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The coexistence of Fox (*Sciurus niger*) and gray (*S. caroliniensis*) squirrels in the Chicago metropolitan area

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Abstract. Two species of tree squirrel inhabit the Chicago region, the fox (*Sciurus niger*) and gray (*S. caroliniensis*) squirrel. Chicago residents submitted squirrel observations and associated landscape variables via a Website, allowing us to map squirrel distributions. Data were analyzed for patterns of correlation. At a smaller scale, we did a foot survey of fox and gray squirrels in the suburb of Oak Park, replicating an earlier study and comparing results. Gray squirrels were associated with densely populated areas, parks and campuses, fox squirrels with suburban areas. Compared to gray squirrels, fox squirrels were more likely to be observed in areas of high cat density. In the suburb of Oak Park, the current trend seems to be an extension of gray squirrel distribution and a decrease in fox squirrel distribution. Our study provides support for the idea that fox and gray squirrel coexistence is facilitated by a trade-off between managing the cost of predation and foraging efficiency, gray squirrels out-competing fox squirrels in areas of high food and low predator (or pet) density.

Keywords: fox squirrel, gray squirrel, *Sciurus*, urban ecology, Chicago Metropolitan Area, coexistence

Introduction

An argument can be made that every organism on our planet lives in the shadow of human activity (witness global climate change). Nowhere is this human impact more evident than in our densely populated metropolitan areas. Worldwide urbanization is increasing at a rapid pace, and increasingly, people use shrinking pockets of conserved and managed land within urban boundaries for outdoor recreation and an opportunity to watch and experience wildlife (Botkin and Beveridge, 1997). In North America, squirrels, rabbits, deer, opossums, raccoons, pigeons and crows represent only a portion of the larger and more noticeable animals that are maintaining thriving populations in urban habitats. For many of these, large numbers of dogs, cats and sometimes humans, represent formidable predators, together with coyotes, hawks and owls. Also prevalent, if not quite as obvious, are the myriads of smaller birds, mammals and invertebrates that live side by side with humans in urban centers. The urban landscape is complex, both on a global and local scale.

How does urban wildlife respond to this varied landscape, and what are the factors that influence the distribution and dynamics of urban populations? A good starting point for answering these questions is to record distribution patterns of the common and easily observed species. Such distribution patterns, and the factors that correlate with them, may suggest important mechanisms that regulate the population dynamics of urban wildlife. Distribution patterns can then suggest the experiments and observations that will be most profitable in furthering our understanding of the processes responsible for observed patterns.

The size of metropolitan areas makes it daunting for a small number of observers to record distribution patterns in an acceptable time frame. However, an interested public can be a valuable resource available to researchers. Wildlife projects that actively involve the public provide an excellent opportunity to instill a sense of public stewardship and awareness in those that participate. This is especially true for wildlife that is active during daytime, colorful or attractive (e.g. birds and butterflies), or that display interesting and easily observed behavior. Squirrels have these qualities and we made use of the Internet to gather squirrel observations from an interested public. Tree squirrels are in many ways ideal candidates for an investigation into urban wildlife distribution patterns. They are both abundant and diurnal, which make them easy to observe. They also display a wide range of behaviors that tend to attract the interest of people. Squirrels are abundant in many urban settings, and human interaction is frequent. Regardless of whether they annoy (by raiding bird feeders and/or damaging plants or structures), or entertain, they are hard to ignore and are part of the public's daily experience. A Website at http://squirrel.bios.uic.edu/ invited people to submit observations of fox (*Sciurus niger*) and gray (*S. caroliniensis*) squirrels (and associated variables of interest) from their own neighborhoods, resulting in hundreds of observations and comments. From the comments it seemed that everyone had a strong opinion, whether positive or negative, about the squirrels in their neighborhoods.

