Spatial distribution of Africanized honey bees in an urban landscape

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A B S T R A C T

Africanized honey bees overlap in resource use with humans in urban environments, creating concerns over public health and safety. We obtained data on Africanized honey bee colony removals from water meter boxes in the greater Tucson metropolitan area from 1996 to 2008 to identify characteristics associated with the spatial distribution of Africanized honey bees across the city. Two generalized linear models were constructed to predict the occupation of water meter boxes based on land use, lot/structure characteristics, and the presence of colonies in neighboring water meter boxes. More than 8000 colonies were removed from water meter boxes during the 12-year study period. Colonies were more likely to occupy water meter boxes associated with residential (versus commercial) locations, smaller lots, older structures, closer distances to vacant land, and higher percentages of neighboring water meter boxes with colonies. Occupied water meter boxes and boxes with multiple occupancies were concentrated in South Central Tucson, suggesting this area provides abundant resources for honey bees and that well-established, source colonies exist in this area. Locating and removing these source colonies may be the best approach for controlling the Africanized honey bee population in the greater Tucson metropolitan area and similar settings. Also, the regular removal of colonies from water meter boxes is important for the control of Africanized honey bees in the greater Tucson metropolitan area.

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1. Introduction

Urban areas often provide resources for wildlife and may be preferred habitat for some species. In the desert southwest, the availability of pollen, nectar, and nesting cavities may be limiting for honey bees in some areas, but urban areas may provide easier and more consistent access to these resources (Baum et al., 2008; Buchmann, 1996; Rabe et al., 2005; Stuart et al., 2006). Overlap in resource use places honey bees in close proximity to humans, prompting public health concerns in areas with Africanized honey bees (Schmidt and Boyer Hassen, 1996). Thus, research on feral honey bee colonies in urban environments is needed to develop strategies for minimizing human interactions with Africanized honey bees.

African honey bees (Apis mellifera scutellata) were introduced into Brazil in the 1950s (Winston, 1992). Matings between African honey bees and European honey bees produced hybrid Africanized honey bees, which rapidly spread through Central America and Mexico, reaching the United States in 1990 (Hunter et al., 1993; Rubink et al., 1996). Africanized honey bees were first recorded in Arizona in 1993 (Guzman-Novoa and Page, 1994; Loper, 1997), and the greater Tucson metropolitan area supports an abundant population (Baum et al., 2008). In areas with Africanized honey bees, the feral population is primarily Africanized (Harrison et al., 2006; Pinto et al., 2004, 2005; Rabe et al., 2005; Schneider et al., 2004).

Africanized honey bees differ from European honey bees by exhibiting stronger defensive behaviors and higher reproductive rates (Schneider et al., 2004; Winston, 1992; Winston et al., 1983). Colony sizes tend to be smaller and Africanized honey bees will use a wider variety of nest sites, including smaller nest cavities, such as water meter boxes (Schmidt and Hurley, 1995; Schneider et al., 2004; Winston, 1992; Winston et al., 1983). This combination of characteristics contributes to the high numbers of Africanized honey bee colonies in the greater Tucson metropolitan area (Baum et al., 2008) and poses unique challenges for controlling Africanized honey bees in urban areas.

We used a dataset of Africanized honey bee colony occupancy of water meter boxes to evaluate the influence of spatial variables on the distribution of Africanized honey bee colonies in the greater
Tucson metropolitan area. We developed logistic and Poisson models to identify factors that influence and predict the occupancy of water meter boxes by Africanized honey bee colonies. These data provide a unique perspective on the distribution of Africanized honey bees because water meter boxes form a network of similarly sized and located sites across the entire greater Tucson metropolitan area that are checked regularly (i.e., monthly) for the presence of colonies.

2. Methods

2.1. Study site and dataset

Tucson (32°08’N Latitude; 110°57’W Longitude) is located in Pima County in southeastern Arizona in the Sonoran Desert at an elevation of approximately 750 m above sea level, where average annual rainfall is 29.7 cm, average annual maximum temperature is 27 °C, and average annual minimum temperature is 12 °C. The area is characterized by flushes of nectar and pollen availability in the spring and late summer/fall (Dimmit, 2000; O’Neal and Waller, 1984). Urban landscaping and irrigation, however, likely extend these flowering periods in the greater Tucson metropolitan area. Sources of nest cavities are relatively uncommon in natural areas, with colonies frequently utilizing rock crevices (Loper et al., 2006; Taber, 1979), but man-made cavities, such as water meter boxes and openings in buildings, are abundant in the greater Tucson metropolitan area (Baum et al., 2008). The city of Tucson began recording the removal of Africanized honey bee colonies from water meter boxes in April 1996. Each time a water meter was checked for billing purposes, occupancy by Africanized honey bee colonies was recorded and colonies were flagged for removal. The resulting data cover a period from April 1996 to May 2008, where each record in the database consists of a date when a colony was found in a water meter box and the address of the location.

