Distribution of exotic monk parakeets across an urban landscape

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Abstract Monk parakeets (Myiopsitta monachus) are the most abundant and widely distributed of the naturalized parrots in the United States. Their presence is simultaneously encouraged by some humans (through use of bird feeders) and discouraged by others (through removal of their nests) and, as a result, they show an interesting spatial distribution across urban areas. We used an online public survey and field surveys to examine the influence of human activities and land use on the distribution of this exotic species around Chicago, IL (USA). These efforts resulted in detection of 249 nesting structures and approximately 778 birds across the region. A CART analysis successfully separated nesting sites from random sites and correctly classified 90 % of the nesting sites. The most important factor in the model was land use, with nests typically found in areas with less than 84 % residential zoning. We found nests on a wide variety of substrates including trees, cell phone towers, and stadium lights. Spatial point pattern analysis indicated that nests in trees and nests in built substrates were significantly dissociated with each other at all scales. Nests on built substrates were closer to railroads and highways or in areas with lower human population density, suggesting either a difference in substrate availability or human tolerance between these settings. While humans may have a positive effect on distribution of monk parakeets at large spatial scales, at the scale of this study we see a potentially negative effect of too many humans on the distribution of monk parakeet nests.

Keywords Introduced species \cdot Habitat suitability \cdot Spatial analysis \cdot Citizen science \cdot Urban ecology \cdot Nest site selection

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Introduction

Investigating habitat relations of introduced species is a key aspect of understanding their distribution and predicting their spread (Peterson and Vieglais 2001; Thuiller et al. 2005). The distribution of exotic species is at least initially linked to human activity (by definition) but the extent to which this connection persists through time varies among species. For highly invasive species, the connection with humans may dissipate shortly after introduction into a novel environment (e.g., Argentine ants; Roura-Pascual et al. 2010). These species spread far beyond their original release locations and may become the focus of intensive control or eradication efforts. Conversely, other species are sought out or cultivated by humans but rarely spread far beyond their original release locations (Rejmánek and Richardson 1996; Van Kleunen et al. 2010). In these cases, such species maintain their spatial association with humans long after the initial introduction. Lastly, a subset of exotic species sustains a dual existence, simultaneously encouraged by some humans but discouraged or eradicated by others. These species may exhibit particularly interesting distribution patterns with respect to human activity.

As Warren (2007) so aptly stated, "One person's pest is often another's livelihood or joy." Monk parakeets (Myiopsitta monachus) provide an excellent example of such a species. These parrots, native to South America, are common birds in the pet trade (Spreyer and Bucher 1998). They established breeding populations in the United States in the late 1960s and early 1970s (Bull 1973; Freeland 1973; Owre 1973; Simpson and Ruiz 1974; Lever 1987) and are now widely distributed and common in many urban areas (Van Bael and Pruett-Jones 1996; Pruett-Jones and Tarvin 1998). In locations with cold climates, such as Chicago, monk parakeets are reliant upon bird feeders during the winter months (South and Pruett-Jones 2000). In turn, many Chicago residents gladly feed them in exchange for a cheerful glimpse of green feathers on a gray winter day (personal observation). The relationship with humans becomes more complex when considering that monk parakeets are reported to be an agricultural pest in their native range (Bump 1971; Bucher 1992). In the early 1970s, the United States Department of Agriculture (USDA) and the United States Fish and Wildlife Service (USFWS) instituted an ultimately unsuccessful control program for monk parakeets that removed 163 (44 %) of the known 367 birds from 30 different states (Neidermyer and Hickey 1977). More recently, monk parakeets have shown an affinity for nesting on electrical utility structures (Avery et al. 2002, 2006) and other built structures (Marcisz 2005). These nests are often removed by people because of the risk of electrical shorts or fires or because of the nuisance factor of loud parakeets nesting near homes and businesses. Therefore, humans may both positively and negatively impact the current distribution and future spread of monk parakeets.