Fox and gray squirrel distributions are interesting from several different perspectives. Squirrels are some of the most conspicuous and abundant of the larger animals that make up the wildlife component in North American towns and cities. Despite occurring in urban parks, campuses and residential areas, fox and gray squirrels must conform to all of the standard processes of population ecology within these habitats. Fox and gray squirrel populations seem to increase and decrease over time, sometimes one species being replaced by the other (e.g. Sexton, 1990), but the extent and manner to which urban changes are responsible for this are not well understood. The two species are ecologically very similar and eat the same types of food and use the same types of shelter (Steele and Koprowski, 2001). They often co-occur in their distribution area, though in their natural habitat gray squirrels are more often associated with densely wooded areas and fox squirrels with more open areas with scattered trees and forest edges. Given their ecological similarity, the mechanism by which these two species share habitats is of great ecological interest (Lanham, 1998). Understanding the coexistence of close competitors remains an inspiration for testing theories of diversity maintenance.

In this study, we ask the following questions: (1) Do fox and gray squirrel distributions in Chicago correlate with tree species, pet (or predator) density, type of land use, or geographic and socio-demographic parameters (e.g. population density or average income)? (2) How do fox and gray squirrel distributions compare at different spatial scales: at the scale of zip codes and variables associated with zip codes in the Chicago Metropolitan Area, at the scale of all the observation sites and variables associated with the observations, or at the scale of a single town (we focused on Oak Park, one of the suburban villages in the Chicago area)? (3) If tree squirrel distribution patterns correlate with any of the variables, does it suggest any hypotheses that may help explain the presence or absence of fox and gray squirrels? (4) How are urban distribution patterns related to the patterns found under natural conditions? (5) Do the distribution patterns suggest anything about possible trade-offs that allow the two species to coexist?

Methods

Study area and study animals

The Chicago Metropolitan area (9557 km^2) includes the Cook (2449 km^2), DuPage (866 km^2), Kane (1348 km^2), Lake (1159 km^2), McHenry (1564 km^2), and Will (2168 km^2) counties (Iverson and Cook, 2000) and is situated in northeastern Illinois next to Lake Michigan. It consists of a mostly flat landscape, and lies at an elevation of about 176 m above sea level. The population count for the city of Chicago during the 2002 census was 2, 886, 251, but its metropolitan area has a population of about 8.2 million people (68% of the population of Illinois and the third largest metropolitan population in the United States) (source: Chicago Fact Book at http://www.cityofchicago.org). Seasons are pronounced, with cold winters and hot and humid summers. January, the coldest month, has an average daily temperature of $-5.5^{\circ}C$ and July, the hottest month, an average daily temperature of $23.3^{\circ}C$. Rain falls throughout the year and averages 897 mm per year. Snow occurs from October to May and averages 970 mm (source: National Climatic Data Center at http://www.ncdc.noaa.gov). Natural vegetation for the area were prairie communities interspersed with deciduous forest communities, which were found mostly along rivers and in sheltered areas. Most of the landscape surrounding the urban areas has been converted to farmland. Within urban areas, forest preserves and parks are common, especially along rivers and streams.

The village of Oak Park, just west of Chicago, was chosen for a more localized and in-depth survey of fox and gray squirrels. Oak Park was chosen for the following reasons: (1) an earlier study (Lanham, 1998) used foot patrols to survey squirrel distribution in Oak Park and provides a valuable reference point against which we can compare our own observations, (2) both fox and gray squirrels occur in Oak Park, and since yards are relatively small, they are easily observed during foot patrols.

Oak Park covers an area of 12.17 km^2 and includes three zip codes (60301, 60302 and 60304). Single-family houses dominate, but multifamily-dwellings are present, especially along larger and busier streets. The 60301 zip code (an area of 0.15 sq miles) covers the main business area where there is a concentration of commercial establishments. The 2000 census gives the population for Oak Park as 52 524 (source: U.S. Census Bureau at http://www.census.gov). Oak Park is divided into a grid by its streets and is thus easily demarcated into blocks for survey purposes. Common tree species include elm and maple and to a lesser degree ash and oak (Lanham, 1998).

Both fox and gray squirrels are common throughout most parts of the Chicago Metropolitan Area. Gray squirrels can be distinguished from fox squirrels by their smaller size (c.