Because the database only provides information for where Africanized honey bee colonies were found (i.e., positive counts), we also obtained a large set of records from the Pima County Tax Assessor’s Office to acquire absence data (i.e., locations of water meters without Africanized honey bee colonies). These data allowed opportunities to be placed in the context of water meter box availability. We used the year a structure was built to deduce when a water meter box became available and was included in our dataset. Since a large majority of the water meter data matched a structure (i.e., parcel of land) described in the Tax Assessor’s dataset, and we assumed that any missing data were Missing Completely at Random (MCAR) (Little and Rubin, 2002), any bias caused by missing data appears to be minimal.

We converted the street address of each water meter to geographic coordinates (longitude and latitude) using a commercial GIS product (ArcGIS® v. 9.3). These points were then used with other GIS layers to quantify variables (Table 1) associated with each water meter. A parcel layer obtained from the Pima County Department of Transportation, Geographic Information Services Division, contained the size of each parcel. Parcels of land without structures (and thus no water meters) were removed from the dataset. Among commercial properties, only information on improved properties was available and included in our dataset. Data from the Pima County Tax Assessor’s Office was used to determine the construction date and presence of a swimming pool for each property represented by a water meter. The presence of a swimming pool represents a water source for honey bee colonies and the availability of water sources can influence cavity selection by honey bee colonies. We used the land use classification for urban and suburban areas developed by Shaw et al. (1998) to identify areas of Tucson as residential, commercial, recreational, natural, vacant, agricultural, transportation, and watercourses (Table 1, Fig. 1). We measured distance from each water meter box to the nearest edge of each land use type using ArcGIS® v. 9.3. We also calculated the percent occupancy of neighboring water meter boxes based on the typical foraging radius and swarm dispersal distance of honey bee colonies.

Table 1

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Variable description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent neighbors with colonies</td>
<td>2.46</td>
<td>2.47</td>
<td>The percent of neighboring water meter boxes within 0.8 km that had been occupied during the 12-year study period for each water meter box</td>
</tr>
<tr>
<td>Construction year</td>
<td>1976</td>
<td>18.73</td>
<td>The year the structure associated with a water meter box was built</td>
</tr>
<tr>
<td>Lot size (ha)</td>
<td>0.466</td>
<td>2.27</td>
<td>The land area of a parcel of land associated with a water meter box</td>
</tr>
<tr>
<td>Distance from “water” (km)</td>
<td>1.42</td>
<td>1.27</td>
<td>Distances calculated as the distance from the center of the lot associated with each water meter box to the nearest edge of the given land use type</td>
</tr>
<tr>
<td>Distance from recreational land (km)</td>
<td>3.73</td>
<td>3.74</td>
<td></td>
</tr>
<tr>
<td>Distance from natural land (km)</td>
<td>2.42</td>
<td>2.51</td>
<td></td>
</tr>
<tr>
<td>Distance from vacant land (km)</td>
<td>1.44</td>
<td>1.67</td>
<td></td>
</tr>
<tr>
<td>Distance from agricultural land (km)</td>
<td>10.92</td>
<td>6.90</td>
<td></td>
</tr>
<tr>
<td>Distance from transportation land (km)</td>
<td>1.36</td>
<td>1.70</td>
<td></td>
</tr>
<tr>
<td>Indicator of pool within 0.8 km</td>
<td>0.737</td>
<td>0.440</td>
<td>Indicator variable for a pool within 0.8 km (i.e., 1 indicates a pool is present and 0 indicates no pool is present). The mean is the percentage of water meter boxes with a pool within 0.8 km</td>
</tr>
<tr>
<td>Indicator of residential location</td>
<td>0.821</td>
<td>0.383</td>
<td>Indicator variable for residential location (i.e., 1 indicates a residential location and 0 indicates a nonresidential location). The mean is the percentage of water meter boxes that were in residential locations</td>
</tr>
</tbody>
</table>

Note: Most of the lots classified as water did not hold water for most of the year; some were washes which fill with water only during the monsoon season (Shaw et al., 1998).