Several coarse-scale studies have found introduced monk parakeet populations to be associated with high human population density (e.g., Munoz and Real 2006; Strubbe and Matthysen 2009), but nest site selection within an urban setting is less well-understood. In this study, we investigated habitat relations of monk parakeets in the Chicago region of northern Illinois. Our goals were to examine the influence of urban land use on habitat selection and nest construction by monk parakeets, and to understand the spatial relationship between humans, the built environment, and monk parakeets. Specifically, we looked at the spatial distribution of nests across the urban area and used classification and regression trees (CART models) to ask (1) which environmental factors explain the presence of monk parakeet nests, and (2) whether we can explain nesting substrate selection based on surrounding environmental factors.

Methods

Study area and focal species This study took place in and around Chicago, Illinois (USA), a metropolitan area that covers almost 600 km² and is home for approximately 8 million residents. The city borders Lake Michigan and is in the transition zone between eastern deciduous forests and the Midwestern prairies, although very little natural habitat remains in the city itself. Rural areas adjacent to Chicago are predominantly agricultural. Average July high temperature is 28.7 °C and average January low temperature is -10.6 °C (NOAA Earth System Research Laboratory).

Monk parakeets were first seen in the Chicago area in 1968, while the first successful breeding colony was established in the Hyde Park neighborhood in 1979 (Spreyer and Bucher 1998; Pruett-Jones et al. 2012). Over the last 30 years, the population of parakeets in this region has expanded in size and distribution (Pruett-Jones et al. 2012). While Chicago winters are cold compared to the birds' native range (where temperatures seldom fall below -13 °C; Bump 1971), monk parakeets have also established populations in similar climates elsewhere in the United States (e.g., Connecticut, New York, New Jersey). It is thought that their year-round use of nests and exploitation of bird feeders allow them to survive the winter months in cold climates (Spreyer and Bucher 1998; South and Pruett-Jones 2000).

Monk parakeets are highly social and may nest solitarily or in colonies; colonies may contain multiple individual and/or compound nests located in close proximity to one another (Spreyer and Bucher 1998). Because nests can either be single or compound, we adopt the terminology of Hyman and Pruett-Jones (1995) whereby a *nesting structure* is a stick structure that contains one or more chambers, an *active chamber* is an unobstructed cavity in a nesting structure that appears to be occupied by birds, and a *substrate* is the physical site where at least one nesting structure is built (tree, pole, etc.).

Nest locations Our goal was to locate all existing monk parakeet nests in the Chicago region. We started by creating a database of possible nest locations. Entries in this database came from two general sources: (1) a historic inventory created in the 1980s and maintained and updated through the years by Marcisz (2005) and two coauthors (SP-J and CA), and (2) a new set of nest observations submitted by Chicago residents and citizen scientists through a web site and online survey launched on 21-Sept-2009 with a press release through each coauthor's institution. The first nest observation was submitted shortly after the press release, and by October 21 of that year 269 nest observations had been submitted. At that point, we stopped adding any additional nests to our database and began to groundtruth the database entries.

Observers went to each location listed in the historic inventory or submitted through the online survey and looked for a nest. If a nest was found, the location was recorded with a GPS or on a paper map. Any nearby nests were also recorded. At each nest location, we recorded the substrate upon which the nest was built, distinguishing between nests that were located in trees ("tree substrates") and nests that were located in built structures ("built substrates"). We recorded the total number of nesting structures and active chambers on each nesting substrate. All confirmed nest observations were entered into a second database, which represented our best estimate of monk parakeet distribution in the Chicago region during the winter and spring of 2010.

To avoid pseudoreplication associated with analysis of adjacent nests, the study area was divided into 500 m×500 m grid cells. All grid cells that contained nests were considered to be suitable habitat and an equal number of non-habitat grid cells were randomly selected for comparison from within a minimum-convex polygon encompassing habitat cells. The non-

habitat cells were technically pseudo-absences since we did not actually confirm the absence of nests. However, we were confident that we identified nearly all nests in the region and thus the vast majority of these cells likely represent true absences. Among the grid cells that contained nests, we classified each cell as containing only tree substrates, only built substrates, or both. This subset of grid cells was used in a separate analysis to examine patterns of substrate selection by monk parakeets.