340–750 g, compared to c. 500–1000 g for fox squirrels), their color (ranging from gray to black, compared to orange or brown) and their white-fringed, as opposed to black-fringed, tails. In their natural habitat gray squirrels prefer mature hardwood forests with significant undergrowth. Fox squirrels prefer less dense forests and forest edges with sparse undergrowth and open areas (Steele and Koprowski, 2001). Both species feed on nuts, insects, fungi, fruit, and vegetation (buds, flowers and bark) (Smith and Follmer, 1976; Korschgen, 1981) and both species scatter-hoard acorns and nuts, especially during fall, throughout their home ranges. They experience pronounced periods of plenty (peaking in spring and fall) followed by periods of scarcity (winter and summer) (Montgomery *et al.*, 1975; Steele and Koprowski, 2001) on the order of weeks or months. Winter is a difficult time for squirrels. The added cost of thermoregulation in colder temperatures and scarcity of food make foraging an energetically expensive activity (Steele and Koprowski, 2001). Tree squirrels do not hibernate and need to forage throughout winter when they also rely heavily on their hoards and bodily fat reserves (Husband, 1976; Havera and Nixon, 1980; Thompson and Thompsen, 1980; Korschen, 1981). Summer is another difficult time for squirrels, since the new growth of spring is over and caches are depleted.

Data collection

Residents from the Chicago metropolitan area submitted fox and gray squirrel observations via our Website, titled “Project Squirrel”, at http://squirrel.bios.uic.edu/. People were made aware of the Website via local newspapers and word of mouth. The site briefly introduced the main objectives of the project, namely quantifying fox and gray squirrel distribution through the Chicago metropolitan area, followed by descriptions of the two species for identification purposes. To maintain independence of observations, we included a description of what should be considered different observation sites, e.g. squirrels observed from a neighbor’s yard should be included with those observed from one’s own yard, but squirrels observed a block away should be considered as a separate observation. A link to the data submission form concluded the introduction to the project. The data submission form recorded the date of the submission, the zip code where the observation took place, the numbers of fox and gray squirrels observed, and several basic environmental variables of interest. The basic environmental variables we wanted the public to include with their observations were land use type, presence or absence of common tree species, and the abundance of dogs and cats in the local area. There was also an area where additional comments could be included.

We differentiated between the following land use types: (1) single family house or duplex, (2) multiple family dwelling, (3) high-rise building, (4) local park, (5) forest or nature preserve, (6) zoo, arboretum or botanical garden, (7) commercial establishment, (8) school, college or university campus, (9) vacant lot, (10) cemetery and (11) farmland. We asked people to indicate the presence of common tree species in the Chicago area. The tree species were (1) elm, (2) hickory, (3) maple, (4) oak, (5) pine and (6) walnut. For each species, the options were (1) present, (2) absent or (3) unsure. Finally we asked people to indicate dog abundance and cat abundance in the area. Options were (1) none, (2) low abundance, (3) medium abundance and (4) high abundance.

All submissions used in this study were received between November 1999 and November 2002. For inclusion in the analyses, we only considered zip codes for which we received at least three independent observations. The following zip code variables were included for analysis: (1) median household income, (2) population density, (3) housing density and (4) median age of population. All data are from the census of 2000 (source: U.S. Census Bureau at http://www.census.gov).

For the squirrel census in Oak Park, we replicated the methods used by Lanham (1998) who conducted five surveys across different seasons between October 1996 and January 1998. Oak Park was divided into 18 rectangular blocks that were delineated by major streets. For each rectangular area we conducted a one-morning foot census that consisted of an observer walking up and down streets and alleyways and recording all squirrel, dog and cat sightings. Surveys were conducted from 13 June 2002 through 15 July 2002, corresponding to a time frame when most of Lanham's (1998) observations were made. Surveys started at 6:30 a.m. and lasted for approximately one hour (this is not necessarily the best time of day for squirrel observations, but conformed to the methods of Lanham 1998). To reduce observer bias, the same observer (MvdM) did all the observation counts.