2.2. Model building

We developed models that use landscape and lot/structure characteristics as explanatory variables to predict the occupancy of the water meter boxes. We used a logistic regression model to predict the presence or absence of Africanized honey bee colonies in water meter boxes over the 12-year study period based on the explanatory variables (Table 1). Of the 275,877 parcels, only 5640 water meter boxes had been occupied at least once during the 12-year study period, so occupancy rates were generally low. However, 1350 water meter boxes were occupied more than once during the study period. To model this behavior, a second model was developed that regressed the number of times a location was occupied against the explanatory variables.

Several assumptions were made when developing these models. First, the water meter dataset was complete. That is, colonies were removed only by the water company and removals were always recorded. We also assumed that for every month, if there was no record of a colony in a water meter box, then none were present. Secondly, some records showed the presence of Africanized honey bee colonies within two weeks of one another. Although the city usually checks water meters once a month for billing purposes, checks may be made more frequently in some cases. To address these irregularities, we selected 30 days as the time required for a new colony to become established (i.e., new workers emerging; Gerig and Imdorf, 1984). Records showing a colony in the same water meter box less than 30 days apart were assumed to be the same colony that had not yet been removed. Conversely, if the records were more than 30 days apart, we assumed there were two separate colonies (i.e., one colony was removed and replaced by another colony the next month). Third, although records contained the construction date for a building, it is possible that water meters were turned off (and therefore not checked) at times during the study period. Similarly, although water meters of new buildings were included in the sample from the year they were built onward, it is possible there were differences between the build date and the date the water meter became active (i.e., the owners of the property take residence). Finally, we assumed there was a linear relationship between the variables and the log odds of having a colony in a water meter box for the logistic regression model, and also a linear relationship between the log of the mean number of times a water meter box was occupied and the other variables for the Poisson regression model.

The logistic model \( \ln(\pi_s/(1-\pi_s)) = \sum_{j=1}^{k} \beta_j x_{sj} \) was used to model the presence or absence of a colony during the 12-year study period. The parameter \( \pi_s \) denotes the probability that a colony ever occupies location \( s \). The explanatory variables, \( x_1, \ldots, x_k \), include the year the structure corresponding to the water meter was built, whether or not a pool was present, lot size (ha), distance from each land use type (km), and the proportion of the locations within 0.8 km radius that were occupied by a colony at least once (Table 1). The \( \beta_j \) are the parameter values. For example, if \( x_2 \) denotes land area, a fitted positive parameter estimate \( \beta_2 \) would indicate that water meter boxes on larger parcels of land were predicted to have a higher probability of colony occupation. An indicator variable is a variable which takes on the value 1 when the item being
described is present and 0 when it is absent. For example, the indicator variable for swimming pools is 1 for those water meter boxes with a swimming pool within 0.8 km. The average of indicator variables is a percentage, and a positive parameter estimate indicates a higher probability of colony occupation when a swimming pool is nearby.

To explain the number of times a water meter box had been occupied during the 12-year study period, we used the Poisson model: \[ \ln(\mu_s) = \sum_{j=1}^{k} \hat{\beta}_j x_{js} \]. The mean, \( \mu_s \), denotes the expected number of times a colony occurred at location \( s \). The explanatory variables were defined as for the logistic model, while the parameter estimate \( \hat{\beta}_2 \) now has the interpretation for this model that larger parcels of land were predicted to have more colony occupations. Because of the high zero count of the data (i.e., there were many locations that never had colonies), we included an over-dispersion parameter that accounted for the mean and variance not being equal as they are in the usual Poisson model.