Environmental variables In each habitat and non-habitat grid cell, we measured a number of environmental variables using ArcGIS 9.3 (Table 1): percent of land zoned as residential, the percent of land in open green space (this included parks, cemeteries, and golf courses but excluded forest preserves, as monk parakeets have not been observed in forests across Chicago or elsewhere (e.g., Sol et al. 1997)), human population density, distance to railroad tracks, distance to the nearest body of water, distance to an interstate highway, and tree canopy cover. These variables have either been reported to be important in previous studies (Sol et al. 1997; Munoz and Real 2006; Strubbe and Matthysen 2009) or were expected to be important based on our personal observations of the nests.

Data analysis We first examined tree and built substrates to determine if they differed in terms of numbers of nesting structures or chambers. Mann-Whitney tests were used to evaluate statistical significance in SigmaPlot 11.0 (Systat Software 2008). We then examined locations of nests and substrates to test for spatial patterns in nest site selection. Ripley's K point-pattern analysis was used to test for clustering of nests and substrates across our study area and to assess the degree to which different nesting substrates (trees versus built substrates) were associated or disassociated with one another. Ripley's K can evaluate spatial point patterns across a range of scales for a single set of points (i.e., a univariate analysis) or for two different sets of points (i.e., a bivariate analysis). We began with a univariate Ripley's K analysis to look at overall pattern of

Environmental variable	Mean value (range)		Source
	Habitat	Non-habitat	
% land zoned as residential	45.5 (0-99)	50.9 (0-100)	CMAP land use dataset ^a
% land in open green space	18.9 (0-92)	11.6 (0–94)	CMAP land use dataset ^a
Human population density (people/ha)	30.4 (0–119)	33.7 (0–123)	TIGER census data ^b
Distance to railroad tracks ^c (m)	466.2 (55-1,890)	559.8 (84-2,249)	TIGER line shapefiles ^b
Distance to nearest body of water ^c (m)	1757.4 (76–6,665)	1377.0 (101–5,876)	National Hydrography Dataset ^d
Distance to nearest interstate highway ^c (m)	2001.1 (88–5,847)	1835.5 (115–6,333)	TIGER line shapefiles ^b
% canopy cover ^c	3.9 (0–20)	5.8 (0-64)	National Land Cover Dataset ^e

Table 1 Environmental variables measured in each grid cell

^a Chicago Metropolitan Agency for Planning (http://www.cmap.illinois.gov/)

^b United States Census Bureau (http://www.census.gov/geo/www/tiger/)

^c Distances and % canopy cover represent a mean value calculated over all 30 m pixels in each 500 m grid cell

^d United States Geological Survey National Hydrography Dataset (http://nhd.usgs.gov/)

e United States Geological Survey Land Cover Institute (http://www.mrlc.gov/)

all substrates. This test included 99 randomizations to compare locations of substrates to random points within the study area. We then used bivariate Ripley's K analysis to look at the associations (or disassociations) of the two substrate types with each other. These tests also used 99 randomizations, but this time randomizations were constrained by fixing points at existing substrate locations and permuting tree and built substrate labels. The Ripley's K statistic was transformed to Ripley's L statistic, which results in an expected value of zero when points are randomly distributed (Dale 1999). Values above zero indicate overdispersion in univariate tests and a negative association between two different sets of points in bivariate tests, while values below zero indicate a clustered pattern in univariate tests and a positive association in bivariate tests. We also used Moran's I to check for spatial autocorrelation among grid cells in number of substrates, number of nests, or number of chambers. Moran's I is used to estimate the strength of autocorrelation between observations as a function of the distance separating them. Random permutations of the data are used to determine whether the empirical pattern differs from random. Spatial patterns were analyzed in PASSaGE v2 (Rosenberg and Anderson 2011).

