \ln Cav * Hab_f + Slope + \ln Cav * Slope + Disturb$	10	-896.23	2.90	0.056	$\beta_1 = -0.060 \pm 0.26$ $\beta_2 = 0.51 \pm 0.18$ $\beta_3 = -0.050 \pm 0.033$ $\beta_4 = 0.018 \pm 0.010$ $\beta_5 = -0.77 \pm 0.44$ $\beta_6 = 0.27 \pm 0.15$ $\beta_7 = 0.11 \pm 0.078$
1)	$\ln Cav + Comm + Hab_f + \ln Cav * Hab_f + Slope + \ln Cav * Slope$	9	-897.30	2.95	0.054	$\beta_1 = -0.063 \pm 0.26$ $\beta_2 = 0.45 \pm 0.18$ $\beta_3 = -0.045 \pm 0.033$ $\beta_4 = 0.018 \pm 0.010$ $\beta_5 = -0.71 \pm 0.44$ $\beta_6 = 0.27 \pm 0.15$

8)	lnCav + Comm + Edge_{tot}	6	-900.51	3.16	0.049	$\beta_1 = 0.60 \pm 0.087$ $\beta_2 = 0.54 \pm 0.16$ $\beta_3 = 0.063 \pm 0.047$
7)	lnCav + Comm + Core_{hab} + lnCav*Core_{hab} + Slope + lnCav*Slope + Disturb	10	-896.43	3.30	0.045	$\beta_1 = 0.039 \pm 0.23$ $\beta_2 = 0.51 \pm 0.18$ $\beta_3 = -0.34 \pm 0.24$ $\beta_4 = 0.13 \pm 0.077$ $\beta_5 = -0.81 \pm 0.44$ $\beta_6 = 0.28 \pm 0.15$ $\beta_7 = 0.11 \pm 0.077$
5)	lnCav + Comm + Core_{hab} + lnCav*Core_{hab}	7	-899.57	3.34	0.045	$\beta_1 = 0.38 \pm 0.14$ $\beta_2 = 0.49 \pm 0.16$ $\beta_3 = -0.31 \pm 0.24$ $\beta_4 = 0.13 \pm 0.077$
4)	lnCav + Comm + Core_{hab} + lnCav*Core_{hab} + Slope + lnCav*Slope	9	-897.55	3.45	0.042	$\beta_1 = 0.030 \pm 0.23$ $\beta_2 = 0.44 \pm 0.17$ $\beta_3 = -0.31 \pm 0.24$ $\beta_4 = 0.13 \pm 0.077$ $\beta_5 = -0.75 \pm 0.44$ $\beta_6 = 0.29 \pm 0.15$
9)	lnCav + Comm + Edge_{tot} + Slope + lnCav*Slope	8	-898.83	3.92	0.033	$\beta_1 = 0.25 \pm 0.21$ $\beta_2 = 0.51 \pm 0.17$ $\beta_3 = 0.042 \pm 0.049$ $\beta_4 = -0.75 \pm 0.44$ $\beta_5 = 0.27 \pm 0.15$
10)	lnCav + Comm + Edge_{tot} + Slope + lnCav*Slope + Disturb	9	-897.81	3.96	0.033	$\beta_1 = 0.23 \pm 0.21$ $\beta_2 = 0.58 \pm 0.18$ $\beta_3 = 0.020 \pm 0.052$ $\beta_4 = -0.83 \pm 0.45$ $\beta_5 = 0.28 \pm 0.15$ $\beta_6 = 0.11 \pm 0.079$
	$\beta_0 + b_{0i}$	3	-923.08	42.17	0.000	

Notes: The intercepts-only model ($\beta_0 + b_{0i}$) is included for comparison.

Table 6. Rankings of models that described the individual, additive, and interactive effects of spatial and temporal factors and conspecific density on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Factors included in models were identified by assessing a range of a priori hypotheses and are the same factors included in the best approximating models for each component. Parameter estimates are in Appendix E.

Hypothesis	Model	K	LL	ΔAICc	*w*
Habitat × Weather + Density	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVI}_{yr}^2 + \mathrm{Density} + \mathrm{lnP}_{yr}*\mathrm{Hab}_f + \mathrm{lnT}_{brood}*\mathrm{Hab}_f + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr}*\mathrm{Hab}_f$	16	-882.99	0.00	0.264
Habitat + Weather × Density	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVI}_{yr}^2 + \mathrm{Density} + \mathrm{lnP}_{yr}*\mathrm{Density}$	14	-885.20	0.15	0.245
Habitat × Weather × Density	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVIyr}^2 + \mathrm{Density} + \mathrm{Frag}_{hab}*\mathrm{Density} + \mathrm{Frag}_{hab}*\mathrm{lnP}_{yr} + \mathrm{Density}*\mathrm{lnP}_{yr} + \mathrm{Frag}_{hab}*\mathrm{Density}*\mathrm{lnP}_{yr} + \mathrm{Hab}_f*\mathrm{Density} + \mathrm{Hab}_f*\mathrm{NDVI}_{yr}^2 + \mathrm{Density}*\mathrm{NDVI}_{yr}^2 + \mathrm{Hab}_f*\mathrm{Density}*\mathrm{NDVI}_{yr}^2$	21	-877.83	0.55	0.201
Habitat + Weather + Density	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVI}_{yr}^2 + \mathrm{Density}$	13	-886.80	1.22	0.144
Habitat × Density + Weather	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVI}_{yr}^2 + \mathrm{Density} + \mathrm{Hab}_f*\mathrm{Density} + \mathrm{Frag}_{hab}*\mathrm{Density} + \mathrm{Comm}*\mathrm{Density}$	16	-884.41	2.84	0.064
Habitat × Weather	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVI}_{yr}^2 + \mathrm{lnP}_{yr}*\mathrm{Hab}_f + \mathrm{lnT}_{brood}*\mathrm{Hab}_f + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr}*\mathrm{Hab}_f$	15	-885.76	3.40	0.048
Habitat + Weather	$\mathrm{lnCav} + \mathrm{Comm} + \mathrm{Hab}_f + \mathrm{lnCav}*\mathrm{Hab}_f + \mathrm{Frag}_{hab} + \mathrm{lnT}_{brood} + \mathrm{lnP}_{yr} + \mathrm{lnT}_{brood}*\mathrm{lnP}_{yr} + \mathrm{NDVI}_{yr}^2$	12	-889.43	4.36	0.030

Habitat × Density	lnCav + Comm + Hab_f + lnCav*Hab_f + $Frag_{hab}$ + Density + Hab_f*Density + $Frag_{hab}$*Density + Comm*Density	12	-892.39	10.29	0.002
Habitat + Density	lnCav + Comm + Hab_f + lnCav*Hab_f + $Frag_{hab}$ + Density	9	-895.75	10.72	0.001
Habitat only	lnCav + Comm + Hab_f + lnCav*Hab_f + $Frag_{hab}$	8	-896.87	10.87	0.001
Weather × Density	$\ln T_{brood}$ + $\ln P_{yr}$ + $\ln T_{brood}$*$\ln P_{yr}$ + $NDVI_{yr}^2$ + $\ln P_{yr}$*Density	9	-908.67	36.56	0.001
Weather + Density	$\ln T_{brood}$ + $\ln P_{yr}$ + $\ln T_{brood}$*$\ln P_{yr}$ + $NDVI_{yr}^2$ + Density	8	-910.41	37.95	0.001
Weather only	$\ln T_{brood}$ + $\ln P_{yr}$ + $\ln T_{brood}$*$\ln P_{yr}$ + $NDVI_{yr}^2$	7	-915.10	45.27	0.001
Density only	Density	4	-920.79	50.49	0.001

FIG. 1. Study area in northwest Mexico showing the distribution of territory patches used by Ferruginous Pygmy-Owls and the location of weather stations considered. Territory patches were located in two major vegetation communities and weather stations were located near Sasabe, Sonoyta, Cucurpe, Magdelena, and Altar. Regional patch occupancy was estimated in 11 regions: San Miguel, upper Magdalena, Magdalena-Coyotillo, Busani, upper Alter, lower Altar, upper Sasabe, lower Sasabe, upper Plomo, lower Plomo, and Sonoyta (see text). Territory patches are 50 ha (not to scale) and the study area was approximately 20,000 km^2 in area.

FIG. 2. Temporal variation and effects of temporal factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Temperature and precipitation were measured at regional scales and normalized difference vegetation index (NDVI) was measured at patch-specific scales and expressed as proportional deviations from mean NDVI by subtracting the mean of all annual estimates across time from each annual estimate and dividing by the mean so as to represent years of relatively high vs. lower productivity. Estimates of reproductive output in the two lower figures are based on model 8 in Table 3.

FIG. 3. Effect of habitat factors on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Lower right figure shows the number of negative heterospecific interactions observed divided by the total number of territory patches in each group across a gradient of increasing abundance of potential nest sites. Filled circles in upper figures are patches in semi-desert grasslands whereas those in the lower figure are patches where we observed negative heterospecific interactions. Estimates of reproductive output are based on model 3 in Table 5. Inset in upper left figure shows means (± SE) in each vegetation community.

FIG. 4. Interactive effects of abundance of potential nest sites and other habitat factors on reproductive output of Ferruginous Pygmy-Owlsin northwest Mexico, 2001-2010.Estimates of reproductive output are based on the top-ranked models that include each of the habitat factors represented as summarized in Table 5.

FIG. 5. Effects of habitat frgamentation (Frag_{hab}) and quantity of woodland vegetation cover (Hab_{f}) on reproductive output (*R*) of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Nine territory patches with high abundance of potential nest sites are illustrated to represent these effects. Black pixels (30-m) were classified as woodland because they had ≥20% fractional woody vegetation cover, whereas gray pixels had <20% woody vegetation cover. Estimates of reproductive output are based on model 3 in Table 5.

FIG. 6. Effects of conspecifics on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Conspecific presence, abundance, and density were measured around each focal patch during each year and regional occupancy was measured as the proportion of patches occupied in each of 11 watershed regions during each year. Estimates of the effect of local conspecific density are based model {Density} in Appendix D, estimates of conspecific presence and abundance are least square means adjusted for patch effects, and estimates of the effect of regional occupancy are adjusted for the effects of local density from model {Density + $\text{Occ}_{\text{region}}$}.

FIG. 7. Estimated reproductive output within individual territory patches occupied by Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Patches are sorted in ascending order basis on the estimated habitat effects and only patches with ≥2 observations (n = 92) are

shown. Upper figure shows predictions based on estimated habitat effects only (model 3, Table 5), and the middle and lower figures show estimates based on habitat and temporal factors, and habitat and conspecific density, respectively (see Table 6). In lower figures, diamonds are average reproductive output and horozontal lines across bars illustrate the range of estimates among years within patches.

FIG. 8. Interactive effects of important factors associated with different environmental components of habitat quality on reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. The hypothetical weather gradient in the top figure was standardized based on annual precipitation and mean maximum temperature during the brooding season so as to represent conditions that ranged from wet and cool to hot and dry. Estimates are based on the top-ranked models that included these interactions in Table 6.

FIG. 9. Effects of vegetation community and fundamnetal habitat quality on density-dependent declines in reproductive output of Ferruginous Pygmy-Owls in northwest Mexico, 2001-2010. Habitat quality was classified as high (>3.0), moderate (>2.4-3.0), or low (0.9-2.4) based on patch-specific predictions of reproductive output from model 3 in Table 5. Slope parameters and SE are from least-squares regression. Estimates are based on the model (Habitat × Density + Weather) in Table 6.

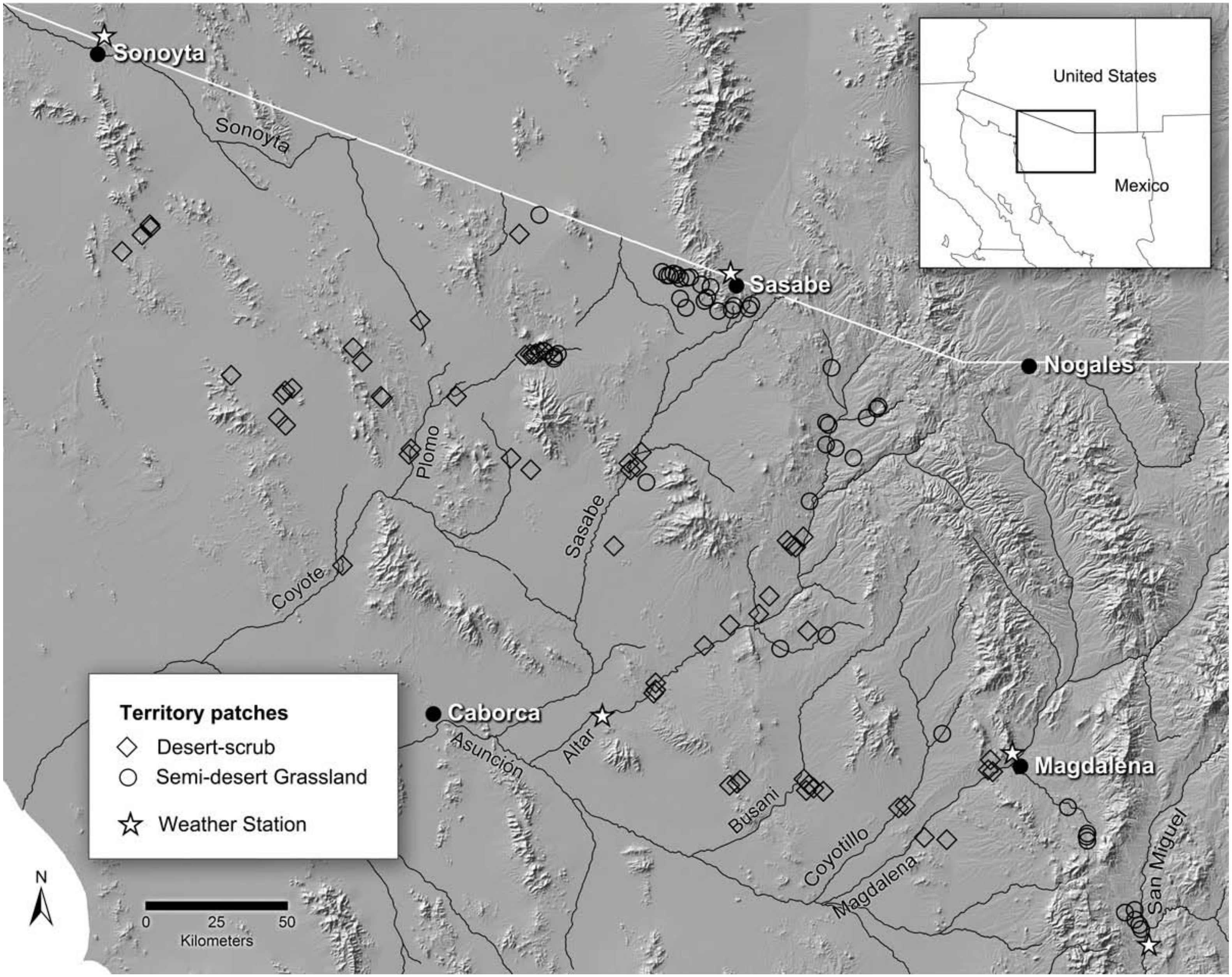
Sonoyta
Sonoyta
Sasabe
Nogales
United States
Mexico
Plomo
Sasabe
Coyote
Caborca
Altar
Asunción
Busani
Coyotillo
Magdalena
Magdalena
San Miguel
Territory patches
Desert-scrub
Semi-desert Grassland
Weather Station
N
0
25
50
Kilometers