To find parameter estimates for both models, the default method of Iterative Reweighted Least Squares (Scales and Gersztenkorn, 1988) for generalized linear models was used. All calculations were done using R v. 2.9.2. After estimating the \( \beta \) parameters for the Poisson model, the final parameter to be estimated was the over-dispersion parameter, \( \phi \). When the mean and variance are equal, as is the case for the usual Poisson distribution, the over-dispersion parameter is equal to 1. When data are over-dispersed, \( \phi \) is greater than 1. To estimate \( \phi \), McCullagh and Nelder (1989) were followed:

\[ \hat{\phi} = \frac{1}{n-p} \sum_{s=1}^{n} \frac{(Y_s - \hat{\mu}_s)^2}{\hat{\mu}_s} \]

where \( n \) is the sample size, \( p \) is the number of variables, \( Y_s \) is the observed number of times a colony had been built at location \( s \), \( \hat{\mu}_s \) is \( \exp(\sum_{j=1}^{k} \hat{\beta}_j x_{js}) \), and \( x_{js} \) is the value of explanatory variable \( j \) corresponding to location \( s \).

Due to spatial correlations for water meter boxes close to one another, variances of parameter estimates derived under independence are likely not appropriate. For this reason, we used a block resampling technique to estimate variances of the parameters, \( \text{Var}(\hat{\beta}) \), as in Heagerty and Lumley (2000). \( P \)-values were then obtained from \( 2P(T > t_{obs}) \), where \( t_{obs} = (\hat{\beta}/\text{se}(\hat{\beta})) \), and \( \text{se}(\hat{\beta}) = \sqrt{\text{Var}(\hat{\beta})} \).

3. Results

On average, about 2.46% of the water meter boxes within 0.8 km of any water meter box were occupied by an Africanized honey bee colony (Table 1), and they tended to be concentrated in South Central Tucson (Fig. 2C). The mean year for housing construction was 1976, with the oldest house being built in 1875 and older houses tending to be clustered in South Central Tucson (Table 1, Fig. 2D). The average lot size was 0.466 ha (Table 1, Fig. 2A). Lot size tended to be largest and water meter box density lowest around the periph-

![Fig. 2. Spatial distribution of selected explanatory variables used in the models. The maps show, for every water meter box in the greater Tucson metropolitan area, the (A) lot size, (B) distance to vacant land, (C) percent neighbors with colonies, and (D) construction year.](image-url)
ery of the city (Figs. 2A and 3). Seventy-four percent of water meter boxes were within 0.8 km of a swimming pool and 82% were in residential locations (Table 1). Colonies were on average closest to transportation land (1.36 km), water (1.42 km), and vacant land (1.44 km), and farthest from agricultural land (10.92 km; Table 1). A total of 8211 colonies were removed from 5640 water meter boxes from April 1996 through May 2008 (Table 2). Eighty-seven percent of these removed colonies were from water meter boxes in residential areas, 6.2% from commercial/industrial/institutional areas, 3.1% from graded vacant land (Fig. 2B), and 2.6% from natural open areas (Table 2). On average, colonies had access to almost all the land use types in less than 3.73 km, except for agricultural land (Table 1).

The percentage of neighboring water meter boxes with colonies in the past 12 years was a significant predictor variable in both the logistic and Poisson models (Tables 3 and 4). The occupancy of a water meter box by a colony was a relatively rare event. However, the probability of a particular water meter box being occupied was significantly greater when neighboring water meter boxes (within 0.8 km) had been occupied. Construction year, lot size, distance from vacant land, and whether the location was classified as residential were also significant in both models. High occupancy probabilities were clustered in South Central Tucson and several isolated residential suburbs away from the city center (e.g., Rancho del Cerro, Tucson Estates; Fig. 4). High multiple occupancy probabilities were primarily clustered in South Central Tucson (Fig. 5). In both models, because of the large sample size, power was sufficient to detect important deviations from zero slope, and it is unlikely that a larger sample size would change our conclusions about model parameters.

Table 2
Number of Africanized honey bee colonies removed from water meter boxes, number of water meter boxes with colonies, number of water meter boxes available, and area for each land use type in the greater Tucson metropolitan area.