The next step was to use classification and regression trees, also known as CART models, to examine the grid cell data in two separate analyses: (1) a habitat suitability analysis and (2) a substrate analysis. The habitat suitability analysis compared habitat grid cells (i.e., containing one or more Monk parakeet nests) with an equal number of randomly-selected non-habitat grid cells. This allowed us to identify the environmental variables most strongly associated with the presence of monk parakeet nests. The substrate analysis included only habitat cells. We compared habitat cells with tree substrates to habitat cells with built substrates to determine which habitat factors were associated with each type of nesting substrate. Individual habitat cells containing both built and tree substrates were excluded from this particular analysis.

CART models can be used to distinguish habitat from non-habitat (or cells with tree substrates from cells with built substrates) by repeatedly splitting the data into progressively more homogeneous groups (called recursive partitioning); at each split in the tree, the process finds the variable that best distinguishes between groups. The recursive nature of the algorithm tends to produce models that are over-fitted to the data used to generate the model, limiting application to other datasets. For this reason, CART models are often simplified by "pruning" to yield a final model that attempts to balance accuracy with robustness to new data. We pruned our model by selecting the tree size that minimized the cross-validated error (using 10 cross-validation groups). CART analyses were performed in the R statistical package (v 2.8.1) using the contributed library Rpart.

Lastly, the output of the habitat suitability analysis was used to create a habitat map for our study area and beyond. We were constrained by the spatial extent of our datasets, so our habitat map extended 25 km beyond the observed nests but did not cross into Indiana, where we have observed nests, due to difficulties standardizing and comparing datasets from the two states. This map identified all grid cells on the landscape that met the criteria for "habitat" as identified by the CART model.

Results

Nest locations Overall, we confirmed the presence of 249 nesting structures on 169 unique nesting substrates (mean nesting structures/substrate=1.5, SD=1.04). These nesting structures contained a total of 389 nesting chambers (mean chambers/substrate=2.3, SD=2.0), suggesting 389 breeding pairs, or a minimum population of 778 birds spread across roughly 933 km² (Fig. 1). Ripley's K point-pattern analysis revealed that substrates, nests, and chambers were significantly clustered at all spatial scales up to 14 km



Fig. 1 Map of study site and monk parakeet nest substrates. In some cases, locations of nest substrates were shifted slightly to display multiple adjacent substrates

(substrates shown in Fig. 2a, nests and chambers not shown). However, there was no spatial autocorrelation (as indicated by Moran's I) among substrates in terms of numbers of nests or chambers per substrate (results not shown).

Monk parakeets used a variety of different substrates as nesting sites. Seventy-one substrates (42 %) were trees (supporting a total of 107 [43 %] nesting structures) and 98 [58 %] were built substrates (supporting a total of 142 [57 %] nesting structures) including railroad overpasses, telephone and light poles, satellite dishes, transmission towers, and structures associated with electrical substrations (Table 2). Tree and built substrates did not differ statistically in terms of mean numbers of nesting structures (Mann-Whitney U=3327.5, p=0.51) or chambers (Mann-Whitney U=3277.0, p=0.49).



Fig. 2 Spatial point pattern analysis (Ripley's K tests) of nest substrates. L(d) is the transformed K statistic for each distance class shown on the x-axis. *Dashed lines* are confidence intervals around expected pattern based on 99 randomizations. *Solid lines* show empirical data; data below confidence intervals indicate a clustered pattern (in univariate tests) or positive association (in bivariate tests), data above confidence intervals indicate overdispersion (univariate tests) or negative association (bivariate tests). **a** univariate test with all nest substrates combined; **b** bivariate test examining association of tree substrates with each other; **c** bivariate test examining association of tree and built substrates to each other