Fig. 1

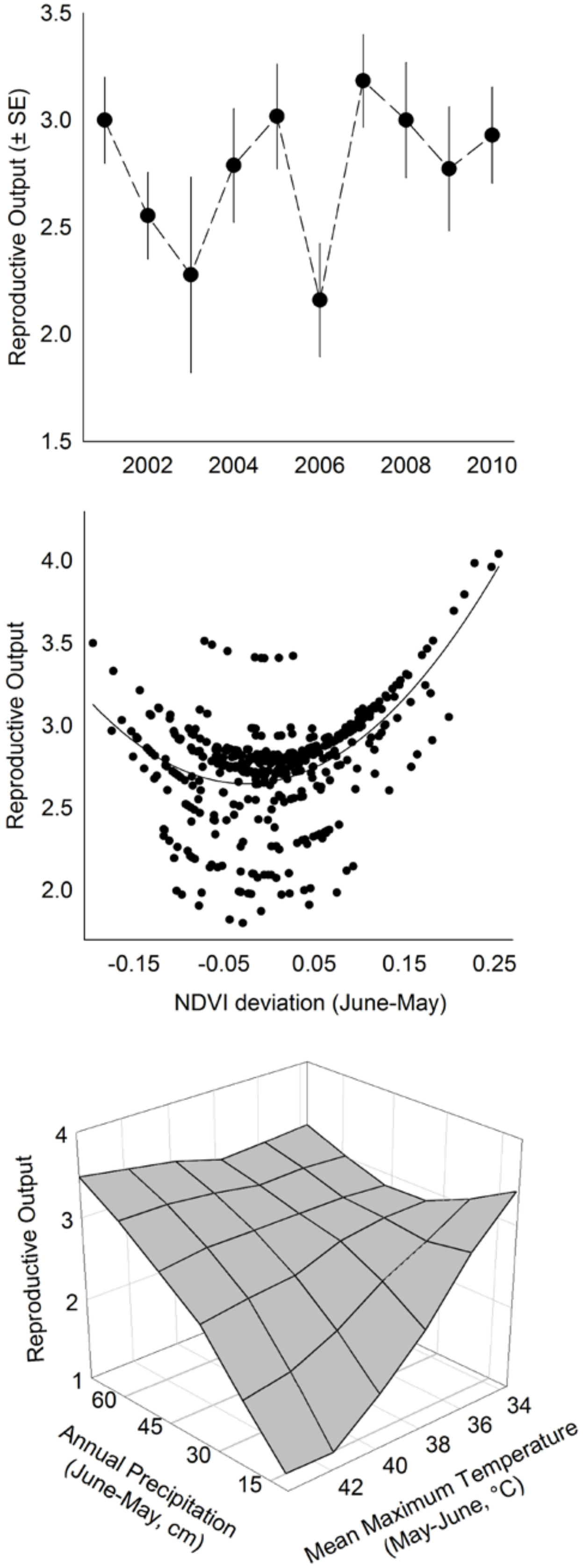
Reproductive Output (± SE)
3.5
3.0
2.5
2.0
1.5
2002
2004
2006
2008
2010
Reproductive Output
4.0
3.5
3.0
2.5
2.0
-0.15
-0.05
0.05
0.15
0.25
NDVI deviation (June-May)
Reproductive Output
4
3
2
1
60
45
30
15
Annual Precipitation (June-May, cm)
42
40
38
36
34
Mean Maximum Temperature (May-June, °C)

Fig. 2

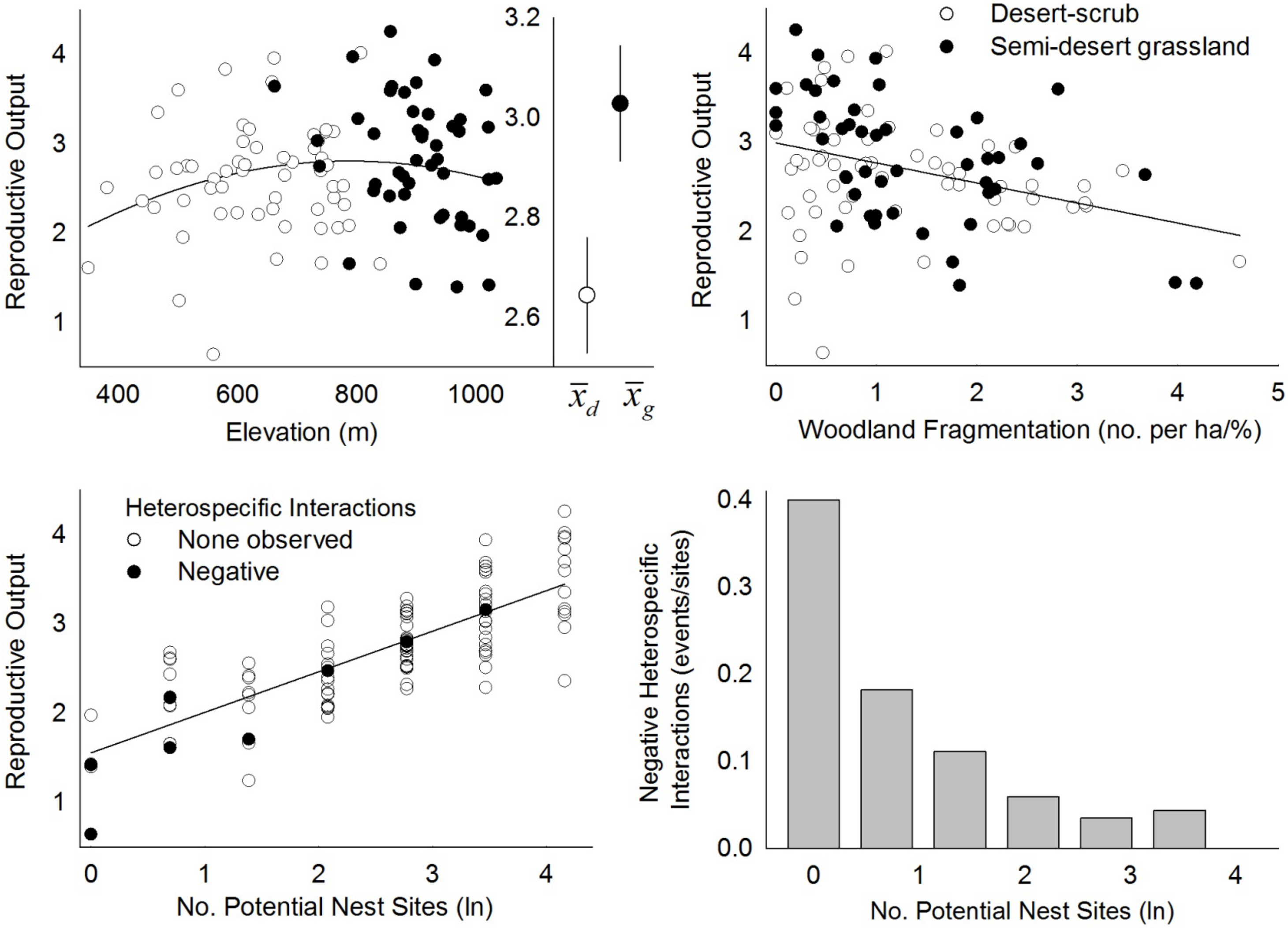
Reproductive Output
1
2
3
4
400
600
800
1000
Elevation (m)
3.2
3.0
2.8
2.6
$\bar{x}_d$
$\bar{x}_g$
Desert-scrub
Semi-desert grassland
Reproductive Output
1
2
3
4
0
1
2
3
4
5
Woodland Fragmentation (no. per ha/%)
Heterospecific Interactions
None observed
Negative
Reproductive Output
1
2
3
4
0
1
2
3
4
No. Potential Nest Sites (ln)
Negative Heterospecific Interactions (events/sites)
0.0
0.1
0.2
0.3
0.4
0
1
2
3
4
No. Potential Nest Sites (ln)

Fig. 3

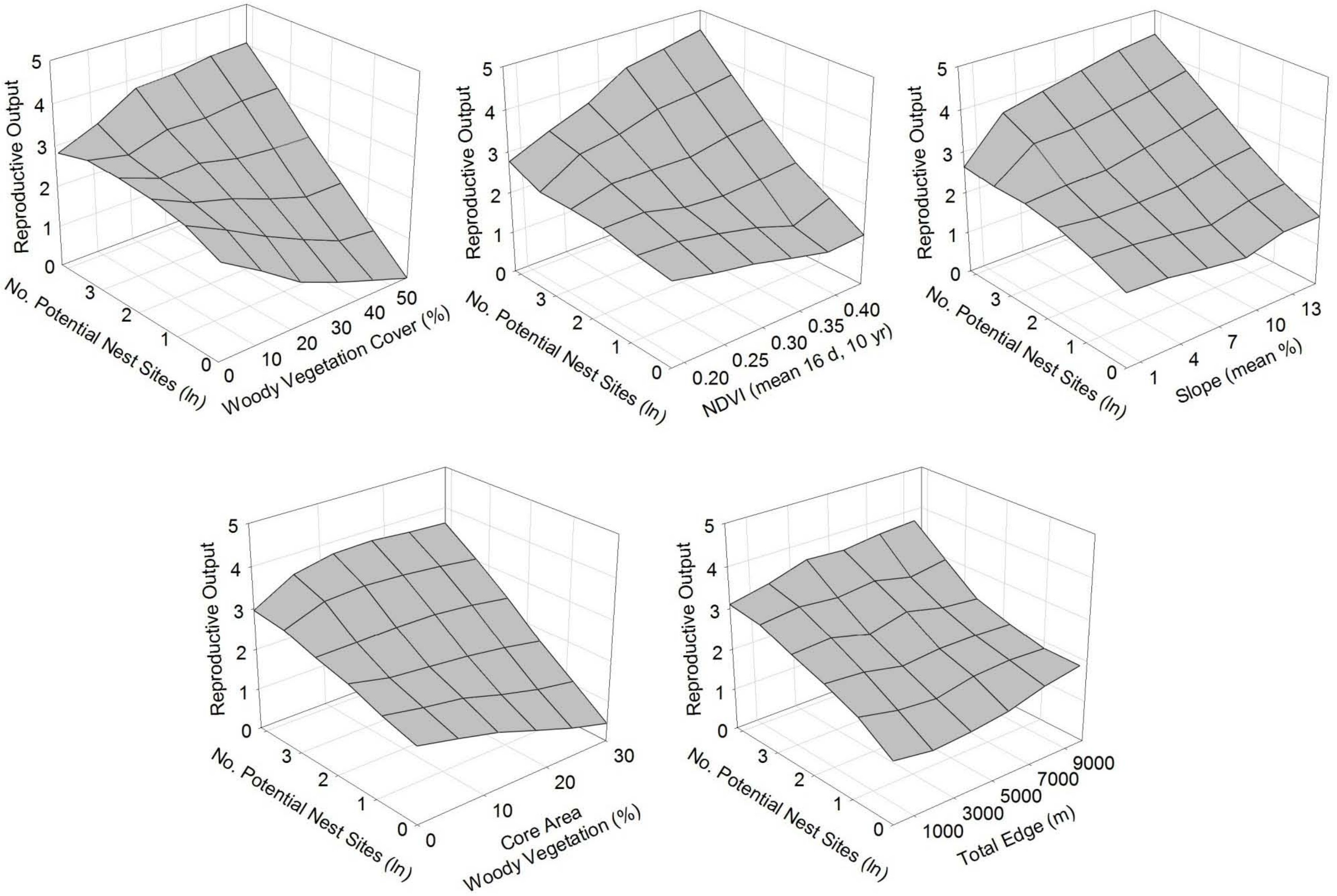
Reproductive Output
5
4
3
2
1
0
No. Potential Nest Sites (ln)
3
2
1
0
Woody Vegetation Cover (%)
0
10
20
30
40
50
Reproductive Output
No. Potential Nest Sites (ln)
NDVI (mean 16 d, 10 yr)
0.20
0.25
0.30
0.35
0.40
Reproductive Output
No. Potential Nest Sites (ln)
Slope (mean %)
1
4
7
10
13
Reproductive Output
No. Potential Nest Sites (ln)
Core Area
Woody Vegetation (%)
0
10
20
30
Reproductive Output
No. Potential Nest Sites (ln)
Total Edge (m)
1000
3000
5000
7000
9000

Fig. 4

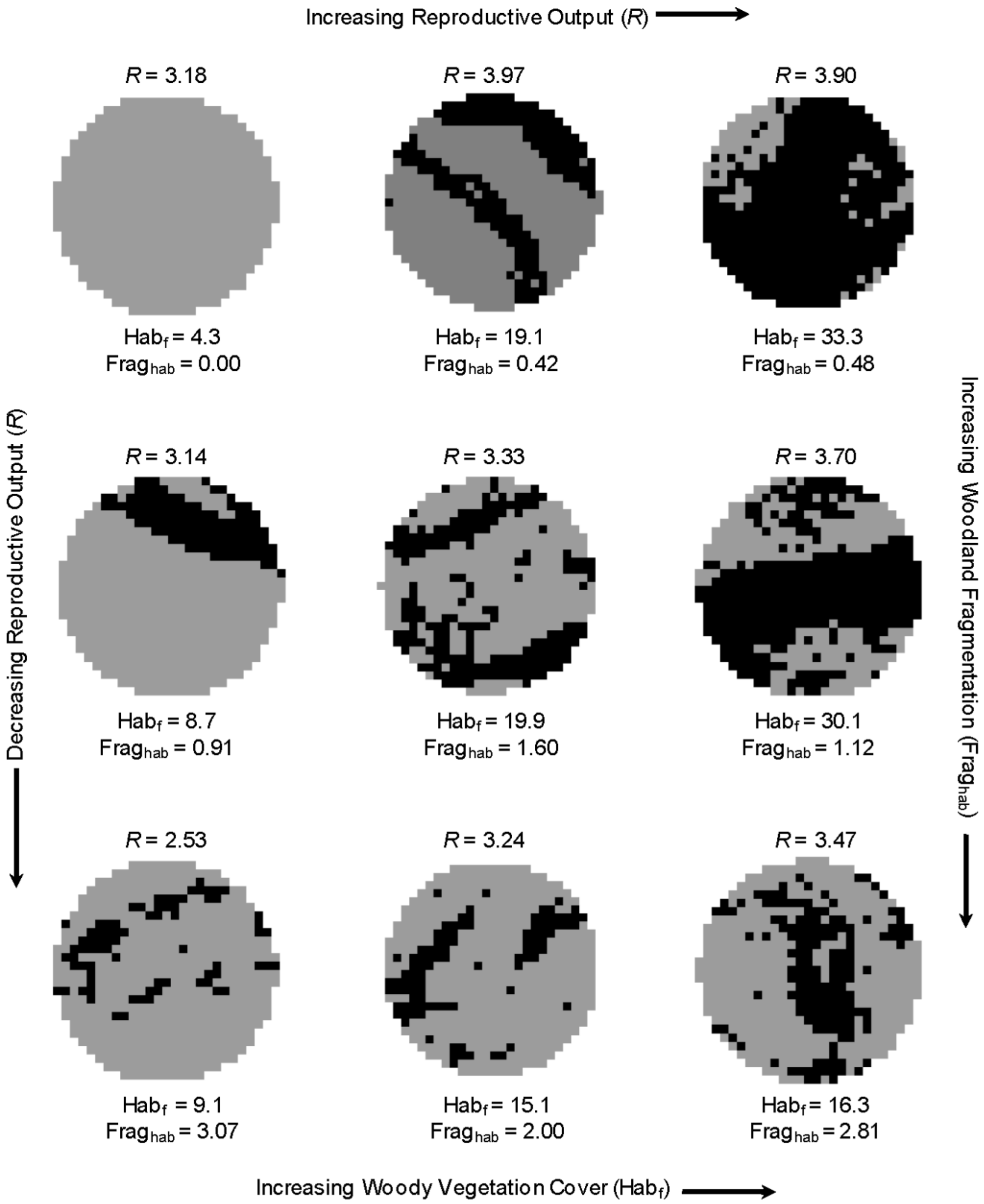
Increasing Reproductive Output (R)
R = 3.18
R = 3.97
R = 3.90
Hab_f = 4.3
Frag_hab = 0.00
Hab_f = 19.1
Frag_hab = 0.42
Hab_f = 33.3
Frag_hab = 0.48
Decreasing Reproductive Output (R)
Increasing Woodland Fragmentation (Frag_hab)
R = 3.14
R = 3.33
R = 3.70
Hab_f = 8.7
Frag_hab = 0.91
Hab_f = 19.9
Frag_hab = 1.60
Hab_f = 30.1
Frag_hab = 1.12
R = 2.53
R = 3.24
R = 3.47
Hab_f = 9.1
Frag_hab = 3.07
Hab_f = 15.1
Frag_hab = 2.00
Hab_f = 16.3
Frag_hab = 2.81
Increasing Woody Vegetation Cover (Hab_f)