<table>
<thead>
<tr>
<th>Land use type</th>
<th># colonies removed</th>
<th># water meter boxes with colonies</th>
<th># water meter boxes available</th>
<th>Area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residential</td>
<td>7116</td>
<td>4860</td>
<td>165,040</td>
<td>38,761</td>
</tr>
<tr>
<td>Commercial and public facilities</td>
<td>510</td>
<td>330</td>
<td>11,744</td>
<td>5901</td>
</tr>
<tr>
<td>Recreation</td>
<td>29</td>
<td>22</td>
<td>2659</td>
<td>38,368</td>
</tr>
<tr>
<td>Watercourses and ponds</td>
<td>70</td>
<td>49</td>
<td>2329</td>
<td>5465</td>
</tr>
<tr>
<td>Natural open space</td>
<td>211</td>
<td>165</td>
<td>23,765</td>
<td>60,718</td>
</tr>
<tr>
<td>Graded vacant land</td>
<td>253</td>
<td>199</td>
<td>18,335</td>
<td>6806</td>
</tr>
<tr>
<td>Agricultural land</td>
<td>16</td>
<td>10</td>
<td>839</td>
<td>1449</td>
</tr>
<tr>
<td>Transportation</td>
<td>6</td>
<td>5</td>
<td>389</td>
<td>5122</td>
</tr>
</tbody>
</table>
Parameter estimates and corresponding two tailed $P$-values from the Poisson model to predict the number of Africanized honey bee colonies in a water meter box.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter estimates</th>
<th>Standard errors</th>
<th>$P$-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>31.71</td>
<td>5.69</td>
<td>$&lt;0.0001$*</td>
</tr>
<tr>
<td>Percent neighbors with colonies</td>
<td>23.43</td>
<td>3.34</td>
<td>$&lt;0.0001$*</td>
</tr>
<tr>
<td>Construction year</td>
<td>−0.018</td>
<td>0.003</td>
<td>$&lt;0.0001$*</td>
</tr>
<tr>
<td>Lot size [La(acre + 0.1)]</td>
<td>0.503</td>
<td>0.039</td>
<td>$&lt;0.0001$*</td>
</tr>
<tr>
<td>Distance from “water” (km)</td>
<td>2.529e−05</td>
<td>2.52e−05</td>
<td>0.316</td>
</tr>
<tr>
<td>Dist from recreational land (km)</td>
<td>4.816e−06</td>
<td>2.260e−05</td>
<td>0.831</td>
</tr>
<tr>
<td>Dist from natural land (km)</td>
<td>1.909e−05</td>
<td>1.686e−05</td>
<td>0.258</td>
</tr>
<tr>
<td>Dist from vacant land (km)</td>
<td>−1.329e−04</td>
<td>2.398e−05</td>
<td>$&lt;0.0001$*</td>
</tr>
<tr>
<td>Dist from agricultural land (km)</td>
<td>2.087e−06</td>
<td>7.540e−06</td>
<td>0.782</td>
</tr>
<tr>
<td>Dist from transportation land (km)</td>
<td>2.990e−05</td>
<td>2.065e−05</td>
<td>0.148</td>
</tr>
<tr>
<td>Indicator of pool within 0.8 km</td>
<td>0.054</td>
<td>0.082</td>
<td>0.508</td>
</tr>
<tr>
<td>Indicator of residential location</td>
<td>0.153</td>
<td>0.009</td>
<td>$&lt;0.0001$*</td>
</tr>
</tbody>
</table>

$^a$ Most of the lots classified as water did not hold water for most of the year; some were washes which fill with water only during the monsoon season (Shaw et al., 1998).

$^*$ Parameter values with a $P$-value $<0.05$.

4. Discussion

Several variables were identified by the models as contributing to the occupancy of water meter boxes by Africanized honey bee colonies, including residential location, lot size, construction year, distance from vacant land, and occupancy rates for neighboring water meter boxes (Tables 3 and 4). Residential location (i.e., the indicator variable for residential locations) and lot size were significant variables in both models (Tables 3 and 4). Each developed lot possessed a water meter, and lots in residential locations tended to be smaller than lots in commercial locations. Thus, residential location and lot size also provided a measure of water meter density (Figs. 2A and 3). All things being equal (i.e., an even distribution of colonies throughout the greater Tucson metropolitan area), areas with high water meter box density (i.e., smaller lots in residential areas) would be expected to have a lower number of colonies per water meter box than areas with low water meter box density (i.e., residential locations with high water meter box density). Distance from vacant land was another significant variable in the models and represented the age of the structure associated with each water meter (Tables 3 and 4). Thus, construction year likely provided a measure of structure condition and the availability of openings in buildings that could serve as nest sites. Older structures likely provided more resources (i.e., cavities) for honey bees than newer structures. Older structures tended to be located in South Central Tucson (Fig. 2D) and their water meter boxes were predicted to be occupied more often than those associated with newer structures (Figs. 4 and 5).