Holding the location of all nest substrates constant, bivariate Ripley's K tests revealed that tree substrates and built substrates were significantly disassociated with each other at all spatial scales up to 14 km, while tree substrates were associated with

Table 2 Nesting substrates used by monk parakeets
Substrate type
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Substrate type	Number of unique substrates with monk parakeet nests		
Metal tower (pylon)	50		
Deciduous tree	45		
Evergreen tree	26		
Light pole	24		
Wooden utility pole	12		
Satellite dish	3		
Elevated train tracks	3		
Power substation	2		
Water tower	2		
Smoke stack	1		
Bridge	1		

each other at scales up to 8 km and built substrates were only associated with each other at spatial scales beyond 5 km (Fig. 2).

Ninety-three of the grid cells contained one or more nesting structures. In these habitat cells, the number of unique nesting substrates ranged from 1 to 8, the number of nesting structures ranged from 1 to 17, and the number of active chambers ranged from 1 to 26. Among these cells, there was no spatial autocorrelation in number of substrates, number of nests, or number of chambers (i.e., Moran's I was not significantly different from zero for any distance class; data not shown). Of the 93 grid cells containing nests, 58 (62 %) contained only built substrates, 29 (31 %) contained only tree substrates, and six cells (6 %) contained both built and tree substrates.

CART analysis The CART analysis identified five variables that distinguished habitat cells from non-habitat cells (Fig. 3). Variance inflation factors were <1.8 for all variables (mean=1.33), indicating a lack of multicollinearity. In a classification tree, the first division at the top of the tree shows the variable that can best distinguish among the groups. Variables that occur successively lower in the tree explain a smaller portion of the variation in the dataset. The tree is plotted according to a set of rules in which each branch is keyed by a condition (e.g., residential zoning <84 %); the "true" reaction to this condition is graphed to the left while the "false" reaction goes to the right.

Our habitat suitability model indicated that residential zoning was the most important variable separating habitat cells from non-habitat cells. All cells with greater than or equal to 84 % cover of residential zoning were classified as non-habitat, although four of those cells in fact contained nests (i.e., were misclassified). Distance to water,



Fig. 3 Classification tree for monk parakeet nesting habitat. Ovals indicate model classification of grid cells as suitable nesting habitat ("NEST") or unsuitable nesting habitat ("NO NEST") and the number of actual cells that contained nests (first number) or did not (second number)

amount of green space, distance to highway, and distance to railroad were also important variables separating habitat cells from non-habitat cells. Nests were found in cells that were farther from water and highways, closer to railroads, and with a higher proportion of open green space than randomly selected cells. The overall classification rate of the habitat suitability model (i.e., % of correct classifications) was 74 % and the number of correctly classified habitat cells was 84 (90 %). Misclassified habitat cells did not differ statistically from correctly classified cells in any of our measured variables nor did they differ in terms of number of substrates, number of nests, or number of chambers (Mann-Whitney Test p>0.05 for all tests). There was no apparent spatial pattern in misclassified habitat cells, although most of them were in the southern portion of the study area.

The substrate model, which examined differences in habitat surrounding built and tree substrates, showed that built substrates tended to be in areas that were either relatively close to a railroad or highway or had a low human population density (Fig. 4). The overall classification rate of the substrate model was 80 %. Cells with tree substrates were misclassified 31 % of the time while cells with built substrates were misclassified only 14 % of the time.

We used the output from our habitat suitability model to create a map of monk parakeet habitat for the entire study area (Fig. 1). This map showed that 1,766 km², or 49 % of the study area, meets the criteria for suitable habitat. Habitat is fairly continuous inside the city but becomes more sparsely distributed and patchy toward the edges of the study area, particularly toward the north. Monk parakeet nests currently occupy only 1.3 % of the apparently suitable habitat on the landscape.