Fig. 5

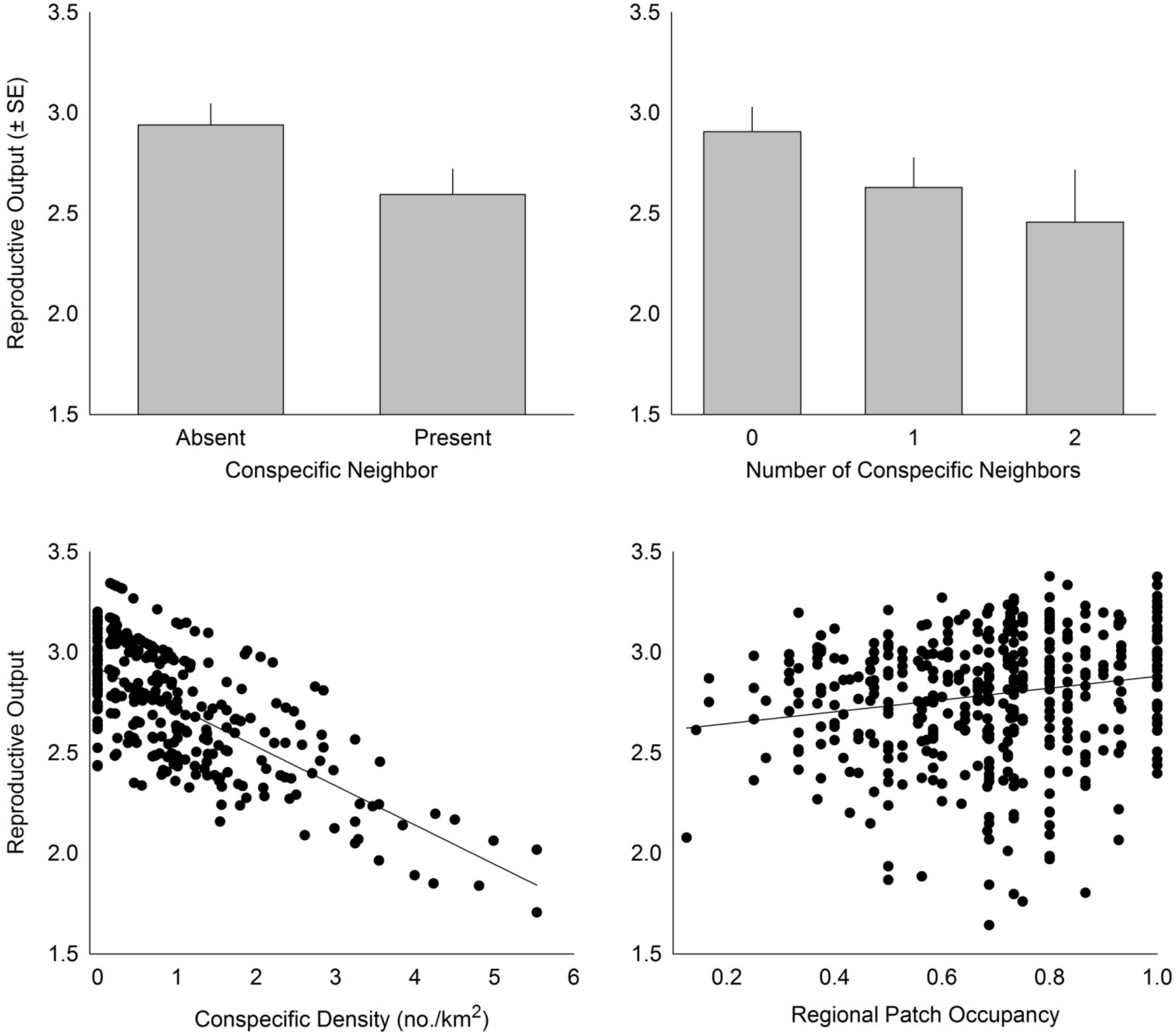
Reproductive Output (± SE)
3.5
3.0
2.5
2.0
1.5
Absent
Present
Conspecific Neighbor
0
1
2
Number of Conspecific Neighbors
Reproductive Output
0
1
2
3
4
5
6
Conspecific Density (no./km^2)
0.2
0.4
0.6
0.8
1.0
Regional Patch Occupancy

Fig. 6

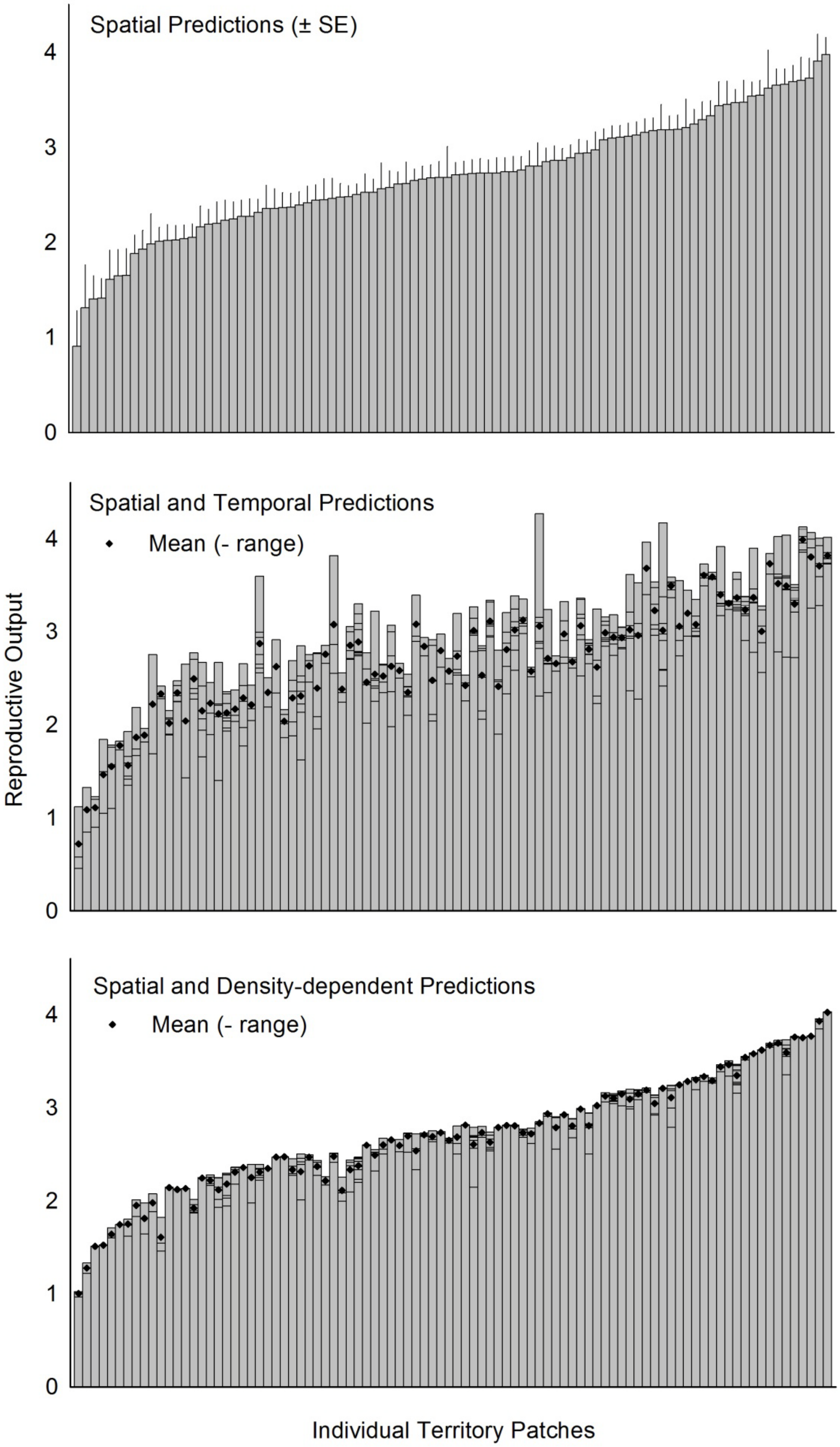
Spatial Predictions (± SE)
4
3
2
1
0
Spatial and Temporal Predictions
Mean (- range)
4
3
2
1
0
Reproductive Output
Spatial and Density-dependent Predictions
Mean (- range)
4
3
2
1
0
Individual Territory Patches

Fig. 7

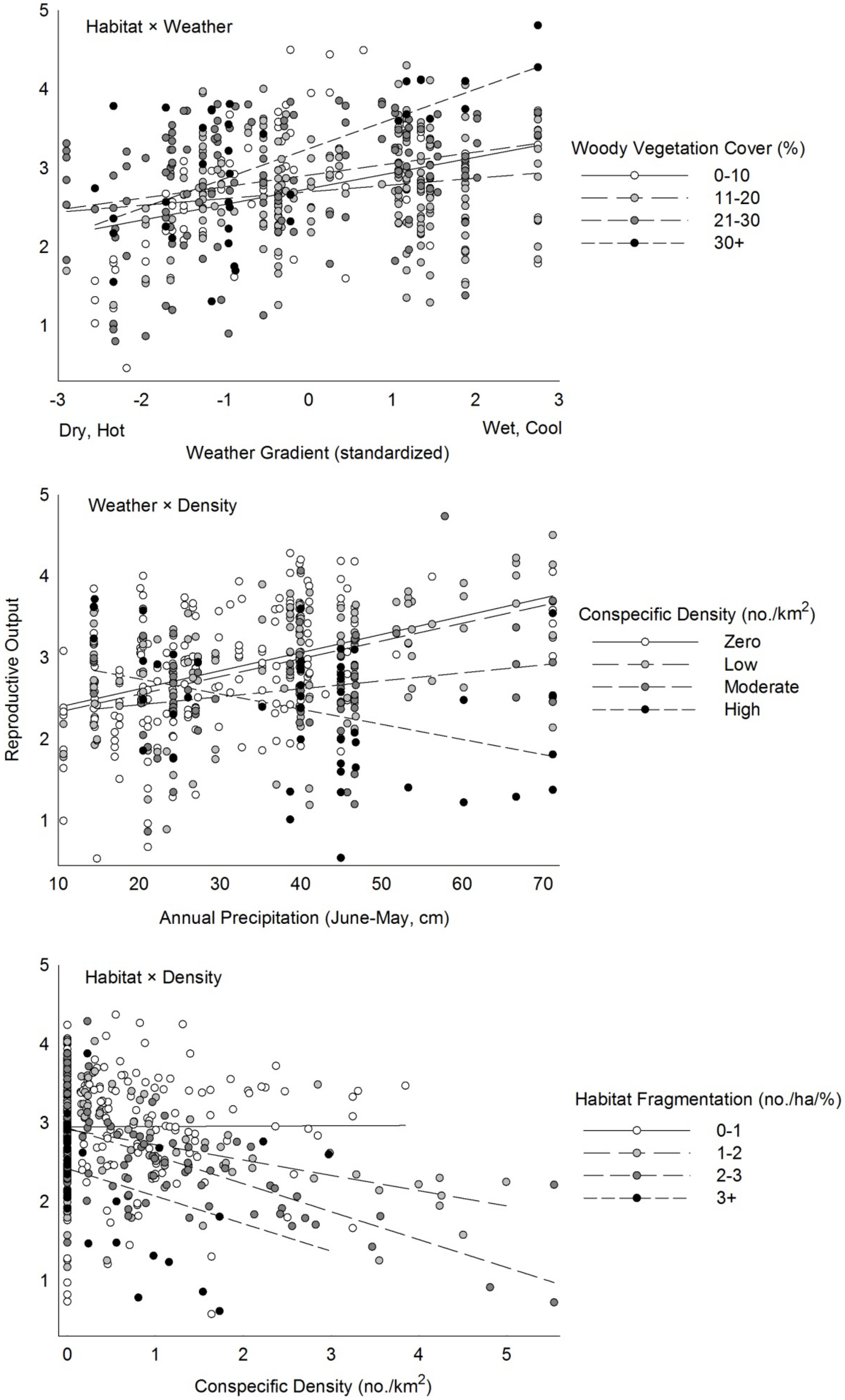
Habitat × Weather
5
4
3
2
1
-3
-2
-1
0
1
2
3
Dry, Hot
Wet, Cool
Weather Gradient (standardized)
Woody Vegetation Cover (%)
0-10
11-20
21-30
30+
Weather × Density
Reproductive Output
10
20
30
40
50
60
70
Annual Precipitation (June-May, cm)
Conspecific Density (no./km^2)
Zero
Low
Moderate
High
Habitat × Density
0
1
2
3
4
5
Conspecific Density (no./km^2)
Habitat Fragmentation (no./ha/%)
0-1
1-2
2-3
3+

Fig. 8

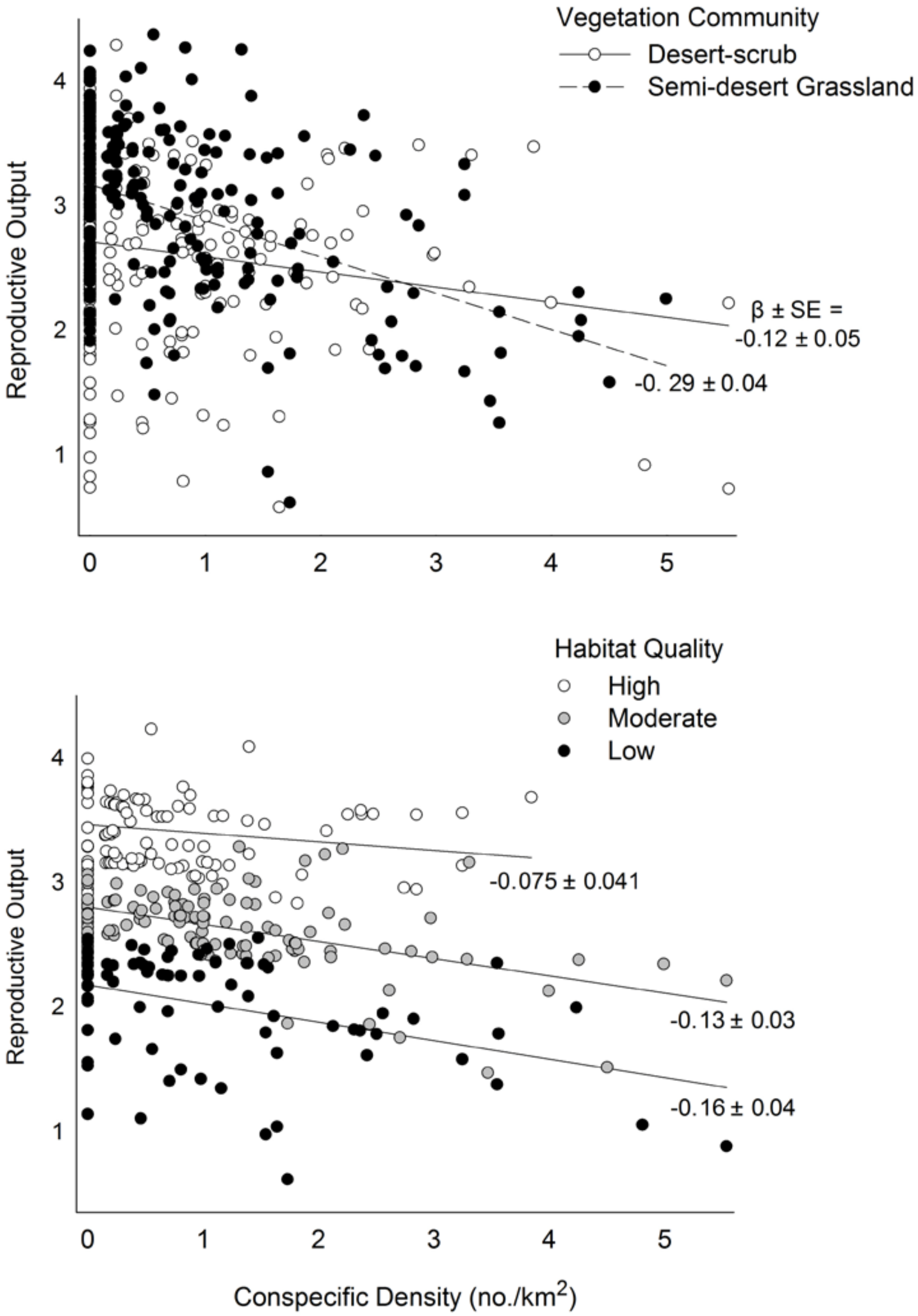
Vegetation Community
Desert-scrub
Semi-desert Grassland
Reproductive Output
1
2
3
4
0
1
2
3
4
5
β ± SE =
-0.12 ± 0.05
-0. 29 ± 0.04
Habitat Quality
High
Moderate
Low
Reproductive Output
1
2
3
4
0
1
2
3
4
5
-0.075 ± 0.041
-0.13 ± 0.03
-0.16 ± 0.04
Conspecific Density (no./km2)

Fig. 9

Appendix A: Description of temporal hypotheses.

