Birds of a feather: Interpolating distribution patterns of urban birds

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Abstract

Geostatistical methods provide valuable approaches for analyzing spatial patterns of ecological systems. They allow for both the prediction and visualization of ecological phenomena, a combination that is essential for the conceptual development and testing of ecological theory. Yet, many ecologists remain unfamiliar with the application of these techniques. Here, we apply the methodology of geostatistics to an urban avian census in order to investigate and illustrate the utility of these tools. We derive habitat probability maps for three bird species known to differentially occupy the urban to rural gradient within the Phoenix metropolitan area and surrounding desert (Arizona, USA). We aggregated avian censuses conducted seasonally at 40 sites over two years and applied two processes of interpolation, ordinary Kriging and indicator Kriging, and compared both methods. Ordinary Kriging interpolates values between measurements; however, it requires normally distributed data, which is commonly invalidated in ecological censuses. While indicator Kriging is not able to produce numerical predictions of measurements, it has the advantages of not requiring normally distributed data and requiring fewer statistical decisions. Each of the species exhibited strong deviations from normality due to many observations of zero. Given the skewness of the data, we anticipated that indicator Kriging would be a more appropriate method of interpolation. However, we found that both methods adequately captured spatial distribution of the three species and are sufficient for creating distribution maps of avian species. With additional census monitoring, Kriging can be used to detect long-term changes in population distribution of avian and other wildlife populations.

Keywords: Interpolation; Kriging; Avian; Urban; Home range; Population distribution

1. Introduction

Effective conservation planning requires a comprehensive understanding of the relationships among organisms and their environment (O’Neil & Carey, 1986). In a rapidly urbanizing world, it has become apparent that understanding the ecological effects of this process is a paramount objective. Urbanization is characterized by dramatic land use transformation, typically across expansive extents. This consequently leads to land cover conversion, which can be a dominant process affecting ecological community structure and population dynamics, generating unique assemblages of organisms (Hostetler, 1997). Typically, researchers find that urban areas tend to harbor biotic communities in which only a few species increase in density relative to the surrounding areas, thereby creating distinct differences in community diversity between these two landscapes (Blair, 1996; DeGraaf & Wentworth, 1981; McKinney, 2002). But how does this process affect the spatial distribution of species within this human-dominated system? Understanding the spatial pattern of such relationships is important for both the development of ecological theory and implementation of conservation strategies.

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Maps illustrating home ranges of a particular species have been extremely useful as a heuristic tool for ecologists. Such distributions overlain with land use and/or land cover maps provide an intuitive device for exploring hypothetical relationships of organisms and their environment (e.g. Robertson, 1987). These patterns have also been used to test existing hypotheses in ecology (e.g. Hodgson, Macrae, & Brewer, 2004; Villard & Maurer, 1996). They have also assisted conservation biologists and environmental planners to identify potential conservation areas and monitor conservation efforts (Price, Droge, & Price, 1995; Scott et al., 1993).

Population distribution maps are increasingly based on geostatistical models, largely due to the explosion of technological innovations provided by GIS. This process is largely contingent on model-based estimations of species distributions, which are typically derived in two ways. First, species occurrences can be predicted based on habitat-suitability models (e.g. Hanski & Simberloff, 1997), in which the predictions of animal population abundances are derived through biologically meaningful environmental variables (i.e. forage abundance, habitat type, water availability). This is an effective method for producing population distribution maps; but only if (1) theory exists supporting the incorporation of particular environmental variables into such models and (2) those variables are collected or modeled across the entire region of interest. As a young discipline, urban ecology lacks habitat-suitability models for many species that occupy urban environments. A second commonly-used approach to population distribution mapping in ecology involves interpolation of observed occurrences of particular species (e.g. Jiguet et al., 2002; Pfeiffer & Hugh-Jones, 2002; Rempel & Kushneriuk, 2003; Royle, Link, & Sauer, 2002; Villard & Maurer, 1996). This process does not require a priori knowledge of habitat relationships; rather, it uses observations of species’ abundances via surveys to construct a spatially-explicit distribution model. Surveys conducted at a series of point locations are a common tool for ecological monitoring, particularly for birds (Bibby, Burgess, & Hill, 1992; Toms, Schmiegelow, Hannon, & Villard, 2006). Thus, this approach may be more useful in urban areas or other situations for which habitat suitability models are lacking. Furthermore, the maps derived from the survey data may provide insights into previously unrecognized habitat associations, thereby facilitating the development of new habitat suitability models.