Data analysis

Public submissions of squirrel observations were screened for duplications, missing data etc. For each zip code, fox and gray squirrel observations were summed, expressed as a percentage and then scored, where 1 = 0% gray squirrels, 2 = 1–25% gray squirrels, 3 = 26–50% gray squirrels, 4 = 51–75% squirrels, 5 = 76–99% gray squirrels and 6 = 100% gray squirrels. Each zip code score was assigned a color and then mapped onto a map of the Chicago Metropolitan Area with the mapping software Microsoft® MapPoint 2002, providing a visual representation of squirrel distributions at our study's largest spatial scale.

We did a regression analysis for the percentage gray squirrels in each zip code against the variables median household income, population density, housing density and median age of population, using the software package SYSTAT (version 10). In order to test for a potentially nonrandom spread of data points we divided observations into 4 categories: (1) a category of high percentage gray squirrels and high focal variable values, (2) a category of high percentage gray squirrels and low focal variable values, (3) a category of low percentage gray squirrels and high focal variable values and (4) a category of low percentage gray squirrels and low focal variable values. Median values were used to distinguish between "high" (above the median) and "low" (below the median) values. Tables of observed vs. expected results (i.e. contingency tables) were then tested with Chi-squared tests for deviations from the null distribution.

Using the observations submitted by the public, we looked for potential relationships of individual observations with land use, tree species and level of cat and dog presence in the immediate area of observation. For this, we constructed tables with the following categories: (1) only gray squirrels observed, (2) only fox squirrels observed and (3) both fox and gray squirrels observed. Only categories for which at least 10 observations were available were included. The number of observations in each category for each of the variable states was then tested with a Chi-squared test to determine whether observed results differed significantly from the expected results.

Percentages of gray squirrels for each delineated rectangular area from the Oak Park squirrel census were represented in pie charts and then superimposed on a map of Oak Park, providing a visual representation of the squirrel distribution at the smallest scale of our study. We did this for both our own census data and the census data from Lanham (1998) for the purpose of comparison.

Results

We received a total of 979 questionnaires (excluding submissions that could not be used due to missing squirrel observation data, repeated submissions etc.) from the public. From this total, 672 observations represented the 114 zip codes for which at least three submissions were received, and these were used to make the distribution map (figure 1) and for data analysis (Tables 1 and 2). The distribution map for the Chicago Metropolitan area showed a trend of gray squirrels dominating in the northern and southern suburbs, the city of Chicago, and the suburbs directly bordering Lake Michigan. Fox squirrels were more likely to be observed in the western and especially southwestern suburbs. There were 27 zip codes where only gray squirrels were recorded, compared to only two zip codes where only fox squirrels were recorded (60104 in the village of Bellwood and 60402 in the village of

Figure 1. Gray and fox squirrel distributions for the Chicago Metropolitan Area. For each zip code, the total number of gray squirrel observations was expressed as a percentage of the total number of gray and fox squirrel observations. Each zip code was assigned a score, where 1 = 0% gray squirrels, 2 = 1–25% gray squirrels, 3 = 26–50% gray squirrels, 4 = 51–75% squirrels, 5 = 76–99% gray squirrels and 6 = 100% gray squirrels.

Table 1. Observed and expected numbers of observations where (1) more than 50% gray squirrels were recorded and (2) less than 50% gray squirrels were recorded for the variables median household income, population density, housing density and median age of population

	Gray squirrels low		Gray squirrels high	
	Observed	Expected	Observed	Expected
Income[a]				
Low	24	23.2	83	83.5
High	1	1.8	6	5.5
Population density[b]				
Low	25	21.7	74	77.3
High	0	3.3	15	11.7
Household density[c]				
Low	25	23.2	81	82.8
High	0	1.8	8	6.2
Median age[d]				
Low	7	7.5	27	26.5
High	18	17.5	62	62.5

[a]The X^2 value for median household income is 0.25 (1 degree of freedom and $p > 0.05$).
[b]The X^2 value for population density is 4.85 (1 degree of freedom and $p < 0.05$).
[c]The X^2 value for household density is 2.42 (1 degree of freedom and $p > 0.05$).
[d]The X^2 value for median age of population is 0.05 (1 degree of freedom and $p > 0.05$).