Table A1. Models representing the hypothesized effects of weather, primary productivity, and seasonal timing of peak primary productivity on reproductive output of Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2001-2010. Rationale for hypotheses is described in the text.

Model	Hypothesis	Expected results
1) Winter Temperature	Low temperatures during the winter stress period explains R	Positive effect of T
2) Nesting Temperature	High temperatures during the nestling stress period explains R	Negative effect of T
3) Precipitation	Precipitation before nesting explains R	Positive or quadratic effect of P
4) Productivity	Primary productivity before nesting explains R	Positive or quadratic effect of NDVI
5) Timing	Timing of peak productivity before nesting explains R	Negative or quadratic effect of S_{NDVI}
6) Nesting Temperature Precipitation	High temperatures during and precipitation before nesting explains R	Negative effect of T, positive or quadratic effect of P, or interaction between T and P
7) Nesting Temperature, Productivity	High temperatures during and primary productivity before nesting explains R	Negative effect of T, positive or quadratic effect of NDVI, or interaction between T and NDVI

8)	Nesting Temperature, Precipitation, Productivity	High temperatures during and both precipitation and primary productivity before nesting explains R	Negative effect of T, positive or quadratic effect of P and NDVI, or interaction between T and P and P and NDVI
9)	Nesting Temperature, Precipitation, Timing	High temperatures during and both precipitation and timing of productivity before nesting explains R	Negative effect of T, positive or quadratic effect of P, negative or quadratic effect of S_{NDVI}, or interactions
10)	Nesting Temperature, Productivity, Timing	High temperatures during and both primary productivity and timing of productivity before nesting explains R	Negative effect of T, positive or quadratic effect of NDVI, negative or quadratic effect of S_{NDVI}, or interactions
11)	Nesting Temperature, Timing, Precipitation, Productivity	High temperatures and precipitation, productivity, and timing of productivity before nesting explains R	Negative effect of T, positive or quadratic effect of P and NDVI, negative or quadratic effect of S_{NDVI}, or interactions
12)	Precipitation, Productivity	Precipitation and primary productivity before nesting explains R	Positive or quadratic effect of P and NDVI, or interaction between P and NDVI
13)	Precipitation, Timing	Precipitation and timing of peak productivity before nesting explains R	Positive or quadratic effect of P, negative or quadratic effect of S_{NDVI}, or interactions
14)	Precipitation, Productivity, Timing	Precipitation, primary productivity, and timing of productivity before nesting explains R	Positive or quadratic effect of P and NDVI, negative or quadratic effect of S_{NDVI}, or interactions
15)	Productivity, Timing	Primary productivity and timing of productivity before nesting explains R	Positive or quadratic effect of NDVI, negative or quadratic effect of S_{NDVI}, or interactions

Notes: positive and negative effects were assessed with both linear and pseudo-threshold ln(x +1) forms of covariates. Each hypothesis was represented by a suite of models that each considered a different related covariate within each variable group in Table 1, and linear, pseudo-threshold, and quadratic forms of covariates.

Appendix B: Description of spatial hypotheses.

Table B1. Models representing the hypothesized effects of spatial habitat factors on reproductive output of Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2001-2010. Rationale for hypotheses is described in the text.

	Model	Hypothesis	Expected results
B)	Cavities, Elevation, Vegetation community	Nest-site availability and environmental harshness explains R	Positive effect of Cav, positive or quadratic effect of Elev, positive effect of semi-desert grassland
1)	Woodland, Topography	Amount of woodland habitat and topography diversity explains R	Positive or quadratic effect of Hab and Topography or interaction between Cav and Hab and/or Cav and Topography
2)	Woodland, Topography, Disturbance	Amount of woodland habitat, disturbance, topography diversity explains R	Positive or quadratic effect of Hab and Topography or interaction between Cav and Hab and Cav and Topography negative effect of Disturbance
3)	Woodland, Fragmentation	Amount and fragmentation of woodland habitat, disturbance, topography diversity explains R	Positive or quadratic effect of Hab and Topography or interaction between Cav and Hab and Cav and Topography negative effect of Disturbance, negative effect of Fragmentation
4)	Woodland, Topography, Fragmentation	Amount and fragmentation of woodland habitat, topography diversity explains R	Positive or quadratic effect of Hab and Topography or interaction between Cav and Hab and Cav and Topography, negative effect of Fragmentation
5)	Core-Area Woodland	Amount of core habitat explains R	Positive or quadratic effect of Core or interaction between Cav and Core
6)	Core-Area Woodland, Topography	Amount of core habitat and topography diversity explains R	Positive or quadratic effect of Core and Topography or interaction between Cav and Core area and Cav and Topography

7)	Core-Area Woodland, Topography, Disturbance	Amount of core habitat, disturbance, and topography diversity explains R	Positive or quadratic effect of Core and Topography or interaction between Cav and Core and Cav and Topography, negative effect of Disturbance
8)	Edge	Amount of edge explains R	Positive or quadratic effect of Edge or interaction between Cav and Edge
9)	Edge, Topography	Amount of edge and topography diversity explains R	Positive or quadratic effect of Edge and Topography or interaction between Cav and Edge and Cav and Topography
10)	Edge, Topography, Disturbance	Amount of edge, disturbance, and topography diversity explains R	Positive or quadratic effect of Edge and Topography or interaction between Cav and Edge and Cav and Topography, negative effect of Disturbance
11)	Primary Productivity	Primary productivity explains R	Positive or quadratic effect of NDVI or interaction between Cav and NDVI

Notes: positive and negative effects were assessed with both linear and pseudo-threshold ln(x +1) forms of covariates. Each hypothesis was represented by a suite of models that each considered a different related covariate within each variable group in Table 2, and linear, pseudo-threshold, and quadratic forms of covariates.

Appendix C. Description of multi-sensor remote sensing methods used to classify land cover and quantify cover of woody vegetation.

Remote Sensing Data Selection and Pre-Processing – The best time of year to create a Landsat based woody cover classification and estimation was determined by examining 250 meter 16-day composite Normalized Difference Vegetation Index (NDVI) time series data from the Moderate Resolution Imaging Spetroradiometer (MODIS) (Fig. C1). A summer time period for which NDVI values were low was considered the best, in order to minimize the impact of the grass cover and avoid the chances of herbaceous vegetation being confused with tree cover. A few periods met the low vegetation signature criteria, but 2007 was chosen for mainly two reasons. The base value for NDVI in 2007 occurred in June which correlated well with cloudless 30 meter Landsat 5 Thematic Mapper (TM) image data. Another plus was that National Agricultural Imagery Program 1 meter

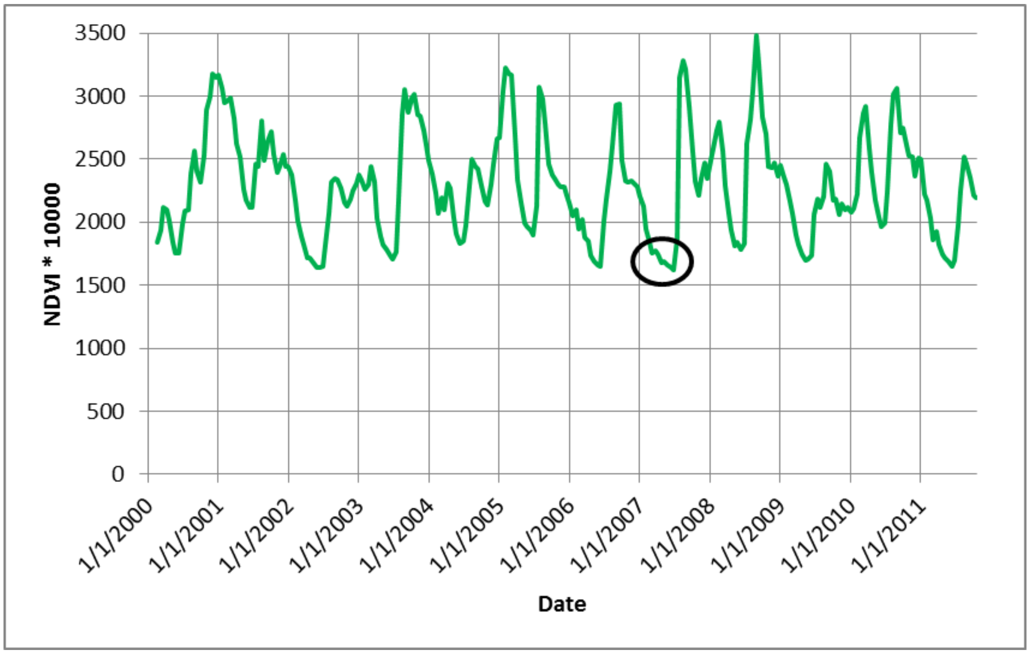

Fig. C1: Example of multiyear MODIS time series data for one of the nest-sites, highlighting the baseline NDVI values during June of 2007.

data (NAIP) was flown for Arizona and parts of Mexico at the end of June 2007. The high resolution NAIP multispectral data allowed us to assess the accuracy of the woody cover product created with the coarser TM image data. Landsat image data were downloaded from: http://glovis.usgs.gov/. The study area was contained within four different Landsat images: Path 35 Row 39, Path 36 Row 38, Path 36 Row 39, and Path 37 Row 38. The majority of the nesting sites fell within Path 36 Row 38 and Path 36 Row 39 which were captured by the TM sensor on June 27 of 2007. The image for Path 35 Row 39 was captured on May 19, 2007, while the image for Path 37 Row 38 was captured on June 18, 2007.

The four images acquired were run through the Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) model (Masek et al. 2006, Masek et al. 2012) to correct for the effects of atmosphere on the reflectance data. The four atmospherically corrected images were then stitched together to create one image of the study area. An NDVI image and a Principal Components Analysis (PCA) image were created from the multispectral image in order to reduce residual noise in the data and better identify woody cover in the region.

Land Cover Classification - A Classification and Regression Tree algorithm was applied to create the land cover classification for this semi-arid region, similar to Villeareal et al. (2012). Training data, to perform the Landsat land cover classification, was acquired from 1 meter multispectral NAIP and high spatial resolution Google Earth data. The NAIP data were collected on June 23 only four days before the majority of the Landsat data was captured making it ideal for training and assessment. Three classes

Table C1: Accuracy assessment of Landsat land cover classification using spectral reflectance, NDVI, and PCA data.

Landcover Class		1	2	3	Total	User	Commission	Kappa
Woody Cover	1	49	0	1	50	98.00%	2.00%	0.97
Non-Woody Cover	2	0	50	0	50	100.00%	0.00%	1.00
Agriculture	3	1	0	49	50	98.00%	2.00%	0.97
	Total	50	50	50	150			
	Producer	98.00%	100.00%	98.00%		148		
	Omission	2.00%	0.00%	2.00%			98.67%	
	Kappa	0.97	1.00	0.97				0.98

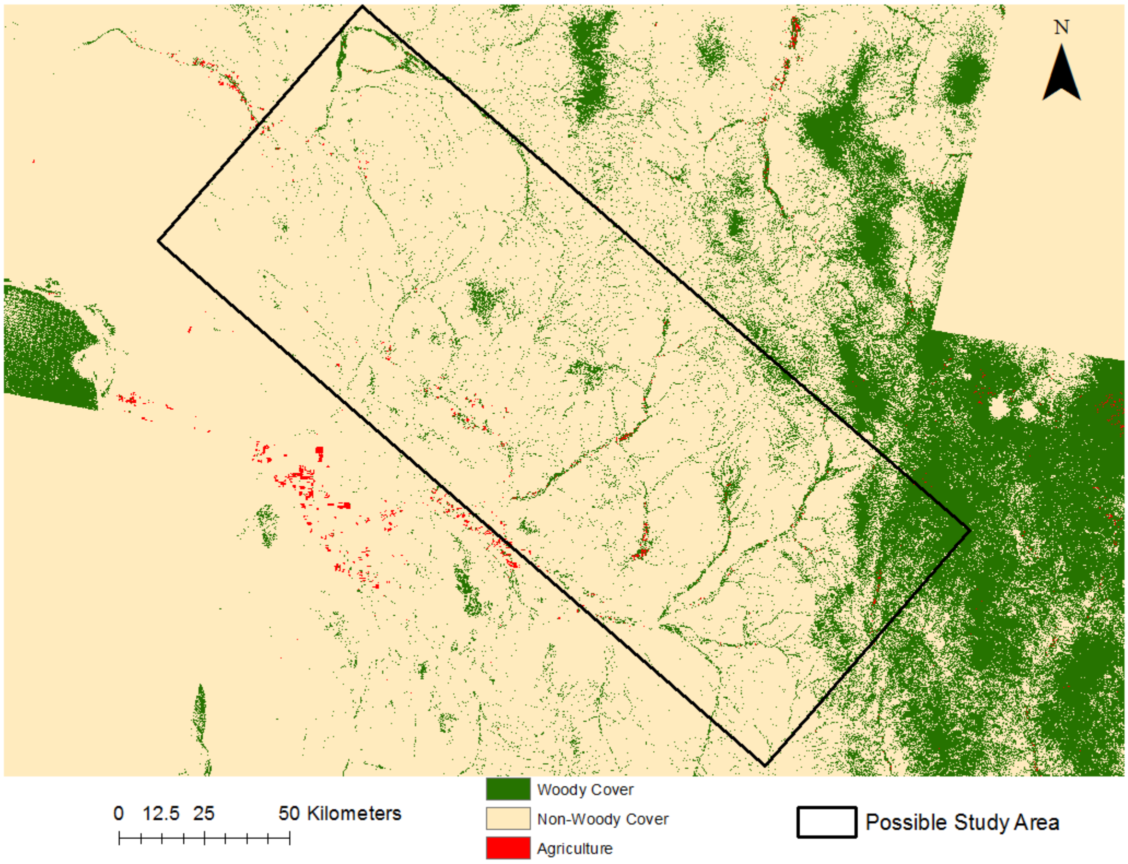

Fig. C2: Land cover classification performed using Landsat spectral data, NDVI data, and a PCA image.

were trained upon: woody cover, non-woody cover, and agriculture. Points were selected for each of the classes taking into account NDVI values in order to help discriminate between classes. Fifty points were also collected for each of the classes in order to assess the accuracy of the land cover classification. The classification was run with CART using the spectral reflectance, NDVI, and PCA data, achieving an overall accuracy of about 99 percent (Table C1; Fig. C2).

Woody cover estimation - Using the NAIP data as reference, a Landsat pixel was selected as a representation of pure woody cover, while another pixel was selected as a representation of pure soil in order to perform a linear Spectral Mixture Analysis (SMA) (Van Leeuwen et al. 1997). The two pixels were selected based on visual interpretation of the NAIP data along with the spectral signatures of the selected Landsat pixels. The output from the SMA results in the fractional abundance of vegetation within each pixel (Fig. C3).