Originally developed for mineral mapping, Kriging is a spatially-based interpolation model which predicts a response at unobserved locations as a linear function of data from the observed locations with the incorporation of a weighting function between points which exponentially decays as the distance between points increases. Other forms of interpolation present specific challenges for ecological analyses. Inverse distance weighting and radial basis functions are largely not used because they are exact, deterministic interpolation techniques, which force the values of the interpolations to be equal to the measured values at those locations, making ecological generalizations difficult. Deterministic, inexact interpolation methods (i.e. global and local polynomial interpolation and splining) allow for enhanced generality; however, they do not provide a mechanism for assessing prediction errors and do not allow for the investigation of autocorrelation. By contrast, Kriging is more flexible than these procedures. The model can be parameterized to be exact or inexact, which can allow for the investigation of spatial autocorrelation, and can produce both probability and prediction standard error maps.

While Kriging is widely used in ecology, the distributions of point count data, such as an avian census, often violate the assumption of normality required by most forms Kriging (Royle et al., 2002). Such data are consistently discrete and positively valued, and consequently, right skewed. This distribution is an especially difficult one to transform to meet the assumptions of normality, making the majority of Kriging techniques (i.e. ordinary, simple, universal) inappropriate. However one form, indicator Kriging, does not assume the data to be interpolated normally distributed. Given the statistically problematic nature of point count data, we compare advantages and disadvantages of modeling spatial distributions of bird populations of three ecologically distinct species in two disparate land uses via a commonly-employed parametric Kriging technique (ordinary) and a non-parametric Kriging technique (indicator).

The major disadvantage of using indicator over ordinary Kriging is that a prediction map can not be generated. However, prediction maps are logically fallible for point count data, as actual abundance can not predicted because the proportion of the population of the sample is always unknown (Royle et al., 2002). Rather, predictions maps represent an index of relative abundance (Link & Sauer, 1998). Another example of an index of relative abundance, which both Kriging procedures are possible of producing, is a probability map. Such maps estimate the probability that any given point will exceed a pre-defined threshold. While this is not useful in calculating an estimate of what the population count is at a particular site, probability maps using avian census counts estimate the range of a given population, not individuals. If a particular species is dominant across the entire study site, the interpolated probability will be high for all areas. However, if a species differentially utilizes a particular study site, the interpolations will subsequently differentiate, producing a more heterogeneous map of population distribution probabilities. This procedure is particularly useful in study sites with disparate landscape types (i.e. forest vs. grassland, urban vs. rural) in which animals differentially occupy space. By comparing probability maps of ordinary and indicator Kriging, we show that either method can be used effectively in order to interpolate avian distribution patterns of the focal species, and discuss the conditions under which each method will be most useful.
2. Methods

2.1. Study area and sampling design

We conducted this work using data collected as part of long-term ecological monitoring by the Central Arizona-Phoenix Long Term Ecological Research project (CAP LTER; http://caplter.asu.edu), a research group studying the effects of rapid urbanization on a Sonoran Desert ecosystem. The CAP LTER study area occupies 6400 km² of the Phoenix metropolitan area, accompanying agricultural lands and Sonoran Desert remnants (Fig. 1). The core monitoring effort of CAP LTER consists of a sampling regime in which a suite of ecological variables are measured at sites falling both within the Phoenix metropolitan area and its surrounding desert. Birds are monitored seasonally at 40 sites, randomly selected using a dual-density tessellation-stratified procedure, with sites in the surrounding desert area occurring at one-third the density of sites in the urbanized areas (Fig. 1; Hope et al. 2003, 2005). This design maximizes the density of points within the highly heterogeneous urban landscape, while maintaining a spatially balanced sample at the regional scale.