Berwyn). There were 85 zip codes for which both fox and gray squirrels were recorded. A regression analysis of the dependent variable (percentage gray squirrels in each zip code) with the independent geographic and demographic variables (median household income, population density, housing density and median age of population) chosen from the Census 2000 Website did not yield any significant correlations.

Table 1 shows observed and expected numbers of observations for the high/low geographic and demographic zip code variable categories for two categories of squirrel data: (1) where more than 50% gray squirrels were recorded and (2) where less than 50% gray squirrels were recorded. A smaller number of low gray squirrel percentages than expected were observed for high population density areas ($X^2 = 4.85$, 1 degree of freedom and $p < 0.05$). In none of the other categories did the number of observations deviate from an expected null distribution.

Table 2 shows the contingency tables for the land use, tree species and pet variable data that were submitted with the Internet questionnaires. Not all submissions recorded all the variable classes, and only those for which data were submitted were included for analysis. In addition, only those variables for which at least 10 observations were submitted were included. Compared to an expected null distribution, fox squirrels were more likely to be observed in areas with single family residences and parks, whereas gray squirrels were likely to be found on campuses, areas with multiple family dwellings and high-rises ($X^2 = 75.5$, 10 degrees of freedom and $p < 0.001$). Gray squirrels were associated more

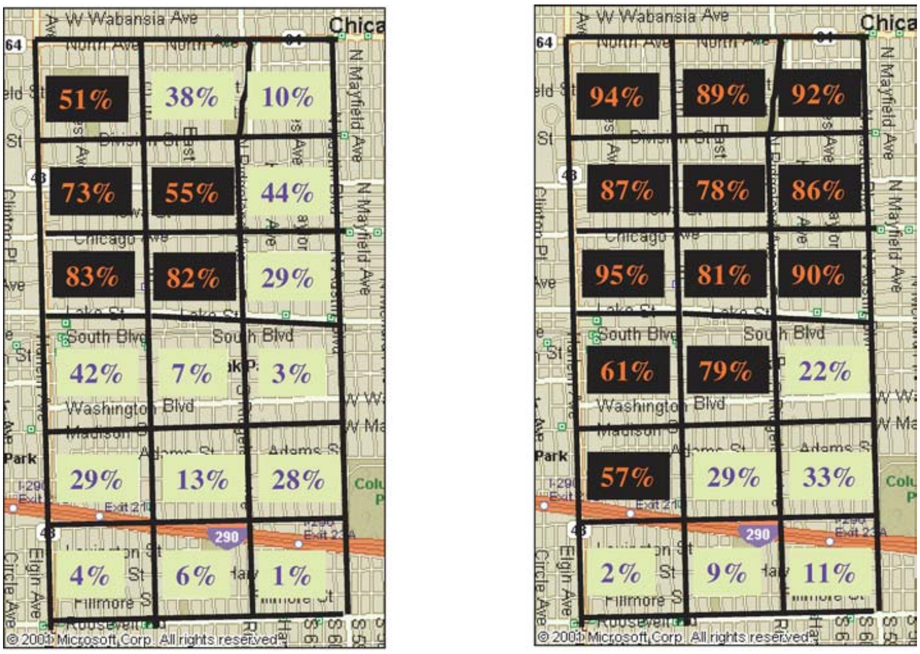
Table 2. The number of observed and expected observations of (1) only gray squirrels, (2) only fox squirrels or (3) both fox and gray squirrels for different land use variables, tree species variables and levels of dog and cat abundances. Only those variables for which at least 10 observations were submitted were included

	Gray		Fox		Both	
	observed	expected	observed	expected	observed	expected
Single[a]	189	233.4	95	72.4	131	109.2
Multiple	66	50.1	12	15.5	11	23.4
Park	42	34.9	2	10.8	18	16.3
Preserve	6	7.3	2	2.2	5	3.4
Campus	46	28.7	1	8.9	4	13.4
High-rise	12	6.8	0	2.1	0	3.2
Elm[b]	39	54.0	25	22.1	60	47.9
Hickory	18	13.1	4	5.4	8	12.0
Maple	87	128.8	81	52.8	128	114.4
Oak	134	102.7	27	42.1	75	91.2
Pine	144	118.8	36	48.7	93	105.5
Walnut	15	19.6	6	8.0	24	17.4
Dogs low[c]	135	131.0	24	30.5	70	67.5
Dogs medium	82	83.0	21	19.3	42	42.7
Dogs high	45	48.1	16	11.2	23	24.8
Cats low[d]	152	149.0	24	33.6	83	76.5
Cats medium	50	52.3	18	26.9	23	26.9
Cats high	20	20.7	8	4.7	8	10.6