The 30m vegetation abundance data were calibrated with classified woody cover data from 1m NAIP multispectral data. Using a 30 meter by 30 meter polygon grid a range of pixels were selected from the vegetation abundance raster representing the following abundance ranges: 0-0.1, 0.1-0.2, .2-.3, ,etc. Percent woody cover was then extracted from the NAIP land cover classification by taking a count of the number of pixels classified as woody cover within the 30 meter by 30 meter grid. This count could range from 0 to 900 so it was divided by 9 in order to get a percent cover. Percent woody cover was estimated based on the SMA vegetation abundance data for the pixels and their

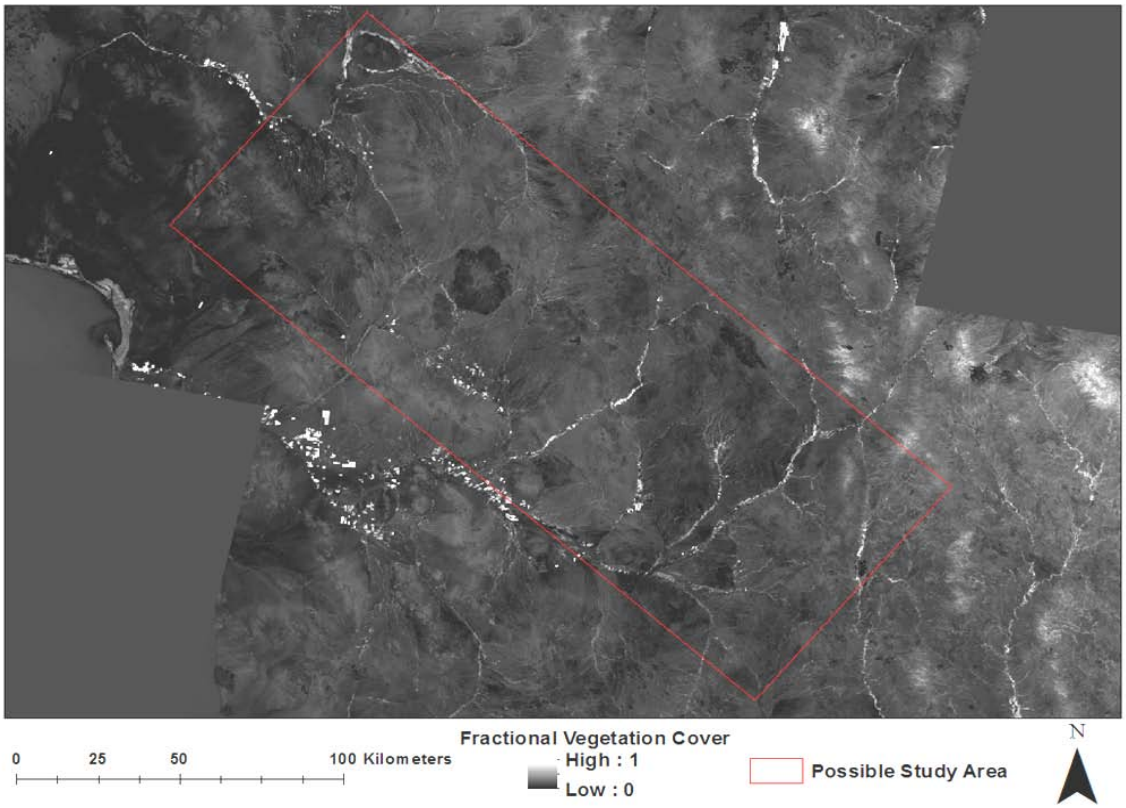

Fig. A3: Linear spectral mixture model - vegetation abundance results for the Landsat mosaic for June 27, 2007. White represents high vegetation cover, while black represents low vegetation cover.

corresponding NAIP-based percent woody cover estimates. Using a linear regression, the relationship between the unmixed pixels and NAIP classification had an R^2 of 0.7881 (Fig. C4). The equation in Figure A5 was applied to the vegetation abundance image to create a map of percent woody cover for the entire study area (Fig. C5).

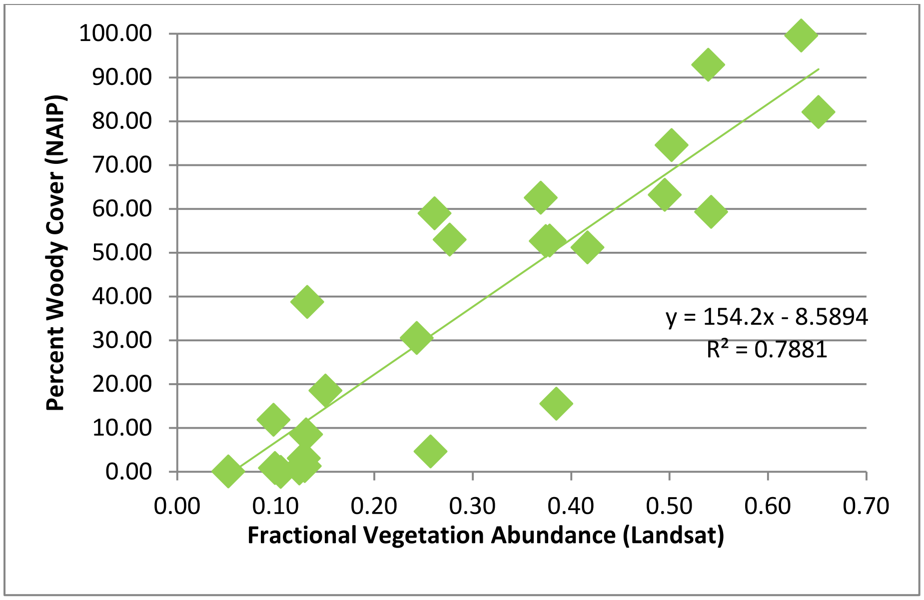

Fig. A4: Results of linear regression of NAIP percent woody cover measurements and the Landsat-based vegetation abundance from the linear spectral mixture model.

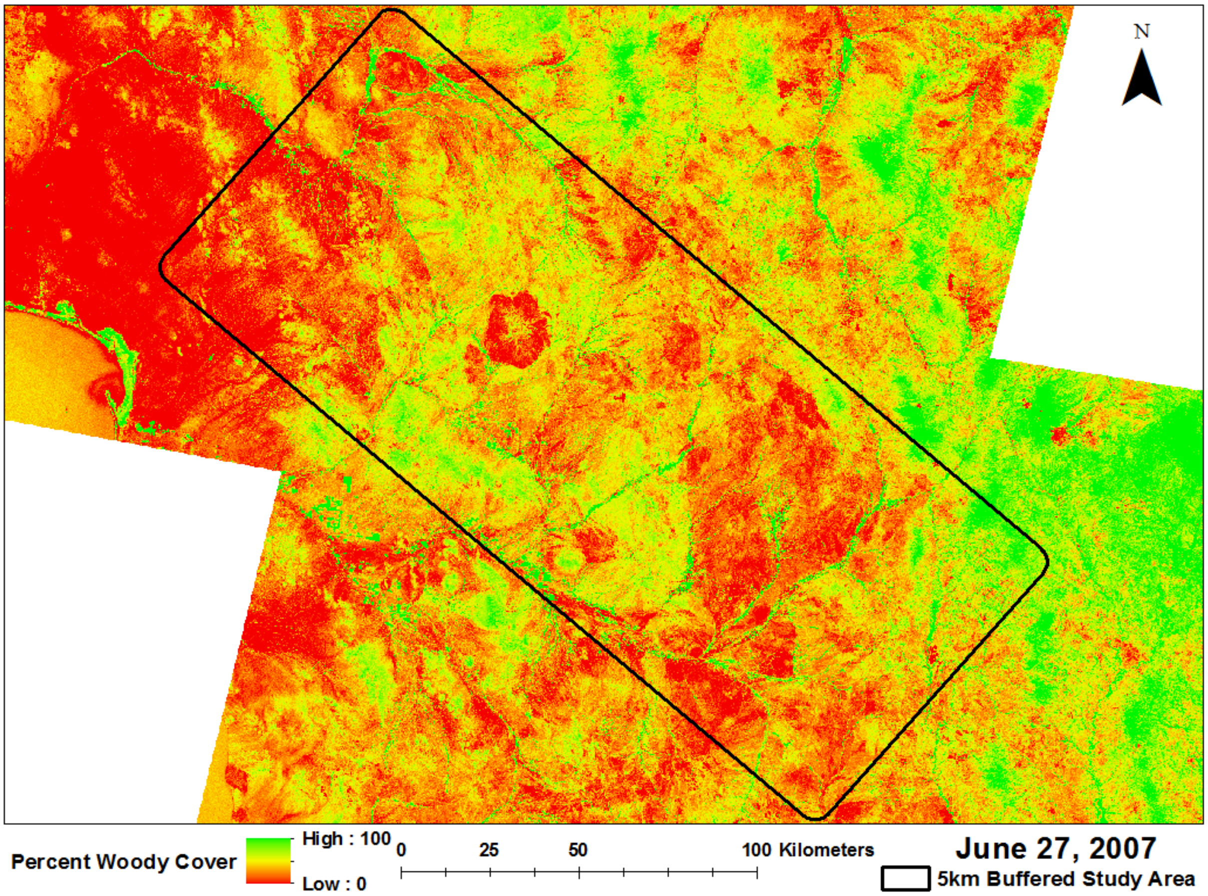

Fig. C5: Percent woody cover image as a result of calibrating the vegetation abundance (LANDSAT) with NAIP-based woody cover data.

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Appendix D: Factor, spatial scales, and models considered to describe the effects of presence and abundance of conspecific neighbors on reproductive output

Table D1. Factors considered when modeling the effects of presence and abundance of conspecifics on reproductive output of Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2001-2010. For presence and number of neighbors we considered a maximum distance of 1.5 km from focal nests because preliminary analyses indicated little effect beyond this distance.

Variable	Scale	Abbreviation	Definition	Units
Total Occupancy	Population	Occ_{total}	Proportion of territory patches occupied across the entire study ineach year	Proportion
Regional Occupancy	Region	Occ_{region}	Proportion of territory patches occupied within each watershed region in each year	Proportion
Presence of neighbor	Local	PresN	Presence or absence of nearest neighbor nesting pair within 1.5 km of focal site	0 or >0 individuals
Number of neighbors	Local	No.pres	Number of nearest neighbor nesting pairs within 1.5 km of focal site	0, 1, or 2 individuals
Density	Local	Density	Number of nearest neighbor nesting pairs per km around focal site (see text)	no./km^2

Table D2. Rankings and estimated slope parameters for 5 hypothesized models that explained the effects of the presence and abundance of conspecifics on reproductive output of Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2001-2010.

Factor - Scale	Formula	K	LL	ΔAICc	w_i	Slope ± SE
Density - Local	Density	4	-920.79	0.00	0.379	$\beta_1 = -0.18 \pm 0.084$
Number of Neighbors Local	No.pres	4	-921.29	1.01	0.229	$\beta_1 = -0.31 \pm 0.17$
Presence of Neighbor - Local	PresN	4	-921.53	1.47	0.181	$\beta_1 = -0.24 \pm 0.13$
Intercepts only	β_0	3	-923.08	2.54	0.106	
Occupancy - Region	Occ_{region}	4	-922.56	3.54	0.065	$\beta_1 = 0.42 \pm 0.41$
Occupancy - Populatio	Occ_{total}	4	-923.06	4.54	0.039	$\beta_1 = 0.12 \pm 0.61$

Appendix E: Parameter estimates from supported models that included interactions between spatial, temporal, and conspecific factors.

Table E1. Estimates of slope parameters in models that described the individual, additive, and interactive effects of spatial and temporal factors and conspecific density on reproductive output of Pygmy-Owls in northern Sonora, Mexico 2001-2010. Model rankings are presented in Table 8. Only estimates for models within 5 ΔAICc points are reported

Model (ΔAICc) Factor	β	SE
Habitat × Weather + Density (0.00)		
lnCav	0.22	0.20
Comm(SDG)	0.33	0.18
Hab_f	-17.8	6.6
$lnCav*Hab_f$	0.019	0.010
$Frag_{hab}$	-0.18	0.084
lnT_{brood}	-135.9	39.3
lnP_{yr}	-133.8	40.0
$lnT_{brood}*lnP_{yr}$	37.0	11.0
$NDVI_{yr}^2$	21.9	8.9
Density	-0.19	0.080
$lnP_{yr}*Hab_f$	4.90	1.83
$lnT_{brood}*Hab_f$	4.87	1.80
$lnT_{brood}*lnP_{yr}*Hab_f$	-1.35	0.50
Habitat + Weather × Density (0.15)		
lnCav	0.22	0.20
Comm(SDG)	0.34	0.18

Hab_f	-0.045	0.034
$lnCav*Hab_f$	0.016	0.010
$Frag_{hab}$	-0.19	0.084
lnT_{brood}	-33.6	13.7
lnP_{yr}	-30.4	13.2
$lnT_{brood}*lnP_{yr}$	8.51	3.64
$NDVI_{yr}^2$	23.0	8.82
Density	0.96	0.65
$Density*lnP_{yr}$	-0.32	0.18
Habitat × Weather × Density (0.55)		
lnCav	0.31	0.21
Comm(SDG)	0.35	0.18
Hab_f	-0.011	0.039
$lnCav*Hab_f$	0.012	0.011
$Frag_{hab}$	-0.86	0.74
lnT_{brood}	-36.1	13.9
lnP_{yr}	-33.3	13.5
$lnT_{brood}*lnP_{yr}$	9.24	3.71
$NDVI_{yr}^2$	38.3	21.5
Density	1.76	1.53
$Density*Frag_{hab}$	0.087	0.842
$Frag_{hab}*lnP_{yr}$	0.23	0.21
$Density*lnP_{yr}$	-0.29	0.41
$Density*Hab_f$	-0.038	0.020
$Hab_f*NDVI_{yr}^2$	-1.89	1.25
$Density*NDVI_{yr}^2$	-22.8	29.9
$Density*Frag_{hab}*lnP_{yr}$	-0.093	0.23
$Density*Hab_f*NDVI_{yr}^2$	2.88	1.71

Habitat + Weather + Density (1.22)		
lnCav	0.23	0.20
Comm(SDG)	0.34	0.18
$\mathrm{Hab}_{\mathrm{f}}$	-0.043	0.034
$\mathrm{lnCav{*}Hab}_{\mathrm{f}}$	0.017	0.010
$\mathrm{Frag}_{\mathrm{hab}}$	-0.18	0.084
$\mathrm{lnT}_{\mathrm{brood}}$	-35.6	13.7
$\mathrm{lnP}_{\mathrm{yr}}$	-32.3	13.2
$\mathrm{lnT}_{\mathrm{brood}}{*}\mathrm{lnP}_{\mathrm{yr}}$	8.99	3.64
$\mathrm{NDVI}_{\mathrm{yr}}^{2}$	23.0	8.8
Density	-0.182	0.080
Habitat × Density + Weather (2.84)		
lnCav	0.30	0.21
Comm(SDG)	0.44	0.21
$\mathrm{Hab}_{\mathrm{f}}$	-0.021	0.038
$\mathrm{lnCav{*}Hab}_{\mathrm{f}}$	0.013	0.011
$\mathrm{Frag}_{\mathrm{hab}}$	-0.078	0.10
$\mathrm{lnT}_{\mathrm{brood}}$	-34.9	13.7
$\mathrm{lnP}_{\mathrm{yr}}$	-31.8	13.2
$\mathrm{lnT}_{\mathrm{brood}}{*}\mathrm{lnP}_{\mathrm{yr}}$	8.84	3.64
$\mathrm{NDVI}_{\mathrm{yr}}^{2}$	21.5	8.89
Density	0.69	0.43
$\mathrm{Hab}_{\mathrm{f}}$*Density	-0.025	0.016
$\mathrm{Frag}_{\mathrm{hab}}$*Density	-0.21	0.11
Comm*Density	-0.18	0.16
Habitat × Weather (3.4)		
lnCav	0.22	0.20
Comm(SDG)	0.34	0.18

$\mathrm{Hab_{f}}$	-17.5	6.60
$\mathrm{lnCav{*}Hab_{f}}$	0.020	0.010
$\mathrm{Frag_{hab}}$	-0.19	0.085
$\mathrm{lnT_{brood}}$	-129.7	39.4
$\mathrm{lnP_{yr}}$	-127.4	40.1
$\mathrm{lnT_{brood}{*}lnP_{yr}}$	35.2	11.0
$\mathrm{NDVI_{yr2}}$	21.9	8.91
$\mathrm{lnP_{yr}{*}Hab_{f}}$	4.79	1.83
$\mathrm{lnT_{brood}{*}Hab_{f}}$	4.80	1.81
$\mathrm{lnT_{brood}{*}ln_{Pyr}{*}Hab_{f}}$	-1.32	0.50
Habitat + Weather (4.36)		
lnCav	0.24	0.20
Comm(SDG)	0.36	0.18
$\mathrm{Hab_{f}}$	-0.047	0.034
$\mathrm{lnCav{*}Hab_{f}}$	0.018	0.010
$\mathrm{Frag_{hab}}$	-0.19	0.085
$\mathrm{lnT_{brood}}$	-31.5	13.6
$\mathrm{lnP_{yr}}$	-28.8	13.2
$\mathrm{lnT_{brood}{*}lnP_{yr}}$	8.01	3.63
$\mathrm{NDVI_{yr}}^{2}$	23.0	8.89

CHAPTER 3

INTEGRATING BEHAVIORAL AND LANDSCAPE APPROACHES FOR UNDERSTANDING ANIMAL DISTRIBUTION

Abstract. Habitat quality, quantity, and connectivity are core drivers of animal distribution but their effects operate at different spatial scales and are rarely measured directly. I integrated behavioral and landscape approaches for explaining distribution by estimating the effects of habitat quantity, habitat configuration, and matrix structure at landscape scales and both direct and indirect estimates of habitat quality at local territory-patch scales on long-term occupancy dynamics of pygmy-owls over 12 years. Direct estimates of habitat quality based on the effects of resources, environmental stochasticity, and conspecific density on vital rates had greater effects on occupancy than landscape factors, but inferences were reversed when habitat quality was measured indirectly based on habitat structure. Although all landscape factors had important effects, habitat quantity had greater effects than habitat configuration and matrix structure that were consistently positive at all levels of habitat quality. Enhancing local habitat quality can be more efficient for conservation than improving connectivity, especially in appropriate landscape contexts.