2.2. Bird counts

Since Fall 2002, seasonal bird counts have been conducted by three observers per site, including winter (January), spring migration (April), summer breeding (July), and fall migration (October). Thus, over a calendar year, each of the 40 sites (Fig. 1) was visited 12 times (three observers by four seasons). Observers employed 15 min open-radius point counts, noting all bird species seen or heard as well as their estimated distance from the observer. In order to maximize numerical robustness for model creation for interpolation, we aggregated results of counts for our three focal bird species across eight seasons, occupying two full calendar years (October 2002 to July 2004, inclusive). The final matrix consists of 40 rows, one for each aggregated observation, and the following columns: latitude, longitude, and the aggregated counts for the three focal bird species.

2.3. Focal species

We selected three commonly occurring, resident birds species to exhibit how these ecologically distinct avian species differentially occupy the urban to rural gradient: Rock Dove (Columba livia), Phainopepla (Phainopepla nitens), and Cactus Wren (Campylorhynchus brunneicapillus). Rock Dove and Phainopepla were chosen to highlight the extremes of avian population distribution within urban and rural land uses, respectively. The Rock Dove is a globally urban species, rarely occurring outside of cities (Marzluff, 2001). Phainopepla, by contrast, are largely desert specialists, occurring primarily in the lowland deserts of California and Arizona. While they appear able to occupy agricultural habitats according to early literature (Crouch, 1943), they are generally not found in urban or suburban areas (Emlen, 1974; Germaine, Rosenstock, Schweinsburg, & Richardson, 1998; Green & Baker, 2003; Rosenberg, Terrill, & Rosenberg, 1987). Cactus Wrens, although nearly iconic as desert dwellers, are more generalists in their habitat preferences than Phainopepla. They are well known to occur in urban areas as well as surrounding desert areas (Emlen, 1974; Germaine et al., 1998; Green & Baker, 2003; Kinzig, Warren, Martin, Hope, & Katti, 2005).
2.4. General approach

Many geostatistical techniques require the assumption of statistical normal distribution of the data to be interpolated in order to supply optimal estimations (Cressie, 1993). Highly skewed data can lead to broad variogram variance and thus may bias the spatial autocorrelation. As predicted of point count data, exploratory analysis indicated that population counts of the three focal species within the study are consistently right skewed (Fig. 2). This is primarily due to the high occurrence of few to no individual records of a particular species at a site and a bias of positively-valued data (Royle et al., 2002). This is a common reality in ecological censuses and presents a significant challenge to researchers interested in producing population distribution maps.

Accordingly, we evaluated our variables for normality using the standardized coefficients of skewness, $z_1$, and kurtosis, $z_2$, calculated as:

$$z_1 = \frac{\sum_{i=1}^{n}(x_i - \bar{X})^3/n}{\sqrt{(6/n)}}$$

and

$$z_2 = \left\{ \frac{\sum_{i=1}^{n}(x_i - \bar{X})^4/n}{\left(\sum_{i=1}^{n}(x_i - \bar{X})^2/n\right)^2} \right\} - 3$$

where the resulting $z$ values were compared against the $t$-value deemed appropriate for the 0.01 level of confidence (Keeping, 1962; Siegel, 1956). Given $n = 40$, the critical value of $t$ is 2.71. In addition, we used the Kolmogorov–Smirnov one-sample test to determine if significant deviations from normality are found in our spatial data (Kolmogorov, 1941).

All three spatial variables suffered from significant deviations from normality. The absolute values for $z_1$ for all species, and $z_2$ for Phainopepla and Rock Dove, exceeded the selected value of $t$; and thus, significant deviations from normality were confirmed. The Kolmogorov–Smirnov one-sample test also showed that all three variables came from non-normal populations. A Box–Cox analysis was conducted for the three species and suggested that a power law was the most appropriate for each species in order to satisfy normality. The fourth root transformation “normalized” the spatial data for the Cactus Wren and Rock Dove distributions while a tenth root transformation was required to “normalize” the Phainopepla data according to our evaluation procedures.