Fig. 4 Classification tree for tree and built substrates. Ovals indicate model classification of grid cells as suitable for built substrates ("BUILT") or tree substrates ("TREE") and the number of actual cells that contained built substrates (first number) and tree substrates (second number)

Discussion

From the earliest establishment of monk parakeets in the United States, nests have most often been observed in urban and suburban areas. In the first known survey of monk parakeets, associated with the removal effort of the Fish and Wildlife Service, 77 % of 367 observations were in urban-suburban areas (Neidermyer and Hickey 1977). More recently, Munoz and Real (2006) found that human activity explained 63.8 % of the variation in monk parakeet distribution across Spain. Another recent study found that establishment success of monk parakeets across Europe was positively associated with human population density (Strubbe and Matthysen 2009). It is difficult to know whether this pattern is due to an inherent preference for urban areas or simply a function of propagule pressure (i.e., numbers of escapees or intentionally released birds), which is likely to be much greater in urban areas. Recent genetic evidence from two introduced populations—one in Florida, the other in Connecticut—indicates that propagule pressure may indeed be high in some locations (Goncalves da Silva et al. 2010). In its native range, monk parakeets are also very common near human habitation (Forshaw 1989).

Within cities, birds show preferences for certain habitat types. In Barcelona, monk parakeets were found near parks and in areas with more palm trees, their preferred nesting substrate (Sol et al. 1997). Palm trees do not occur in Chicago but we expect that several other factors might affect nest distribution in our study population. First, proximity to foraging areas may be important. Monk parakeets have a diverse diet (Spreyer and Bucher 1998; South and Pruett-Jones 2000) but are thought to rely on bird feeders in the Chicago winter and thus may be limited by the distribution of feeders. In our study, human population density and residential zoning are proxies for bird feeders, green space may represent foraging sites, and railroad tracks may also provide foraging opportunities in the form of spilled grain from train cars. Second, monk parakeets require a suitable substrate to support their frequently large and heavy nests. While canopy cover provides a measure of tree substrate availability, we were unable to measure the availability of built substrates in the study area. However, the association of nests with railroad rights-of-way may suggest that these rights-of-way contain a large number of suitable built structures. A third factor is whether a given nest persists over time. Because nests are often removed by humans, nests in heavily populated areas may be less likely to persist than nests in less populated areas.

At the scale at which this study was conducted, the third factor may play a large role in determining nest locations. If the proportion of households with bird feeders is similar to numbers observed in England (~40-50 %; Gaston et al. 2007; Davies et al. 2009) and elsewhere in the Midwestern United States (~66 %; Lepczyk et al. 2004), bird feeders are likely to be abundant and widely distributed across the metropolitan area. Monk parakeets have been known to forage up to 24 km from their nest site during the non-breeding season (Spreyer and Bucher 1998), making them more unlikely to be limited by proximity to bird feeders in this region. Given the diversity of nest substrates we have observed (trees, light poles, telephone poles, cell phone towers, buildings, etc.), nest substrates are also unlikely to be limiting to monk parakeet distribution. Furthermore, canopy cover was not identified as an important variable in the CART model. However, we know of many occurrences of nests being removed by home owners, utility companies, and businesses. This may explain why, in our study area, nesting substrates were rarely found in areas with greater than 83 % residential cover. Therefore, while humans appear to have a positive effect on distribution of monk parakeets at large spatial scales, at the scale of this study we see a potentially negative effect of too many humans on the distribution of monk parakeet nests.