Key words

Connectivity, distribution, fragmentation, habitat area, habitat quality, habitat selection, isolation, matrix structure, occupancy.

INTRODUCTION

Understanding processes that drive animal distribution is a core aspect of ecology with major implications for conservation. Approaches for explaining distribution, however, often focus on different processes and spatial scales, which yield varying insights and implications (Armstrong 2005, Hodgson et al. 2009a). Behavioral approaches for explaining distribution invoke the principles of habitat selection to assess how environmental variation affects patch choices by individuals at small spatial scales (Wiens et al. 1993, Thomas 1994). In contrast, landscape approaches invoke the principles of island biogeography, metapopulation theory, and landscape ecology, and assess how the amount and connectivity of habitat affect occupancy and extinction-colonization dynamics at larger scales (Hanski and Gaggiotti 2004). Integrating these approaches is important for understanding distribution and for focusing conservation on the most important processes and scales.

Under habitat approaches, the quality or fitness potential of habitat is thought to drive distribution. This is because habitat selection has important fitness consequences, and animals are thought to select territory patches (e.g., habitat patch large enough to support a breeding pair) in an ideal manner so that distribution precisely reflects patch quality (Fretwell 1972). Perceptual errors in assessing patch quality, however, can decouple choices from their fitness consequences and create non-ideal patterns of distribution if cues used to assess quality are unavailable, future conditions associated with those cues are not realized due to stochastic factors, or evolutionarily novel cues promote selection of poor habitats (Wiens 1985, Orians and Wittenberger 1991, Schlaepfer et al. 2002). Moreover, as spatial scale increases from groups of nearby territory patches to complex landscapes, perceptual constraints on detecting high-quality habitats or fitness tradeoffs associated with colonizing them can cause patches to be occupied more or less than expected based of their quality (Morris 1987, Pulliam 2000).

Under landscape or metapopulation approaches, variation in the size and isolation of habitat patches (e.g., habitat areas distinct from the surrounding matrix) are thought to drive distribution. Classically, this is thought to be because extinction probability declines with increasing patch area, as larger populations are less vulnerable to extinction, and because colonization probability declines with increasing patch isolation (MacArthur and Wilson 1967, Hanski and Gaggiotti 2004). Moreover, as habitat amount increases at landscape scales, potential colonists become more abundant, habitat typically becomes less isolated, and immigration rates and population persistence increase (Brown and Kodric-Brown 1977, Hanski and Ovaskainen 2000, Fahrig 2003).

Despite differences, both habitat and landscape approaches have successfully explained distribution patterns, albeit in different ways. Habitat approaches indicate general conformance to ideal expectations because when the proportion of years a territory patch is occupied is plotted against estimates of its quality, there is virtually always a positive relationship (Levin et al. 2000, Zimmerman et al. 2003, Sergio and Newton 2003, Burgess et al. 2008). However, there are also distributional “mismatches” characterized by patches with lower or higher occupancy than expected based on their quality. Although, explanations of mismatches include both local and landscape processes (Arlt and Pärt 2007, Burgess et al. 2008) our understandings of their relative roles is limited.

Landscape approaches in a broader range of systems indicate important effects of habitat area and occasionally isolation (Hanski and Gaggiotti 2004, Prugh et al. 2008). Nonetheless, because habitat isolation often declines as habitat area increases and because isolation is a function of habitat configuration (e.g., fragmentation), matrix structure, and movement behavior, assessing the independent effects of area and isolation is challenging and isolation is often defined in terms of functional connectivity, which is the degree to which landscapes foster movement and immigration (Harrison and Bruna

1999, Fahrig 2003, Hodgson et al. 2009a). Moreover, a growing number of studies show important effects of habitat attributes that are thought to be linked to habitat quality, thus effectively broadening landscape approaches (Thomas et al. 2001, Thornton et al. 2011).

Despite growing recognition that neither approach is sufficient alone, integrating them is complex (Armstrong 2005, Hodgson et al. 2009b). Because habitat choices are made by individuals and may depend on the surrounding landscape context, processes at both local and landscape scales must be considered. Delineating territory and larger habitat patches from the surrounding matrix and characterizing landscape attributes with potential to affect movements, however, is rarely straightforward and often subjective (Fahrig 2013). Moreover, because habitat quality represents contributions to population growth by individuals in specific habitats, which is driven by the effects of resources, conspecifics, and stochastic factors on vital rates, these factors should be considered when estimating habitat quality and evaluating its role relative to other factors (Franklin et al. 2000, Armstrong 2005). Although habitat approaches often estimate habitat quality directly based on vital rates (Sergio and Newton 2003), virtually all landscape approaches consider indirect estimates based on habitat attributes or density, which may underestimate the relative importance of habitat quality vs. landscape processes (Mortelliti et al. 2010).

Here, I consider hypotheses based on processes fundamental to both habitat and landscape approaches to explain long-term occupancy dynamics of Ferruginous Pygmy-Owls (*Glaucidium brasilianum*) at territory-specific scales. Specifically, I assessed the degree to which occupancy dynamics matched ideal expectations based on habitat selection theory and how stochastic and density-dependent processes affected this relationship. Additionally, I assessed the effects of habitat amount and overall quality, habitat configuration, and matrix structure at landscape scales, potential interactions between local and landscape factors, and compared the relative effects of direct and indirect estimates of habitat quality and landscape factors on occupancy dynamics. To address these questions, I defined habitat based on observed patterns of use by owls, explicitly estimated habitat quality at local and landscape scales based on the estimated effects of important environmental factors on reproductive output measured over 10 concurrent years, and considered estimates of habitat configuration that were uncorrelated with habitat amount.

If animals distribute themselves ideally in space, then variation in occupancy should precisely reflect habitat quality. Thus, the *habitat hypothesis* states that spatial variation in resources that drive habitat quality explain distribution. When this ideal expectation is not met, three general explanations of distributional mismatches exist: 1) animals make perceptual errors when assessing habitat quality, 2) researchers estimate quality inaccurately, or 3) landscape processes drive distribution. If animals make errors in assessing habitat quality, cues that promote patch choice may not be well matched with their fitness consequences. Thus, the *environmental stochasticity hypothesis* states that stochastic factors such as weather, which can temporarily degrade performance in otherwise good habitats, explain distribution, and the *trap hypothesis* states the effects of human activities, which can create evolutionarily novel cues (Robertson and Hutto 2006), explain distribution. If researchers estimate patch quality inaccurately, one possibility is the *density-dependence hypothesis*, which states the effects of conspecifics on vital rates must be considered when estimating quality. If landscape processes drive distribution, a range of potential explanations are possible. If colonization probabilities are higher or extinction probabilities are lower in landscapes with larger populations, or if individuals prefer to settle near conspecifics, the *habitat amount hypothesis* states the area or effective area (*sensu* Hanski 1994) of habitat within landscapes explains distribution. If movement and colonization are affected by landscape structure, the *habitat configuration hypothesis* states that habitat fragmentation (e.g., breaking apart of habitat independent of amount, *sensu* Fahrig 2003) explains distribution, whereas the *matrix structure hypothesis* states matrix attributes that affect movement explains distribution. Finally, if habitat configuration is important only below some critical threshold in habitat amount (*nonlinear configuration hypothesis*; Andren 1994), interactions between factors explain distribution. More broadly, if patch choices by individuals or local probabilities of extinction or colonization depend on the surrounding landscape context, interactions between local and landscape factors explain distribution.

MATERIALS AND METHODS

Study system

Ferruginous Pygmy-Owls are residents of the lowland Neotropics north to Arizona. In the arid Sonoran Desert region of northwest Mexico, breeding habitat includes various types of riparian woodland, adjacent uplands of desert-scrub, thorn-scrub, or semi-desert grassland, and associated stands of giant saguaro cacti (*Carnegiea gigantea*), which provide nest cavities. Thus, habitat includes multiple land cover types, is challenging to delineate into discrete patches using the habitat-patch concept that dominates landscape approaches (Fahrig 2013), and is best defined by observed patterns of space use by owls. Conveniently, detectability is nearly perfect so that occupancy can be efficiently estimated with standardized techniques (Flesch and Steidl 2007). Because dispersal movements and colonization success are affected by landscape structure (Flesch et al. 2010) landscape processes should affect distribution. Moreover, because pygmy-owls have declined to endangered levels in neighboring Arizona, where unoccupied habitat is present but often found in degraded landscapes, information on the relative effects of local and landscape factors on distribution has important management implications.

Design

I considered a random sample of territory patches that spanned broad gradients of habitat quality and a large number of independent landscapes of varying structure and anthropogenic disturbance across an approximately 20,000 km^2 region of northwest Mexico. In 2000 and 2001, I selected random points across the study area, surveyed transects around points and in other regions selected opportunistically where owls were rare (see Flesch and Steidl 2007), and searched for nests exhaustively in occupied areas until I located the nests of most pairs. During subsequent years, I surveyed areas around nests (or observation points if nests were not initially found) and searched for nests at occupied sites. To delineate territory patches, I plotted nest coordinates across time, identified clusters of owl use in space, and placed a 50-ha circle around average coordinates for each cluster, which matches the area of a home range during the breeding season (Chapter 2). Because distribution of potential nest sites was clumped, owls used the same general areas over time, and abundance was highest at the start of the study (Chapter 1), this approach allowed easy identification of territory patches across a broad range of quality. I defined landscapes based on observed patterns of dispersal by placing a 5-km radius circle around territory patches, which is ≈0.3 times the length of maximum dispersal distance and thus an appropriate scale to assess landscape effects (Jackson and Fahrig 2012, Fahrig 2013, Flesch, *unpubl. data*).

Density-dependent habitat quality in a stochastic environment

In a separate study, I identified factors that explained habitat quality by modeling the effects of habitat resources, stochastic factors (weather and primary productivity), and conspecific density on reproductive output at territory-patch scales over 10 concurrent years (see Chapter 2). This model-based approach provided explicit estimates of territory quality based on the additive and interactive effects of these factors, and inference to patches that were rarely occupied and landscape scales. In this system, habitat quality increases with increasing nest-site abundance, presence of semi-desert grassland, and woodland aggregation within territory patches, and woody vegetation cover has increasingly positive effects as nest-site abundance increases, but landscape structure immediately around patches has no effects. Additionally, reproductive output increases with decreasing conspecific density and brooding-season temperature, and increasing precipitation and primary productivity (Appendix S1, Chapter 2).

Virtually all studies that assess the effects of habitat quality, quantity, and connectivity on distribution use indirect estimates of habitat quality, which may underestimate its importance. Thus, I compared inferences on the relative effects of habitat quality measured directly based on vital rates and indirectly based on resources that affect habitat selection. In this system, owls select areas with higher abundance of potential nest sites and greater cover of woody vegetation (Flesch and Steidl 2010), which I collapsed into a single continuous index of habitat quality by summing their standardized values.

Landscape factors

I estimated indices of habitat amount and overall quality, habitat configuration, and matrix structure that were largely uncorrelated in a large number of independent landscapes (Appendix S2). I used multispectral data from 30-m-resolution Landsat images to estimate woody vegetation cover because it is an essential component of owl habitat and classified pixels with ≥20% cover as woodland (see Chapter 2). I used Google Earth imagery to classify 3 land cover types that represent anthropogenic land use (agriculture or large clearing, housing or urban development, roadway corridor). To quantify habitat amount, I estimated the number of potential territory patches in each landscape based on maps of woody vegetation cover and field observations of pygmy-owls and saguaros. Because woodlands are often arranged linearly along drainages and only areas with woodlands and saguaros provide habitat, this procedure allowed easy estimation of habitat amount. Because population size at landscape scales and thus colonization potential may best be characterized by both habitat amount and quality, I calculated habitat effective area by multiplying habitat amount by landscape quality and dividing by maximal quality (Hanski 1994). To quantify landscape quality, I applied the same model-based approach used to estimate habitat quality at territory scales. To quantify habitat configuration, I used an index of woodland aggregation that was uncorrelated with habitat amount termed the “clumpiness” index, which ranges from -1 (maximal fragmentation) to 1 (maximal aggregation; McGarigal et al. 2012). To quantify matrix structure, I computed area, edge length, and largest patch indices (% landscape of largest patch) for each land cover class representing anthropogenic land use. I used program Fragstats (McGarigal et al. 2012) to estimate landscape factors.

Analyses

I developed statistical models to represent hypotheses and used an information-theoretic approach based on Bayesian information criterion (BIC) to evaluate support among them. To represent the *habitat hypothesis*, I considered the effects of habitat quality based on the estimated effects of important habitat resources only. To represent the *stochasticity* and *density-dependence hypotheses*, I considered the effects of habitat quality based on the estimated effects of important habitat resources and stochastic factors or conspecific density, which I also considered together to assess their combined effects. Because in this system high-quality resources buffer the negative effects of conspecifics and amplify the benefits of favorable weather, and positive effects of favorable weather are offset by competition at high densities (Chapter 2), I also considered the effects of habitat quality based on the interactive effects of habitat, stochastic, and conspecific factors (Appendix S1). Finally, to assess the *trap hypothesis*, I predicted increasing anthropogenic land use within territory patches would explain the presence of traps. To assess the *habitat amount hypotheses*, I considered the effects of habitat amount and habitat effective area and used the best model and to assess the *matrix structure hypothesis*, I considered the effects of each matrix factor separately, assessed combinations of factors from the best models, and used the top-ranked model

I used mixed-effects logistic regression for binomial counts to fit models and estimate parameters with a response variable equaled the number of years patches were occupied vs. the number of years surveyed. Because this approach weights samples by the number of trials, I used data from all patches including some not surveyed in later years due to accessibility constraints. I assigned territory patches to landscape regions based on their spatial arrangement, which I fit as a random effect. All models were fit with the lme4 library in R 2.15.3 (R Development Core Team 2013). Spatial autocorrelation was undetectable in all models.

I considered the effects of local and landscape factors separately and then evaluated their combined effects. For local factors, I first identified the best description of habitat quality and then considered the trap hypotheses. At landscape scales, I considered each hypothesis separately and most additive combinations of hypotheses. To evaluate the combined effects of local and landscape factors, I considered the best model of local effects with all possible additive and interactive combinations of factors from supported landscape models. To assess the relative effects of local and landscape factors and direct and indirect estimates of habitat quality, I computed standardized regression coefficients.

RESULTS

I monitored 112 territory patches in 29 landscape regions that included an average 3.9 ± 0.5 (±SE) patches. Patches were monitored over an average of 10.2 ± 0.2 years and occupied during 6.1 ± 0.3 years. Anthropogenic land use covered 0-29% of landscapes and total area of territory patches (n = 1-26) cover 1-15% of landscapes.

Local effects

Occupancy dynamics were best explained by estimates of habitat quality that considered the interactive effects of habitat resources, stochastic factors, and conspecific density on reproductive output (Table 1). Although occupancy was highly associated with all direct estimates of habitat quality in the predicted direction, support for the habitat hypothesis was lowest overall (ΔBIC = 5.27) and considering the effects of stochastic factors and conspecific dependence greatly improved correspondence between observed and ideal distribution patterns (Fig. 1). In contrast, relative support for the effects of habitat quality measured indirectly based on important habitat attributes was much lower (ΔBIC ≥11.73) despite strong positive effects (*β* ± SE = 0.18 ± 0.06). There was no evidence for the trap hypothesis.

Landscape effects

All landscape factors had important effects on occupancy (Fig. 1). Evidence for the habitat amount hypothesis was strongest overall and its predicted effects were included in all models with high support (Table 1). The habitat amount hypothesis was better represented by habitat effective area than by unadjusted estimates of habitat amount (e.g., number of territory patches in landscapes; ΔBIC = 4.71) as occupancy increased with landscape quality at a greater rate in landscapes where habitat was common vs. rare (Fig. 1). Habitat configuration and matrix structure also had important effects that did not depend on habitat amount. Occupancy decreased as both area of agriculture (*β* ± SE = -0.068 ± 0.027; 100 ha) and area of the largest road (-0.74 ± 0.38) increased within landscapes (Fig. 1). On average, occupancy decreased as woodlands became increasingly aggregated within landscape (-2.8 ± 1.3).