Geostatistics (including both deterministic and stochastic methods) rely on the assumption that measurements of neighboring samples are more similar than locations further away (Tobler, 1970) and is fundamentally based on the theory of regionalized variables (Matheron, 1971). A regionalized variable is an intermediary between an exact, deterministic variable and a random variable that varies in a continuous manner from one location to another. Kriging is an interpolation technique that assumes the variable being interpolated can be treated as a regionalized variable, and is generally expressed as:

$$Z(s) = \mu(s) + \delta(s) + \varepsilon$$

where $Z(s)$ is the variable being interpolated, and $\mu(s)$ is the deterministic function, $\delta(s)$ is the stochastic, but spatially dependent regionalized variable, $\varepsilon$ represents a residual with a spatially independent Gaussian noise term with zero mean and variance, and $s$ is a geographic location (Cressie, 1993).

2.5. Ordinary vs. indicator Kriging

Ordinary, simple and universal Kriging are not permissible interpolation techniques for data that do not conform to normality. Ordinary Kriging assumes that $\mu(s)$ is constant over space and estimates the mean of the sampled population. Simple Kriging assumes that $\mu$ and $\delta$ are known exactly, which is not true for point count data (Royle et al., 2002). Universal Kriging relaxes the assumption of a constant mean, but often does not produce more accurate results because additional parameters must be introduced to describe the changing mean. We chose to do interpolation of the transformed data with ordinary Kriging because $\mu$ and $\delta$ are not known exactly. Ordinary Kriging is a commonly used geostatistical method that estimates values across a study region in which the variogram is known, and assumes a constant mean. It is calculated as:

$$Z(s) = \mu + \delta(s)$$

where $Z$ is an estimated value based on the variogram model, $\mu$ is some unknown constant, and $\varepsilon$ is assumed to be zero (Cressie, 1993; Matheron, 1971).

An alternative approach is to use indicator Kriging with the untransformed data (Journel, 1983). Indicator Kriging does not assume normal distribution. Rather, it builds the cumulative distribution function at each point based on the

![Fig. 2. Frequency distributions of untransformed data.](image-url)
behavior and correlation structure of indicator-transformed data point. This is accomplished through a series of threshold values between the smallest and largest data values, which are used to create an estimation of the cumulative distribution function. In this way, indicator Kriging proceeds just like ordinary Kriging, only for binary (indicator) variables. Indicator Kriging predicts the probability that a given location is above some predetermined threshold value, and is calculated as:

\[ I(s) = \mu + \delta(s) \]  

where \( I \) is the binary variable being selected (\( I = 0, 1 \)) and \( \mu \) is an unknown constant, and \( \delta \) is assumed to be zero (Cressie, 1993). For each species \( I \) was the probability that a given point would exceed the mean (\( I = 1 \)). The largest advantage of indicator Kriging is that the method does not require normality distributed data. Thus, analysis of indicator Kriging with the bird census data was done with the untransformed data. If the outputs of these methods are similar, this will indicate that the need to transform data in order to satisfy normality of most Kriging methods is unnecessary, and thus indicator Kriging is a more simple and reliable method. Interpolations were conducted in the Geostatistical Analyst extension of ArcGIS v. 9.1.

3. Results

3.1. Ordinary Kriging

To satisfy the assumption of normality, ordinary Kriging was conducted with the transformed data as suggested by the Box–Cox procedure. The first step was to determine what threshold to select in order to determine the probability that a given point will exceed that threshold. We selected the mean of the transformed variables for ordinary Kriging (Table 1). Second, we determined if trend removal was necessary. We did so by selecting varying levels of trend removal and selecting the one that maximized the height of the partial sill. For all three species, the calculated partial sill was maximized by no trend removal (see Table 2).

We next analyzed the semivariograms and began model fitting (Fig. 3). The semivariogram is a scatter diagram with the differences squared. We would assume that points close together are more similar than points far apart, but this spatial dependence or spatial autocorrelation varies considerably from surface to surface.