Distance from vacant land was the most important land use variable in the models (Tables 3 and 4). Vacant land was located in isolated areas throughout the greater Tucson metropolitan area (Figs. 1 and 2B). Therefore, the presence of Africanized honey bee colonies was associated with shorter distances from vacant land. The proportion of neighboring water meter boxes with colonies during the 12-year study was a strong positive predictor of the presence of a colony in a water meter box in both models (Tables 3 and 4, Fig. 2C), supporting the view that colonies tend to form aggregations and indicating the density of water meters. Colonies may be aggregated if swarms from an originating colony select nearby cavities, which may occur when cavities are abundant (Jaycox and Parise, 1980, 1981; Seeley and Morse, 1977). Water meter boxes are abundant, providing an ideal habitat to allow colonies to select nearby cavities if such a preference exists. The aggregation of nectar and pollen resources also may contribute to the aggregation of colonies. However, land use type was controlled for in the model, so aggregated resources cannot completely explain why the colonies were aggregated in the greater Tucson metropolitan area. Other factors also may have contributed to the presence of aggregations, such as swarms being attracted to existing colonies, increased mating efficiency, or increased colony defense (Baum et al., 2005;
Fig. 4. Spatial distribution of Africanized honey bee colony occupancy probabilities predicted by the logistic model. Brown/dark areas show parts of the greater Tucson metropolitan area predicted to have high occupancy rates based on the results of the logistic model. Yellow/light areas are predicted to have low occupancy rates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

McNally and Schneider, 1996; Oldroyd et al., 1995; Seeley et al., 1982). Perhaps the most plausible explanation is the presence of nearby, well established colonies in some other type of cavity, such as an opening in a building or a tree cavity, which was not checked monthly for the presence of an Africanized honey bee colony. These well established colonies would produce swarms regularly, and these swarms may colonize nearby water meter boxes.

The indicator variable for swimming pools was not significant for either model, suggesting sources of water were likely not limiting for honey bees in the greater Tucson metropolitan area (Tables 3 and 4). Distances to recreational, natural, agricultural, and transportation land also were not important predictors in the models. Recreational land was concentrated in large expanses outside the greater Tucson metropolitan area (e.g., Coronado National Forest, Saguaro National Park, Catalina State Park, Tucson Mountain County Park, etc.) and limited to smaller, isolated areas within the study area (Fig. 1). Distance from natural land was related to distance from the center of Tucson (i.e., natural land use types were more often located in the outskirts of the greater Tucson metropolitan area). Agricultural land (e.g., orchards, vineyards, cattle ranches, etc.) was uncommon and restricted to a few isolated areas around the outskirts of the study area (Fig. 1). Transportation land would not provide resources for honey bees and the associated noise and activity could be disruptive to Africanized honey bee colonies.

Africanized honey bee colony occupancies of water meter boxes were concentrated in South Central Tucson (Fig. 4), suggesting that either a denser population of honey bees occurred in this area or that more colonies were utilizing water meter boxes as cavities in this area (the opposite would be expected for areas with few colony occupancies). Because we do not expect cavities (i.e., water meters or other types of cavities) to be limiting in the greater Tucson metropolitan area, we assume the former explanation is more reasonable. Africanized honey bees use many different types of cavities in urban areas, including tree hollows, openings in buildings, trash cans, tires, and other spaces of adequate size (Baum et al., 2008). Water meter boxes in residential areas are, on average, the same size and shape (i.e., approx. 31.115 cm \( W \times 48.26 \text{ cm } L \times 20.32 \text{ cm } H \)) and are usually composed of concrete, although a few may be cast iron. Water meter boxes for large apartment complexes and commercial buildings may be larger to accommodate multiple water meters within the same box. If water meter boxes and other cavities are relatively constant in quality and colonies do not exhibit a preference for water meter boxes or other cavities, then based on a random-encounter model, we would expect water meter box occupancy to be positively related to the availability of water meter boxes relative to other types of cavities. Because we expect other urban sources of cavities to be relatively abundant throughout the greater Tucson metropolitan area (Baum et al., 2008), locations with higher occupancy rates likely represent areas with a denser population of Africanized honey bees. However, there are likely microclimatic differences among water meter boxes which could influence suitability for honey bee colonies, such as exposure to sunlight which could melt comb and cause honey bees to reject water meter boxes located in full sun.
Multiple occupancies of water meter boxes by Africanized honey bee colonies also were concentrated in South Central Tucson (Fig. 5). Honey bee colonies are likely to reuse cavities for several reasons. First, colonies likely use similar criteria to select cavities, so a cavity selected by one colony is also likely to be selected by other colonies when it is unoccupied. Second, colonies tend to form aggregations (Baum et al., 2005, 2008; McNally and Schneider, 1996; Oldroyd et al., 1995; Seeley et al., 1982; see discussion above). Lastly, colonies are attracted to and may even prefer previously occupied cavities (Seeley and Morse, 1978), which is why pest control companies usually fill cavities with foam after a colony is removed.