[a]The X^2 value for the land use variables is 75.5 (10 degrees of freedom and $p < 0.001$).
[b]The X^2 value for the tree species variables is 73.2 (10 degrees of freedom and $p < 0.001$).
[c]The X^2 value for the dog abundances is 4.7 (4 degrees of freedom and $p > 0.05$).
[d]The X^2 value for the cat abundances is 10.0 (4 degrees of freedom and $p < 0.05$).

often than expected with oaks and pines, whereas fox squirrels were associated more often than expected with elms and maples. Walnut and hickory observations were relatively few and made a minor contribution to the overall pattern ($X^2 = 73.2$, 10 degrees of freedom and $p < 0.001$, the total contribution of walnut and hickory observations to the X^2 value was 7.1). Though not as strong as for land use and tree species variables, there was a pattern in the data that suggests an association of fox squirrels with higher levels of cats ($X^2 = 10.0$, 4 degrees of freedom and $p < 0.05$ for cat observations). The pattern for dog observations was not significant ($X^2 = 4.1$, 4 degrees of freedom and $p > 0.05$).

Figure 2 shows two maps of Oak Park: superimposed on map A are pie diagrams indicating the ratio of gray to fox squirrels recorded for each survey area during the 2002 survey, and superimposed on map B are the pie diagrams indicating the ratio of gray and fox squirrels recorded for each survey area during Lanham's (1998) 1996–1998 surveys. The data from the 1996–1998 surveys (six surveys in total) were pooled, which is the way it



A. B.

Figure 2. Gray and fox squirrel distributions for the village of Oak Park. Numbers represent percentage gray squirrels observed for each study block. Map (A): census data collected between June and July 2002. Map (B): census data collected by Lanham (1998) between October 1996 and January 1998.

is represented in Lanham (1998). The 1996–1998 data show fox squirrels dominating in all areas except for an area extending from central Oak Park into the northwest corner of Oak Park. Currently gray squirrels seem to be replacing fox squirrels and the 2002 survey showed that gray squirrel percentages increased in 16 of the 18 survey areas. In the two areas where gray squirrel percentages decreased, the changes were small (1% and 2% changes). In 2002 gray squirrels were predominant in all of northern Oak Park and most of central Oak Park. Fox squirrels still predominate in five of the six most southern survey blocks. Few gray squirrels were observed (in either survey) south of the Eisenhower expressway (I-290).

Discussion

Though still underutilized, public observations can make very valuable contributions to wildlife research. This has been amply demonstrated, particularly with bird monitoring programs, but many other groups of animals are noticed and appreciated by the public on a regular basis. Urban areas, with their higher densities of potential observers, are especially well suited to studies involving public volunteers. The large number of squirrel observations and comments that we received for this study underscores the suitability of conspicuous urban wildlife, like tree squirrels, for public monitoring. Public involvement in squirrel research has been successfully used before and made possible research projects that covered much larger geographic areas than would otherwise have been feasible. Bowers and Breland (1996) used public volunteers to measure giving-up-densities on sunflower seeds (a technique measuring foraging costs) in artificial food patches along an urban-rural gradient in northern Virginia. By involving the public, they managed to measure giving-up-densities at 78 different sites representing different levels of urban impact.