The semivariogram can become a science unto itself. A curve fitted to the scatter pattern should have an intercept and a point where it flattens and becomes parallel to the \( x \)-axis. The intercept (point on the \( y \)-axis above zero) is called the nugget. In theory, the point of zero separation should have a semivariogram value of zero. It rarely is zero, and referred to as the nugget effect and is theoretically caused by measurement errors or spatial sources of variation at distances smaller than the mean sampling interval. The range or span is the distance where the fitted curve is parallel to the \( x \)-axis. At distances less than the range, the points are spatially autocorrelated; while at distances greater than the range, the points are not autocorrelated. The sill is the \( y \)-axis value of semivariance associated with the range. The range is used to determine the neighborhood, which is used in estimating the value for a given point. The two dimensional view of the semivariogram shows for any direction and distance from the center of the surface tend to fall into the color-coded bin. The empirical semivariogram surface indicated anisotropic conditions for all three species. This occurs when the semivariance changes as a function of direction, in which the theoretical model reaches the sill more rapidly in some direction than others (Isaaks & Srivastava, 1989; Journel & Huijbregts, 1978). There was a directional trend in the data from northwest to southeast, which corresponds to the overall direction of the city (see Fig. 1), which is blocked in the southwest and northeast by mountain ranges and creosote flats. Theoretical anisotrophies were estimated empirically and then embodied successively within each model.

Once the anisotrophies were accounted for each species, we then determined which theoretical variogram model best fits each of the three empirical semivariograms (Fig. 3). Statistical comparison between original and indicator Kriging can only be done with root mean square error (RMSE), which is a measure of the deviation of the predicted value from the actual value; where values close to zero indicate the theoretical model closely fits the measured values. We created a variety of models and compared the RMSE of each (Table 3). We selected the variogram model with the lowest RMSE for each species.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Median</th>
<th>Standard deviation</th>
<th>( z_1 )</th>
<th>( z_2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cactus Wren</td>
<td>19.15</td>
<td>9.50</td>
<td>22.85</td>
<td>2.77</td>
<td>-0.32</td>
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<tr>
<td>Phainopepla</td>
<td>3.38</td>
<td>0.00</td>
<td>8.06</td>
<td>7.82</td>
<td>12.30</td>
</tr>
<tr>
<td>Rock Dove</td>
<td>113.20</td>
<td>39.00</td>
<td>193.10</td>
<td>7.73</td>
<td>12.39</td>
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</table>

### Table 2

<table>
<thead>
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<th>Trend removal</th>
<th>RD</th>
<th>CW</th>
<th>PH</th>
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<tr>
<td>0</td>
<td>2.89</td>
<td>0.60</td>
<td>0.33</td>
</tr>
<tr>
<td>1</td>
<td>1.41</td>
<td>0.06</td>
<td>0.16</td>
</tr>
<tr>
<td>2</td>
<td>0.29</td>
<td>0.039</td>
<td>0.14</td>
</tr>
<tr>
<td>3</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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Values indicate partial sills with varying levels of trend removal. Ordinary Kriging used transformed data while indicator Kriging used the original data, where Rock Dove (RD), Cactus Wren (CW), and Phainopepla (PH).
Phainopepla and Cactus Wren both had lowest RMSE values for a hole-effect variogram. Phenomena associated with this model are typically represented by spatial periodicity (Journel & Huijbregts, 1978). However, the suggestion of a hole-effect model for these two species is not due to a periodic process continuing ad infinitum, but is more an artifact of the configuration of the sampling extent. CAP LTER’s study area is centered around the Phoenix metropolitan surrounded on all sides by desert. The strength of the hole-effect model, along with empirical evidence, indicates that these species are prevalent in the desert, decrease as one moves into the city, and then increase as one moves out of the city. Rock Dove had the lowest RMSE for the rational quadratic variogram model. This model works best for data that exhibit high correlations between short distances (Cressie, 1993). The RMSE value for hole-effect variogram model is also low for Rock Dove, suggesting spatial periodicity for this species. Interpolated values created with ordinary Kriging are presented as probability maps in Fig. 4a, c, and e.