Despite large, continuous patches of potentially suitable habitat across the study area (Fig. 1), nesting substrates were clustered at all spatial scales. This is not surprising for a species known to be a colonial breeder (Eberhard 1998; Burger and Gochfeld 2005). What is more surprising is the spatial disassociation between built and tree substrates (Fig. 2d). The CART model showed that built substrates were found in areas that were closer to railroad tracks or highways or in areas with lower human population density (Fig. 4). In fact, a few monk parakeet nests are built directly under the elevated train tracks associated with Chicago public transit (Table 2). These results may reflect a difference in available substrates between these settings or, conversely, a difference in human tolerance to nests on built structures. Either way, the result would be a separation of built substrates from tree substrates. We found that built substrates were associated with each other at larger spatial scales and tree substrates were associated with each other at smaller spatial scales, suggesting that these substrates are used in large and small "patches," respectively. Without a detailed map of possible nesting substrates, it is difficult to do more than speculate about these patterns. However, it is important to keep in mind that nests on built substrates are more likely to be torn down. This means that many nests have probably been torn down over the years and cells that currently contain only tree substrates may have also contained built substrates at one time. This could explain why tree cells are misclassified as built cells proportionally more often than vice versa; the misclassified cells may be locations where nests on built substrates have been removed in the past. Nest removal might also explain why cooccurrence of tree and built substrates was uncommon.

Slightly more than half (58 %) of the nests in our study were constructed on built substrates. A previous study in our area (Marcisz 2005) also found a large number of monk parakeet nests on built substrates, particularly cell towers, although that study was admittedly focused on surveying towers for nests. Nevertheless, both the survey by Marcisz (2005) and our study clearly show the common use if not preference of monk parakeets for placing nests on built structures.

Our results are not dissimilar from those of Burger and Gochfeld (2009), who examined 51 nest structures in New Jersey and found that 45 % of them were on built structures. Monk parakeets also use built substrates in Mexico (MacGregor-Fors et al. 2011) and South America (Bucher and Martin 1987), although apparently not to the same extent as they do in the United States. Forshaw (1989) reports that monk parakeets are a nest-site generalist in their native range. However, in both Barcelona, Spain (Sol et al. 1997) and south Florida, USA (Burger and Gochfeld 2000), monk parakeets appear to be nest-site specialists, preferring either punk trees (*Melaleuca quinquenervia*) in Florida or palm trees in both locations. Our data and general impressions are more in line with the conclusions of Forshaw (1989) that the species is a nest-site generalist. Even among trees, substrates included a diversity of deciduous (n=45 substrates) and evergreen (n=26) trees (Table 2).

The overall accuracy of our habitat suitability model, including classification of both habitat and non-habitat grid cells, was 74 %. However, we were able to correctly classify 90 % of the observed habitat cells. This means we had a higher rate of commission error (false positives) than omission error (false negatives), more frequently predicting species to occur where they did not (Fielding and Bell 1997; Guisan and Zimmermann 2000). These commission errors may occur for several reasons: (1) we excluded relevant variables from our habitat model, (2) "non-habitat" cells contained suitable habitat but monk parakeets have not colonized them yet, (3) "non-habitat" cells contained suitable habitat but monk parakeet nests have been removed from them, (4) "non-habitat" cells contained suitable habitat and monk parakeet nests were in fact present but we did not observe them. Reasons '2' and '3' above seem more likely to us. Although we know we missed a few parakeet nests in our

survey, we are confident that we did not miss so many as to bias the results of the CART model. It is also possible that monk parakeets are responding to finer-scale variables (such as specific plant resources) that we did not measure. Regardless, in the case of exotic species with expanding distributions, only omission errors are considered serious flaws (Guisan and Thuiller 2005).

Our map indicates that monk parakeets currently occupy less than 2 % of the apparently available habitat in the area. Fifteen years ago, monk parakeets occupied only a small fraction of the sites they currently occupy in the Chicago region (Pruett-Jones et al. 2012). We predict a continuing expansion of the population and of the geographical range of nesting sites over the next decade or two. Although there is continuing concern that monk parakeets will become an agricultural pest, as yet the parakeets do not occur in agricultural areas in northern Illinois. It is possible that the lower density of humans (and backyard bird feeders) in rural areas outside Chicago will slow or limit the range expansion of the species. On the other hand, the parakeets could nest in areas with higher human densities and then forage in neighboring agricultural areas. Nonetheless, we predict that humans will continue to have a strong influence on both the location and substrate selection of nesting monk parakeets for many years to come.

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