An ongoing research program (information at: http://www2.brevard.edu/whitesquirrel) in the city of Brevard, North Carolina, employs teams of volunteers to do annual population counts of Brevard's white squirrel morphs (species *S. caroliniensis*). In southern California, California State University is currently inviting the public to submit observations of fox squirrels and California gray squirrels (*S. griseus*) (at: http://instructional1.calstatela.edu/amuchli/squirrelform.htm) in an attempt to monitor the spread of the introduced fox squirrel. The Lab of Ornithology (Website at http://www.birds.cornell.edu) and the Audubon Society (Website at http://www.audubon.org) involve bird-watching citizens from all over North America in leading examples of the potential scale of possible projects. There is great opportunity for insights into large-scale patterns of animal distributions with the help of an interested public. This is especially true for metropolitan areas where there are large sources of human volunteers. In a real sense these people are custodians of a rich urban wildlife, and for the scientific community to gain their support and interest is of great consequence.

When evaluating the results from this study, it is useful to be mindful of the different spatial scales involved. At the largest scale, we have the Chicago area distribution map of fox and gray squirrels that can be visually inspected for any obvious trends. Also at this scale is the regression analysis of squirrel distribution with the demographic variables from the Census of 2000. When looking at the distribution map (figure 1), it is obvious that fox and gray squirrels were not randomly distributed. Most areas were more likely to contain gray squirrels than fox squirrels, and a few areas were more likely to contain fox squirrels. Correlations between zip code squirrel distributions and zip code demographic variables could have supported certain mechanistic hypotheses in favor of others, but a regression analysis failed to show any correlation (at least not for the variables considered in this study).

After categorizing the data for demographic variables, the contingency table analysis (Table 1) showed that the only instance where observed data differed from expected data was when we expected more than the observed number of observations of low gray squirrel percentages in densely populated areas (this particular cell contributed 3.29 of a total X^2 value of 4.85). High human population densities are concentrated in the city of Chicago and tend to decrease with distance from the city (U.S. Census Bureau at http://www.census.gov). In accordance with this pattern, the map showed that fox squirrels are relatively rare in the city, whereas gray squirrels dominate in the city (as well as many suburban areas). In their natural habitat, gray squirrels are associated with densely forested areas containing significant undergrowth, whereas fox squirrels are more likely to be found in open forest or forest edges (Steele and Koprowski, 2001). Thus the obvious question: are the areas in and around Chicago where mostly gray squirrels were observed associated with higher forest or tree cover? A study by Iverson and Cook (2000) assessed 29 municipalities in the Chicago Metropolitan Area for 10 land cover classes, including forest and residential areas with trees. There is some overlap with areas for which squirrel observation data are available and the municipalities for which tree cover has been determined (10 municipalities). A regression analysis for this small data set failed to show any significant correlation of percentage gray squirrels observed with any of the tree cover variables. These results are preliminary, and it may be that we need more forest cover data for a truly representative sample of the study area. It may also be, as suggested by the regression analysis of the zip code demographic variables, that an explanation of urban gray and fox squirrel distributions at this large scale is not practical. The variation within zip codes may simply be too large for a comparison between zip codes, and at this large scale the only pattern that emerged from our data is the one of gray squirrels being associated with areas of high human population density.

At a smaller scale, we have the land use, tree species and pet variables submitted by the public together with their individual squirrel observations. At this scale, the emerging patterns were more clearly defined. Results include more fox and fewer gray squirrels than expected in areas with single-family homes. The incidence of both species together was also higher than expected in these areas. This is in contrast to multiple-family units, high-rise buildings, parks and campuses, where the pattern was reversed and where more than the expected number of gray squirrel observations and fewer than expected fox squirrels observations were made. Amongst multiple-family units, high-rises and on campuses, fewer than the expected number of observations that included both species was recorded. Results for multiple-family units and high-rises were in accordance with the pattern of gray squirrels being more common in areas of higher population density. However, parks and campuses are not always situated in areas of high population density, and the gray squirrel association with these areas may be more closely tied in with the results for different tree species.