The interpretation of model results is constrained by potential challenges and sources of bias associated with the dataset. Explanatory variables were selected from existing spatial data layers and were not specifically designed to quantify ecologically important landscape characteristics, although these layers were selected because they are good approximations of landscape characteristics important to honey bees. For example, the age of a structure may be associated with structure condition and the availability of openings in buildings that could serve as nest sites for honey bee colonies. Although relationships exist between the quantities measured in the spatial data layers and factors of direct ecological relevance to honey bees, these relationships have not been quantified and the influence of these variables must be carefully interpreted.

The dataset also may possess patterns of socio-economic bias. For example, more affluent residential areas may provide more floral resources for bees, as perennial plant species richness typically increases with median family income (Martin et al., 2004). At the same time, the source population of Africanized honey bees (i.e., colonies located in other types of cavities that are not removed on a monthly basis) may be smaller in more affluent residential areas because residents may be more likely to request and pay for pest removal services (Baum et al., 2008). Some of this bias may be controlled for by lot size, as larger lots may be associated with larger median family incomes. Any bias is likely small compared to data collected from pest control companies, which are based on the ability/willingness of residents to pay for pest removal services (e.g., Baum et al., 2008).

A potential challenge is that water meters are not evenly spaced throughout the greater Tucson metropolitan area (i.e., water meter density ranges from approximately 0–179 per ha; Fig. 3), so sampling effort was variable throughout the study area. However, this issue was resolved by using the appropriate logistic and Poisson regression models that included both presence and absence data (i.e., when modeling occupancy of neighboring water meter boxes, we used the percent of neighbors that had been occupied rather than a count of the number of neighbors that had been occupied).

This extensive dataset provides a unique perspective on the ecology of Africanized honey bees in urban areas. The expanse of the dataset is large (i.e., 275,877 water meter boxes spread across the study area that were checked monthly for billing purposes) compared to the number of sampling locations and frequency of sampling that would be logistically possible with any experiment.
we could have designed to evaluate the distribution of Africanized honey bees across the greater Tucson metropolitan area. A common weakness of such large data sets is that models identify meaningless deviations in slope from zero as being significant. However, our models did not identify any multiplicative factors between 0.9 and 1.1 as being significant for the odds of occupancy in the logistic model or expected number of occupancies in the Poisson model.

The 12-year dataset highlights areas that were consistently high in Africanized honey bee colony occupancy, suggesting these areas are extremely attractive to Africanized honey bees (i.e., contain abundant nectar, pollen, and cavity resources) and/or that source colonies exist nearby. The areas of highest occupancy and highest multiple occupancy are located within South Central Tucson (Figs. 4 and 5). Thus, it is likely that resource availability is high in this area and that a source population of well established colonies exists in this area. Locating and removing these well established colonies may be the best approach for controlling the Africanized honey bee population in the greater Tucson metropolitan area and similar settings. Our dataset also emphasizes the importance of the monthly removal of colonies from water meter boxes for control of the Africanized honey bee population in the greater Tucson metropolitan area. Without access to water meters, Africanized honey bee colonies would nest in other locations where detection and removal would likely not occur on a monthly basis, which could lead to an increase in the size of the Africanized honey bee population.

An evaluation of honey bee colony removals from multiple sources (e.g., water companies, pest control companies, etc.) would provide additional insight into the ecology of Africanized honey bees in urban areas. Comparing different types of spatial data (e.g., lattice/grid data represented by water meter boxes, point data represented by removals by pest control companies, etc.) with different limitations/constraints would expand our understanding of how Africanized honey bees respond to spatial and temporal variability in the environment. Furthermore, a detailed analysis of cavity use in different land use types could lead to improved strategies for controlling Africanized honey bees in urban areas. This study also identifies and uses data from a nontraditional source to address an important issue in urban ecology, suggesting a new direction for future landscape level research in urban environments.

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