3.2. Indicator Kriging

Semivariogram analysis indicated anisotrophic conditions similar to ordinary Kriging with trends from a NW to SE direction for all species. Model selection was done by analyzing RMSE values of different models (Table 3). For each species, the lowest RMSE value was for the hole-effect model, indicating spatial periodicity of each dataset. The indicator data were then interpolated using

<table>
<thead>
<tr>
<th>Model</th>
<th>Ordinary Kriging</th>
<th>Indicator Kriging</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RD</td>
<td>CW</td>
</tr>
<tr>
<td>Spherical</td>
<td>0.3987</td>
<td>0.4185</td>
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<tr>
<td>Exponential</td>
<td>0.3947</td>
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<td>Gaussian</td>
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<td>Rational quadratic</td>
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<tr>
<td>Hole-effect</td>
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<td>0.4067</td>
</tr>
<tr>
<td>Circular</td>
<td>0.3997</td>
<td>0.4173</td>
</tr>
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</table>

By comparing root mean square values of theoretical variogram models for ordinary and indicator Kriging of Rock Dove (RD), Cactus Wren (CW), and Phainopepla (PH), the model with the lowest RMS value was selected.
the variogram models to estimate the probability that a given point was above or below that defined threshold value. Interpolated values created with indicator Kriging are presented as probability maps in Fig. 4b, d, and f.

3.3. Comparison of ordinary and indicator Kriging

To assess the robustness of different interpolation methods, the deviation of the model from the measured values was calculated and compared. Cross validation is a common method to optimize model variograms to experimental variograms (Johnston, Ver Hoef, Krivoruchko, & Lucas, 2001). This was accomplished by removing a single data point, and predicting the associated value, and then repeating this procedure for all data points. Predicted values are compared with actual values in order to assess the strength of the model (Table 3).

4. Discussion

Our exploratory analysis of two Kriging methods, indicator and ordinary Kriging, indicates that both are viable tools for mapping species distributions along an urban–rural gradient, using data from point count censuses. However, it is imperative that researchers utilizing this approach understand and adhere to the model assumptions of the geostatistical techniques which they employ. Biological census data are usually heavily right-skewed, generally caused by many samples with few to no observations. The advantage of using indicator Kriging over ordinary Kriging is twofold for data of this nature. First, it does not require the satisfaction of the assumption of normality; and thus there is no need for data transformation. Second, there are fewer decisions to make during variogram analysis and model fitting. Indicator Kriging has the disadvantage of not producing implicit predictions as ordinary Kriging does. Instead it estimates the probability that a given location will be above or below a threshold. We maintain that indicator Kriging, while not implicitly predictive, could be an useful tool for researchers and urban wildlife managers who desire habitat probability maps from an urban to rural gradient, or other landscape gradients more generally.

An analysis of cross validation of three ecologically distinct species (Table 3) supports the use of either Kriging
method with point count data. Distribution maps and model accuracy were essentially the same for ordinary and indicator Kriging for all three species, indicating that the results are not particularly dependent on the method used for spatial interpolation. Keeping in mind that ordinary Kriging was performed with transformed data and indicator Kriging was performed with untransformed data, the similarity of RMSE indicates overall robustness for each model. Thus, either model could be used to achieve the same outcome.

The advantage of ordinary Kriging is that once those decisions are made, one can make actual prediction of population densities instead of predicting the probability of exceeding some threshold. However, it is important to reiterate that probability distribution maps do not serve to predict population abundance; rather, they exist as indices of relative abundance, or probability of existence. Both prediction maps and probability maps serve this purpose and are appropriate estimates of population distribution barring that the assumptions of the interpolation model are satisfied. Garrison and Lupo (2002) found that model-based distribution maps are most accurate for species that are (1) relatively abundant, (2) have relatively large breeding ranges, and (3) are territorial. The effects of these attributes must be considered when interpreting such prediction or probability maps. All three of the species that we modeled met these criteria. Equivalent results should not be expected from bird species that are relatively rare or habitat specialists (i.e. riparian species). Habitat suitability models would be a more appropriate spatial distribution model of such species.

4.1. Mapping an urban–rural habitat gradient

Interpolation of bird count data across the urban–rural gradient encompassed by the Phoenix metropolitan area and surrounding Sonoran desert illustrates striking trends in avian population distribution. The Rock Dove is a flagship urban species, and the maps show it adhering strongly to the urban ecosystem. It exhibits elevated levels of the abundance within the urbanized areas and a sharp decline of probability into the outlining desert regions. The opposite is true for the Phainopepla, with very strong probability values in the desert with an even sharper gradient into the city relative to the Rock Dove. The Cactus Wren is an interesting intermediary. Kriging suggests that this species has a much broader gradient from rural to urban, indicating that the Cactus Wren is more able to penetrate the urban ecosystem than the Phainopepla. However, this native species does tend to occupy the desert areas surrounding the Phoenix metropolitan with greater probability than the city.