Gray squirrels were found more often than expected in association with oaks and pines, whereas fox squirrels were associated with elms and maples. The acorns from oak trees are an important food source for tree squirrels, and as a general rule, areas with large numbers of oak trees can probably support higher squirrel densities than areas with few oak trees. The cacheability of acorns is especially important for winter survival (Husband, 1976; Havera and Nixon, 1980; Thompson and Thompsen, 1980; Korschen, 1981). The noticeable abundance of oaks in parks and campuses of the Chicago Metropolitan area may be tied in with the preponderance of gray squirrels in these land use types. Pines, though not as important as oaks, also provide cacheable food. Trees like maples and elms provide food in the form of new spring growth, but the lack of cacheability of these food types restricts their importance to shorter time periods. Taken together, the data for land use and tree species variables seem to support the notion that gray squirrels are strongly associated with areas of high human population density and an abundance of oak trees. Fox squirrels are more likely to be associated with lower human population densities in areas with single-family homes and where elms and maples are the dominant tree species.

Could high human population densities and oak trees have anything in common that may suggest a mechanism favoring gray squirrels? One could argue that both these conditions lead to situations of high food abundance for tree squirrels. Tree squirrels foraging in garbage cans and dumpsters are a familiar sight in Chicago. This may be especially true for large dumpsters, which seem to be easier for squirrels to get into compared to garbage cans (pers. obs.). Dumpsters are mostly found in areas of high human population density (where they service multiple family units and high-rises), whereas garbage cans are more abundant in suburban residential areas with single-family homes. More garbage, as well as easier access to garbage, are thus both associated with high human population density and also a higher incidence of gray squirrels. Similarly, oak trees are probably the single most important tree species providing food for tree squirrels and these are more abundant in the areas where gray squirrels dominate. A study based in St. Louis County, Missouri reported a population of fox squirrels being replaced by gray squirrels in a new subdivision (Sexton, 1990). Sexton (1990) also notes that the replacement was accompanied by an increase in food abundance through an increase in bird feeders and the planting of trees.

Apart from high human population density and oak trees being associated with gray squirrels, there was also a significant pattern with cat abundance. The number of observations where only fox squirrels were observed was different from the expected number. Fox squirrels were more likely to be observed in areas of high cat abundance and less likely to be observed in areas of low cat abundance. Though not significant, the same trend was found for dogs: the public made more fox squirrel observations than expected in areas of higher dog abundance. Fox squirrels are larger than their gray squirrel counterparts, and differences in body size have been suggested to result in trade-offs that could promote coexistence (Kotler, 1984; Lima *et al.*, 1985). Larger and more mobile prey is more difficult to subdue by predators, whereas smaller foragers can be more efficient due to lower metabolic foraging costs. This mechanism is supported by all the observed patterns from our study. In areas where predation risk is relatively minor and where food is abundant, gray squirrels may have the competitive advantage due to being more efficient foragers. In areas where pets (as potential predators) are more prevalent, the larger fox squirrels may have a competitive advantage over gray squirrels. This is in accord with the favored natural habitats of the two species, where fox squirrels do better in the more risky open areas and forest edges, and gray squirrels prefer denser forest.

At the smallest scale of our study, we have the squirrel surveys from the village of Oak Park. Both fox and gray squirrels are abundant in Oak Park, and the area is ideal for an investigation into potential mechanisms of fox and gray squirrel coexistence. Mechanisms of coexistence were the main focus of Lanham's (1998) study, and the data from our own survey provide additional insight into the changes that seem to be occurring in Oak Park. Though only two time periods are represented for Oak Park in figure 2, it seems as if gray squirrels are in the process of replacing or at least gaining ground on fox squirrels. From giving-up-density data (measuring quitting harvest rates in artificial food patches), Lanham (1998) concluded that gray squirrels were more efficient foragers than fox squirrels (food giving-up-densities were lower in areas where gray squirrels dominated). Due to the potentially confounding factors of squirrel densities (areas where gray squirrels are dominant may be able to support higher squirrel densities) and predation risk (areas where gray squirrels dominate are safer, as was concluded from Oak Park pet registration records), this conclusion should be viewed with some caution. However, it is consistent with the hypothesis that the main mechanism determining fox and gray squirrel coexistence is a trade-off between predator vulnerability and foraging efficiency. A future line of investigation documenting changes in pet abundance, pet control (e.g. leash laws) and squirrel food abundance in Oak Park will be valuable in settling this question.

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