Integrated effects

When considered together, habitat quality at local scales, and habitat effective area, habitat configuration, and matrix structure at landscape scales all had important additive effects on occupancy (Table 1). Moreover, evidence for interactions between local habitat quality and both landscape habitat configuration and matrix structure was high (ΔBIC = 0.53) but not for habitat effective area, which had positive effects at all levels of local habitat quality (ΔBIC = 5.23). As area of agriculture increased within landscapes, occupancy declined at a much greater rate in low-quality patches than in those of moderate quality and increased somewhat in high-quality patches (Fig. 2). As woodland habitat became increasingly aggregated within landscapes, occupancy in low-quality patches increased whereas that in high-quality patches decreased.

Local habitat quality had greater relative effects on occupancy than landscape factors but its importance depended on the processes and estimation procedure considered. When habitat quality was estimated directly based on the interactive effects of habitat resources, stochastic factors, and conspecific density on reproductive output, its effect was 1.5 times greater than that for habitat effective area and >2 times greater than that for habitat configuration or matrix structure based on magnitudes of standardized regression coefficients (Table 2). When habitat quality was estimated directly based only on the effects of important resources, however, the relative magnitude of its effect declined to 1.2 and >1.7 times greater, respectively. In contrast, the effect of habitat effective area was 1.5 times greater than indirect estimates of habitat quality, with similar effects for habitat configuration or matrix structure (Table 2). Among landscape factors, the effect of habitat effective area was 1.4-1.7 times greater than that for habitat configuration or matrix structure.

DISCUSSION

Understanding how habitat quality, habitat amount, habitat configuration, and matrix structure affect animal distribution is of great theoretical and applied importance. Nonetheless, because habitat quality is difficult to estimate and because habitat typically becomes more fragmented as overall habitat amounts decline, few studies have evaluated their independent and relative effects, even fewer consider the simultaneous effects of matrix structure, and to my knowledge, no study has assessed all these effects by considering explicit estimates of habitat quality based on vital rates (Fahrig 2003, Prugh et al. 2008, Mortelliti et al. 2010). I estimated the effects of habitat amount and overall quality, habitat configuration, and matrix structure at landscape scales and both direct and indirect estimates of habitat quality at local territory-specific scales on long-term occupancy dynamics of pygmy-owls across broad gradients in territory quality and landscape structure in a large number of independent landscapes. I found that all landscape factors affected occupancy but that habitat amount had greater effects than habitat configuration or matrix structure, which corresponds generally to findings from studies framed at larger scales (Fahrig 2003, Prugh et al. 2008, Hodgson et al. 2009a). Local habitat quality, however, had greater effects than landscape factors but only when habitat quality was estimated directly based on vital rates. Moreover, my results suggest that the effects of habitat connectivity depended on local habitat quality. Although the relative effects of landscape factors may be somewhat higher when estimated at different scales, these findings confirm important roles of both local habitat quality and landscape processes in driving distribution. Because in this system local territory quality is not affected by landscapes attributes (and only weakly correlated with habitat effective area at landscape scales) and because estimates of habitat configuration were uncorrelated with habitat amount (Appendix S1), inferences were largely unconfounded.

Habitat approaches for explaining animal distribution are based on the expectation that patch choices are driven by the quality or fitness potential of habitat. Thus, patches that support the highest population growth rates are thought to be selected first and used more consistently over time so that distribution precisely reflects patch quality. Although distribution patterns often conform generally to ideal expectations, distributional mismatches characterized by patches that are occupied more or less than expected on the basis of their quality are common in nature (Tregenza 1995, Sergio and Newton 2003) and were clearly apparent in this system (Fig. 1). Although natural selection should favor the ability to accurately assess habitat quality, settlement choices are often made on the basis of cues associated with future conditions (especially in seasonal environments) that may not be realized due to environmental stochasticity. In the Sonoran Desert, pygmy-owls select territories with high woody vegetation cover, in part, because it provides important habitat for prey. Nonetheless, temporal variation in precipitation and temperature affect prey abundance and activity, which might explain why owls perform poorly in some years even in good places (or well in poor places; Chapter 2). Moreover, territories with higher vegetation cover amplify the positive effects of favorable weather on realized habitat quality (Chapter 2). Thus, considering the additive and especially interactive effects of weather on habitat quality better explained distribution patterns. Although evolutionarily novel cues such as those created by humans can promote settlement in poor habitats and also explain mismatches (Robertson and Hutto 2006), this pattern was not apparent.

Mismatches between distribution and patch quality can also result from inaccurate estimates of habitat quality by researchers. The effects of conspecifics for example, are rarely considered when estimating habitat quality despite broad recognition that individual performance is density dependent. In my system, reproductive output declined with increasing conspecific density around focal patches (Chapter 2) and estimates of habitat quality that were adjusted these effects better explained distribution. Moreover, because the negative effects of conspecifics are buffered by high-quality resources and also mediated by weather effects, interactions among these factors can better explain realized habitat quality (Chapter 2) and distribution. Because habitat quality represents individual contributions to population growth from specific habitats, considering both reproduction *and* survival could provide even higher conformance with ideal expectations than observed here.

Landscape approaches for explaining distribution focus on the effects of habitat amount and habitat connectivity on occupancy and extinction-colonization dynamics at scales typically much larger than individual territory patches. Thus, when processes that drive distribution are approached from an integrated perspective, landscape factors should affect distribution at local scales and explain distributional mismatches revealed by habitat approaches. This is especially relevant in systems where territory patches are imbedded in complex landscapes with varying quantities and configurations of habitat surrounded by matrices of variable permeability to focal organisms (Ricketts 2001, Hanski and Gaggiotti 2004). In these cases, perceptual barriers, dispersal limitation, and fitness trade-offs associated with movement and search costs and variation in the number of potential colonists in the surrounding landscape can affect distribution independent of local patch quality (Morris 1987, Stamps 2001, Wiens 2001). My results showed that when all core factors that are the focus of landscape approaches were considered simultaneously with local territory quality, all factors had important effects on occupancy dynamics, which is plausible given the system. In this system, habitat is fragmented into areas of variable size and accessibility by moisture gradients that affect woodland distribution, topographic gradients that affects saguaro distribution, and by anthropogenic disturbance. Like other resident woodland birds, pygmy-owls disperse short distances by flying near ground level and dispersal movements and colonization success are affected by landscape structures such as large agricultural fields and roads, which is likely why these same structures also affected occupancy dynamics (Harris and Reed 2002, Moore et al. 2008, Flesch et al. 2010). Thus, increasing woodland fragmentation had positive effects on occupancy independent of habitat amount likely because more dispersed habitat fosters movement and because habitat amounts at landscape scales were too low to drive interactions with habitat configuration (Andren 1994, Fahrig 2003). Regardless, habitat amount had greater effects on occupancy than habitat configuration or matrix structure, which was best represented by habitat effective area that scales habitat amount by the overall quality of habitat at landscape scales and is thus more closely associated with abundance of potential colonists (Schooley and Branch 2011). Generally, habitat effective area should have greater effects than habitat connectivity, because production of new individuals occurs only within habitat and because it is closely linked to carrying capacity.

My findings also add to a small but growing literature indicating the effects of some landscape factors depend on local habitat quality (Schooley and Branch 2007, Jaquiéry et al. 2008, Hodgson et al. 2009b). Evidence for interactions between habitat quality and both matrix structure and habitat configuration were high but not for habitat effective area, which had consistently positive effects on occupancy at all levels of habitat quality (Fig. 2). Because animals often persist longer in high-quality habitat and may have the ability to target it during dispersal, the effects of habitat connectivity could generally depend on local habitat quality. In this system, occupancy declined markedly with increasing agricultural development at landscape scales only in low-quality territories where declining colonization rates likely fail to keep pace with higher extinction rates. Although the effects of habitat fragmentation can be positive or negative (Fahrig 2003) and were positive on average, fragmentation had negative effects on occupancy in low-quality territories and positive effects in high-quality territories, likely due to differential effects on colonization and persistence. Potential interactions between local and landscape factors highlight the importance of integrating habitat and landscape approaches for understanding distribution.

Habitat quality at local scales had greater effects on occupancy than landscape factors but its relative importance depended on how it was estimated. When habitat quality was measured indirectly based on resources known to affect habitat selection, habitat effective area at landscape scales had greater effects. In contrast, when habitat quality was measured directly based on the estimated effects of important resources, weather, and conspecific density on reproductive output, its relative effect nearly doubled and was much greater than landscape factors. Because habitat quality depends on individual contributions to population growth from specific habitats, which is driven largely by how the environment affects vital rates (Franklin et al. 2000), these processes should be considered when estimating habitat quality and evaluating its role in driving distribution (Armstrong 2005). Nonetheless, because virtually all studies that consider habitat quality at either local focal patch or regional source patch scales estimate habitat quality indirectly (e.g., Thomas et al. 2001, Jaquiéry et al. 2008, Mortelliti et al. 2010, but see Frankin and Hik 2004) due likely to logistical constraints, its overall role in driving distribution has likely been underestimated.

Distribution patterns represent sums of individual choices projected onto landscapes (Lima and Zollner 1996). Therefore, understanding processes that drive distribution requires an appreciation of how behavioral decisions by individuals at local scales are mediated by landscape processes. Efforts to integrate behavioral and landscape approaches for understanding distribution have been underway for some time but few studies focus at scales relevant to individual animals (Wiens et al. 1993, Armstrong 2005). From a landscape perspective, general support for the effects of habitat area and occasionally isolation provide a useful framework for explaining distribution but its generality may limit more mechanistic understandings. From a behavioral perspective, variation in habitat quality should drive patch choices by individuals because high-quality habitats confer greater fitness on occupants thereby affecting distribution at a range of scales. This is because by driving the birth and death rates individuals, high-quality habitats attract more immigrants, have lower extinction probabilities, and contribute more individuals to regional populations, which enhances colonization potential.

As threats to biodiversity accelerate, identifying key processes that drive distribution is critical for conservation (Lindenmayer and Fisher 2007). Nonetheless, because landscape and habitat approaches focus on different factors and spatial scales and because distributional mismatches reduce population growth rates, integrated approaches will help guide conservation (Armstrong 2005). My findings suggest that efforts to augment local habitat quality will be more efficient than efforts focused at landscape scales, especially given lower anticipated costs. Nonetheless, landscape factors also had important effects on occupancy that sometimes depended on local habitat quality, suggesting local management should consider the broader landscape context. Thus, local efforts that improve habitat quality in landscapes with more habitat and greater habitat connectivity should bolster occupancy the most whereas strategies focused only on connectivity will be least effective. Nonetheless, because anthropogenic disturbance was fairly low in my study region, connectivity could be more important in more altered landscapes. This is especially true in landscapes that support little habitat and population networks close to an extinction threshold (Hodgson et al. 2009a), which may be the case in portions of southern Arizona where pygmy-owls are endangered, large areas of riparian bottomland habitat has been lost, and owls are relegated to small habitat fragments on adjacent outwash plains. Strategies focused on processes with the greatest effects on distribution should enhance conservation efforts.

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Table 1. Effects of local and landscape factors on distribution of Ferruginous Pygmy-Owls in northwest, Mexico 2001-2013. Distribution was estimated annually based on territory-specific estimates of occupancy. Local processes considered the effects of anthropogenic disturbances that drive the presence of ecological traps, and the effects of habitat quality based on the estimated additive and interactive effects of habitat resources, stochastic factors, and conspecific density on reproductive output monitored over 10 years in the same territory patches. An indirect estimate of habitat quality based on resources important to habitat selection was also considered. Landscape processes considered the effects of habitat amount and overall habitat quality, habitat fragmentation, and matrix structure at a landscape scale around territory patches. All models are based on mixed-effects logistic regression for binomial counts where the response was number of years a territory patch was occupied vs. number of years surveyed; landscape was fit as a random effect.

Scale Hypothesized Factors	K	BIC	ΔBIC	w_i
Local Processes				
Habitat × Stochasticity × Density	3	277.19	0.00	0.53
Habitat × Stochasticity × Density + Traps	4	279.66	2.47	0.15
Habitat + Stochasticity + Density	3	279.67	2.48	0.15
Habitat + Stochasticity	3	281.33	4.14	0.07
Habitat + Density	3	281.42	4.23	0.06
Habitat	3	282.46	5.27	0.04
Indirect Habitat	3	294.19	17.00	0.00
Null	2	300.50	23.31	0.00
Traps	3	302.19	24.99	0.00
Landscape Processes				
Habitat Amount + Matrix Structure	5	292.40	0.00	0.48
Habitat Amount	3	294.03	1.62	0.21

Habitat Amount + Habitat Configuration	4	294.41	2.00	0.18
Habitat Amount + Habitat Configuration + Matrix Structure	6	295.46	3.05	0.11
Null	2	300.50	8.09	0.01
Matrix Structure	4	301.35	8.95	0.01
Habitat Configuration	3	302.48	10.08	0.00
Nonlinear Habitat Configuration	6	304.81	12.41	0.00
Habitat Configuration + Matrix Structure	5	304.98	12.58	0.00
Local and Landscape Processes				
Hab. Quality + Hab. Amount + Hab. Configuration	5	275.54	0.00	0.25
Hab. Quality + Hab. Amount + Matrix Structure	6	275.58	0.04	0.24
Hab. Quality + Hab. Amount + Hab. Quality × Hab. Configuration + Hab. Quality × Matrix Structure	9	276.07	0.53	0.19
Hab. Quality + Hab. Amount	4	277.05	1.51	0.12
Hab. Quality + Hab. Amount + Hab. Configuration + Matrix Structure	7	277.65	2.11	0.09
Hab. Quality + Hab. Quality × Hab. Amount + Hab. Quality × Hab. Configuration	6	277.78	2.24	0.08
Hab. Quality + Hab. Quality × Hab. Amount + Hab. Quality × Hab. Configuration + Hab. Quality × Matrix Structure	10	280.77	5.23	0.02
Hab. Quality × Hab. Amount	5	281.75	6.20	0.01
Hab. Quality × Hab. Amount + Hab. Quality × Matrix Structure	8	283.51	7.97	0.00

Table 2. Standardized regression coefficients for the effects of local and landscape factors on distribution of Ferruginous Pygmy-Owls in northwest, Mexico 2001-2013. Coefficients are from three different models that considered the effects of habitat quality estimated based on two different procedures. Indirect estimates of habitat quality were based on abundance of resources associated with habitat selection in this system. Direct estimates of habitat quality considered the effects of important habitat resources only and the effects of habitat resources, stochastic factors, and conspecific density on reproductive output monitored over 10 years. Coefficients are based on model {Habitat Quality + Habitat Amount + Fragmentation + Matrix} and mixed-effects logistic regression for binomial counts where the response was number of years a territory patch was occupied vs. number of years monitored.

	Indirect - Habitat Only		Direct - Habitat Only		Direct - Habitat × Stochasticity × Density	
Factor	β	SE	β	SE	β	SE
Local Habitat Quality	0.191	0.086	0.319	0.075	0.360	0.076
Habitat Effective Area	0.284	0.100	0.258	0.092	0.248	0.090
Largest Road Index	-0.137	0.088	-0.139	0.085	-0.151	0.084
Area of Agriculture	-0.240	0.111	-0.188	0.103	-0.177	0.100
Habitat Fragmentation	-0.149	0.097	-0.177	0.092	-0.146	0.089

Figure Captions

Figure 1 Effects of local and landscape factors on distribution of Ferruginous Pygmy-Owls in northwest, Mexico 2001-2013. Distribution was estimated annually based on territory-specific estimates of occupancy. Top row shows the effects of local habitat quality based on the estimated effects of habitat resources only, and based on different additive and interactive combinations of habitat resources, stochastic factors, and conspecific density on reproductive output monitored over 10 years in the same territory patches. Bottom row shows the effects of habitat effective area, matrix structure, and habitat configuration at a landscape scales.

Figure 2 Interactive effects of local habitat quality and landscape factors on distribution of Ferruginous Pygmy-Owls in northwest, Mexico 2001-2013. Distribution was estimated annually based on territory-specific estimates of occupancy. Effects of area of agriculture and habitat configuration are based on model {Habitat Quality + Habitat Amount + Habitat Quality × Fragmentation + Habitat Quality × Matrix Structure} whereas effects of habitat effective area are based on model {Habitat Quality + Habitat Quality × Habitat Amount + Habitat Quality × Fragmentation} at three levels of habitat quality. Lines show changes in predicted occupancy based on models at average values of other covariates; direction and magnitude of effects were largely unaffected at different covariates values.