It is interesting to note that Rock Dove and Phainopepla have consistently lower RMSE values than Cactus Wren. We interpret this as indicating that Rock Dove and Phainopepla are more specialized in their habitat associations, urban and desert, respectively. Their RMSE values are lower due to strong spatial autocorrelations between points close together. Cactus Wren’s RMSE is higher due to decreased spatial autocorrelation indicating this species is more of a generalist, preferring desert habitats but also using urban habitats. Thus, the model fit for these species confirms our a priori assessments of their habitat preferences.

Relative to all other variogram models, the hole-effect model tends to have the lowest RMSE values for each species in both types of Kriging. The minor exception is ordinary Kriging with Rock Dove. Rational quadratic was the lowest indicating strong spatial autocorrelation, but hole-effect is second lowest. The strong model fit with the hole-effect hints at the spatial periodicity over the study region. This is an artifact of the sampling area being a metropolitan area surrounded on all sides by desert, except to the Southeast (Fig. 1). The configuration of urban growth in Phoenix is clearly having a direct influence on the spatial distribution of these three species.

Implementation of this process with longer term data sets will allow research and wildlife managers the opportunity to analyze changes in population distributions over time. This is especially relevant for analyzing the impact of urbanization on species that utilize both urban and rural ecosystems and on species that are inhibited by urban growth. The output of this process creates probability maps that estimate the distribution of a given population of a species, and these maps can be compared in a temporal sequence to analyze change over time, either seasonally or annually. Likewise, the maps could be beneficial in prioritizing areas for additional research, conservation, and restoration efforts. Distribution maps can assist in communicating urban ecology to the public. For example, the maps we developed are currently being used by environmental educators involved in CAP LTER to illustrate the concept of an urban–rural gradient for K–12 schoolchildren in Phoenix.

Properly constructed maps from count survey data can assist the development of establishing habitat associations, by generating visualizations of spatial patterns that can help infer ecological processes. For example, comparing standardized maps of species distribution probabilities and overlaying habitat classification maps can provide researchers insights into habitat usage by particular species. For species that preferentially utilize specific habitats, one can infer rates of percolation from one habitat to another by comparing the isolines of the interpolated probabilities of a species existence atop overlaying habitat types (e.g. forest vs. grassland, urban vs. rural). Analysis of such isolines can also supplement non-spatial analyses by suggesting potential ecological corridors utilized by species. For example, two relatively large patches of high probability are connected by a narrow strip of high probability, suggesting a potential ecological corridor.

5. Conclusions

Urbanization has clear impacts on the population distribution of particular native and exotic species. This process
creates a new dynamic ecosystem with greatly altered biotic community composition. It is clear there are species of birds that are ecosystem specialists in both extremes of the urban–rural gradient within the Phoenix metropolitan and surrounding deserts. There also appear to be species native to the Sonoran desert that are able to encroach and thrive in the urban ecosystem. However, it seems that these species are more partial to their native habitat than the constructed ecosystem. This is an example of how directly humans can impact ecological community composition.

Performing geostatistical analyses for wildlife populations has always been difficult as population data tend to be highly skewed with many random points having no observations and other points potentially having many observations. Indicator Kriging offers a valuable alternative to more common Kriging methods with the advantages of fewer decision-making steps and no assumption of normality. Population estimates can also be interpolated through ordinary Kriging. However, the data must be transformed, if necessary, in order to satisfy the assumption of normality. It also requires additional decision-making throughout the variogram analysis during modeling. Both of these approaches should be generalizable to other animal functional groups and other systems. However, further analyses are necessary to validate whether or not these techniques are transferable to other ecological systems. The reliability of these techniques in this system with these bird species is robust, as suggested by the RMSE. This is likely due to these species being relatively abundant and relatively dispersed across the region, two factors important in producing reliable interpolations. Therefore, future monitoring of the species should provide for temporal analyses of habitat use. This is especially important considering the current rapid expansion of Phoenix into the surrounding desert.

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