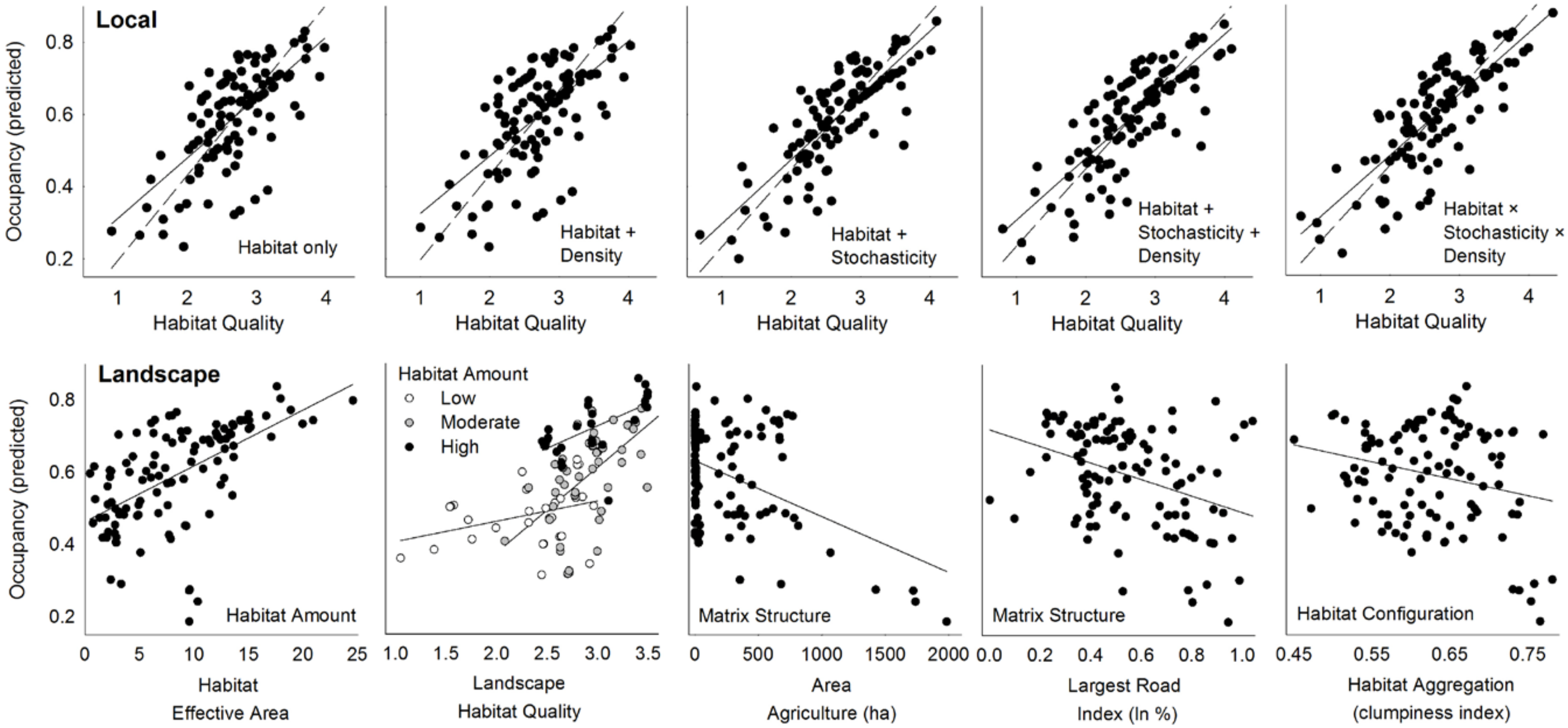
Local
Occupancy (predicted)
0.2
0.4
0.6
0.8
Habitat only
Habitat + Density
Habitat + Stochasticity
Habitat + Stochasticity + Density
Habitat × Stochasticity × Density
1
2
3
4
Habitat Quality
Landscape
Habitat Amount
Habitat Amount
○ Low
● Moderate
● High
Matrix Structure
Matrix Structure
Habitat Configuration
0
5
10
15
20
25
Habitat Effective Area
1.0
1.5
2.0
2.5
3.0
3.5
Landscape Habitat Quality
0
500
1000
1500
2000
Area Agriculture (ha)
0.0
0.2
0.4
0.6
0.8
1.0
Largest Road Index (ln %)
0.45
0.55
0.65
0.75
Habitat Aggregation (clumpiness index)

Fig. 1

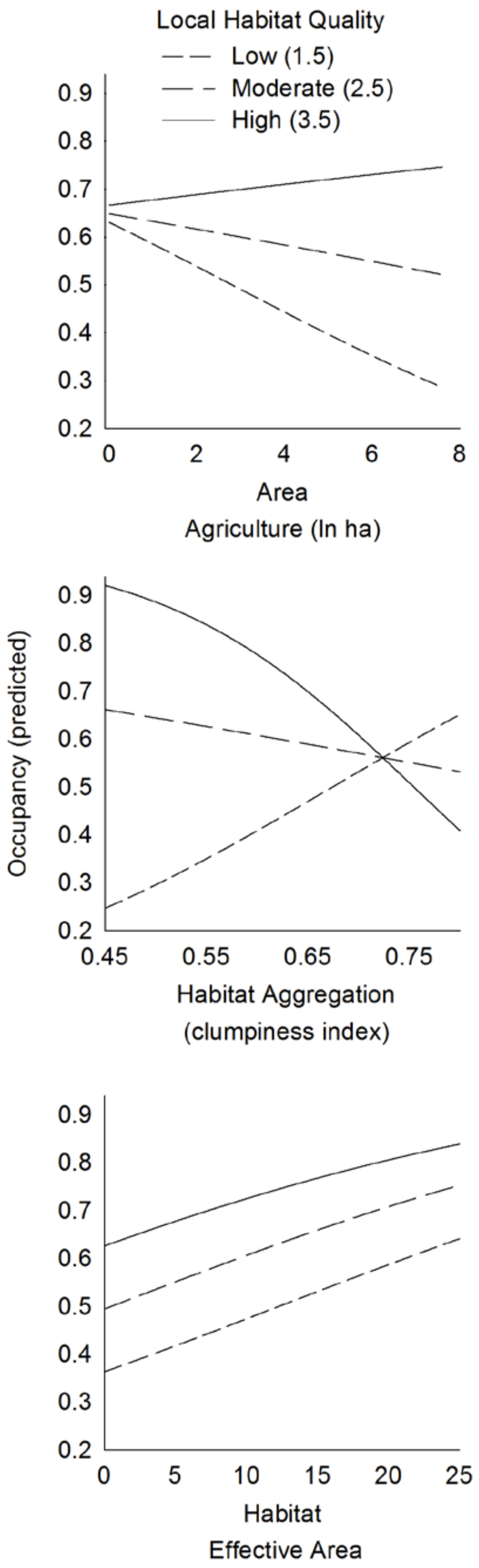
Local Habitat Quality
Low (1.5)
Moderate (2.5)
High (3.5)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0
2
4
6
8
Area
Agriculture (ln ha)
Occupancy (predicted)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.45
0.55
0.65
0.75
Habitat Aggregation
(clumpiness index)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0
5
10
15
20
25
Habitat
Effective Area

Fig. 2

APPENDICES

Appendix S1: Models and factors used to estimate habitat quality:

In a separate study (see Chapter 2), I identified environmental factors that drove habitat quality (HQ) by assessing a range of hypothesized relationships between reproductive output and patch-specific environmental factors over 10 years. Environmental factors included habitat resources, weather-related factors, and local conspecific density, which are defined below. All models are based on linear mixed-effects models where the response was the number of young produced during each year within each occupied territory patch, and territory patch was fit as a random effect. I predicted patch quality with these models for all 112 territory patches, which included 5 patches where demographic monitoring was not completed. Models are listed in order of their power to explain long-term occupancy dynamics.

Table S1.1: Models used to estimate habitat quality.

Hypothesis	Model
Habitat × Weather × Density	$HQ = 131.6 + 0.31(\text{lnCav}) + 0.35(\text{Comm(SDG)}) – 0.011(\text{Hab}_f) + 0.012(\text{lnCav*Hab}_f) – 0.86(\text{Frag}_{hab}) – 36.1(\text{lnT}_{brood}) – 33.3(\text{lnP}_{yr}) + 9.24(\text{lnT}_{brood}\text{*lnP}_{yr}) + 38.3(\text{NDVIyr}^2) + 1.76(\text{Density}) + 0.087(\text{Frag}_{hab}\text{*Density}) + 0.23(\text{Frag}_{hab}\text{*lnP}_{yr}) – 0.29(\text{Density*lnP}_{yr}) – 0.093(\text{Frag}_{hab}\text{*Density*lnP}_{yr}) – 0.038(\text{Hab}_f\text{*Density}) – 1.89(\text{Hab}_f\text{*NDVI}_{yr}^2) – 22.8(\text{Density*NDVI}_{yr}^2) + 2.88(\text{Hab}_f\text{*Density*NDVI}_{yr}^2)$
Habitat + Weather + Density	$HQ = 130.4 + 0.23(\text{lnCav}) + 0.34(\text{Comm(SDG)}) – 0.043(\text{Hab}_f) + 0.017(\text{lnCav*Hab}_f) – 0.18(\text{Frag}_{hab}) – 35.6(\text{lnT}_{brood}) – 32.3(\text{lnP}_{yr}) + 8.99(\text{lnT}_{brood}\text{*lnP}_{yr}) + 23.0(\text{NDVI}_{yr}^2) – 0.18(\text{Density})$
Habitat + Weather	$HQ = 115.5 + 0.24(\text{lnCav}) + 0.36(\text{Comm(SDG)}) – 0.047(\text{Hab}_f) + 0.018(\text{lnCav*Hab}_f) – 0.19(\text{Frag}_{hab}) – 31.5(\text{lnT}_{brood}) – 28.8(\text{lnP}_{yr}) + 8.01(\text{lnT}_{brood}\text{*lnP}_{yr}) + 23.0(\text{NDVI}_{yr}^2)$

Habitat + Density	$HQ = 2.53 + 0.13(\ln Cav) + 0.47(Comm(SDG)) – 0.067(Hab_f) + 0.023(\ln Cav*Hab_f) – 0.17(Frag_{hab}) – 0.12(Density)$
Habitat only	$HQ = 2.43 + 0.15(\ln Cav) + 0.46(Comm(SDG)) – 0.068(Hab_f) + 0.023(\ln Cav*Hab_f) – 0.18(Frag_{hab})$

Table S1.2: Definitions of environmental factors used to describe habitat quality. Habitat resources, primary productivity, and conspecific density were measured at the scale of individual territory patches and weather factors were measured at five weather stations, most of which were within 1-30 km from patches.

Category Variable	Abbreviation	Definition	Units
Habitat resources			
Cavities	Cav	Number of saguaros with at least one suitable nesting cavity	no.
Vegetation Community	Comm	Dominant community type in patches; either desert-scrub or semi-desert grassland (SDG)	category
Habitat Amount	Hab_f	Mean fractional woody vegetation cover among all 30 × 30 m grid cells across patch	%
Habitat Fragmentation	$Frag_{hab}$	Number of patches of woody vegetation per ha divided by Hab_f	no./ha/%
Stochastic factors			
Temperature	T_{brood}	Mean daily maximum temperature during the brooding season (May and June), no lag time	^0C
Precipitation	P_{yr}	Total precipitation from June of the current year to May of past year	cm
Primary Productivity	$NDVI_{yr}$	Deviation from mean normalized difference vegetation index (NDVI) from June of the current year to May of past year	Proportion
Conspecifics			
Local Density	Density	Number of nearest neighbor nesting pairs per km immediately around each focal territory patch	no./km^2

Appendix S2: Correlation between local and landscape factors.

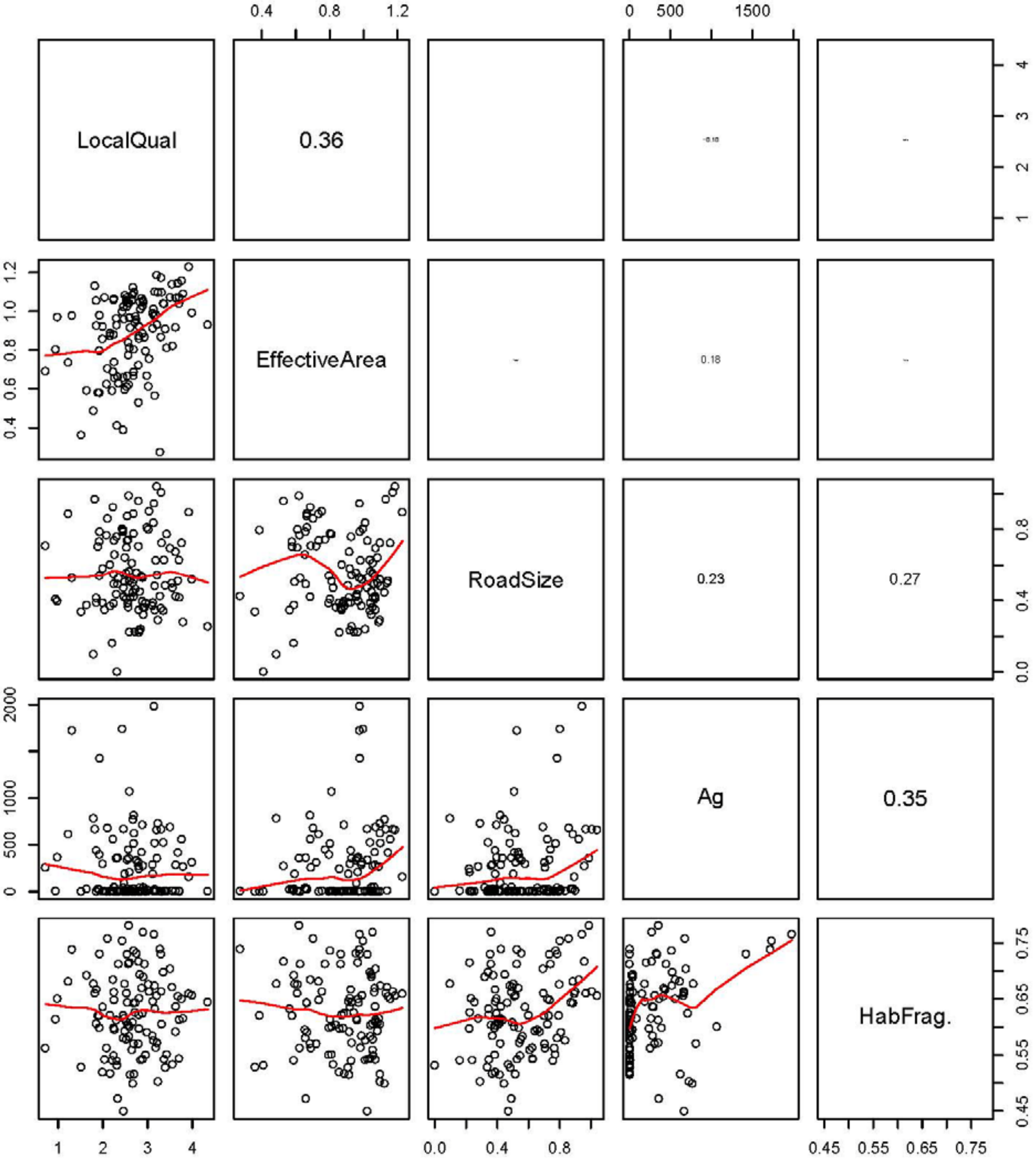

Table S2.1: Pair-wise correlation between important local and landscape factors.

	Local Habitat Quality		Habitat Effective Area		Matrix-Road Size		Matrix-Agriculture		Habitat Aggregation	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Local Habitat Quality			0.36	<0.01	0.00	0.97	-0.10	0.30	0.02	0.81
Habitat Effective Area	0.36	<0.01			-0.03	0.74	0.18	0.06	-0.05	0.60
Matrix-Road Size	0.00	0.97	-0.03	0.74			0.23	0.01	0.27	<0.01
Matrix-Agriculture	-0.10	0.30	0.18	0.06	0.23	0.01			0.35	<0.01
Habitat Aggregation	0.02	0.81	-0.05	0.60	0.27	<0.01	0.35	<0.01		