EFFECTS OF URBANIZATION ON THE RELATIVE ABUNDANCE OF HUMMINGBIRDS (*ARCHILOCHUS ALEXANDRI* AND *ARCHILOCHUS COLUBRIS*) AS MEASURED BY RESOURCE REMOVAL RATES

by

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ABSTRACT

Urbanization has led to a loss of natural habitat, an increase in impervious surfaces, and subsequently, an increase in the provisioning of food sources for local wildlife. One common scenario of supplementary feeding includes artificial nectar feeders for hummingbirds, which can be so successful at attracting hummingbirds as to cause an increase in local abundance past natural carrying capacity. While previous studies have investigated persistence of hummingbird populations across an urban-rural gradient, mine is the first to use sucrose solution removal from hummingbird feeders as a proxy variable for relative hummingbird abundance. I deployed nectar feeders (N=27) in locations encompassing various intensities of imperviousness (i.e. percent of impervious surfaces, which is an indicator of urbanization intensity) and canopy cover around San Marcos, Texas, USA, to determine whether these factors affect the relative abundance of *Archilochus alexandri* and *Archilochus colubris* within 100, 200, and 400 m spatial scales. Extraneous variables including Julian date, resource availability, precipitation, and temperature were considered, but ultimately none of these individually had an effect on solution consumption ($P > 0.05$). Imperviousness had a negative significant effect on solution consumption across all three spatial scales, indicating that hummingbirds are less abundant in areas of greater urban development ($P \leq 0.05$). Canopy cover had a non-significant effect on solution consumption at all spatial extents ($P > 0.1$). In addition to developing a reliable new method for surveying hummingbirds, my findings show that urbanization, despite warmer local temperatures and increased food provisioning, may negatively affect some hummingbird populations.

I. INTRODUCTION

Urbanization, the shift in human population toward cities that results in an increase in size of urban areas, can affect bird species in a variety of ways. The development of urbanized areas leads to a loss of natural habitat, the addition of impervious surfaces, an increase in local temperatures, and a potential increase in the availability of food sources. The latter is represented by the introduction of non-native plants that may continue to flower, fruit, or seed into the winter, and the presence of supplementary feeders (McKinney, 2000; Rizwan et al., 2008; Greig et al., 2017). Supplementary feeders, in particular, are so popular that roughly half of all households in the U.S.A, U.K., and Australia provide supplementary food to birds (Hanmer et al., 2016).

One common scenario of provisioning food sources to wild birds occurs when people in urbanized areas set out artificial nectar feeders to attract hummingbirds. Hummingbirds cannot survive longer than a few hours without food, except at night and during torpor when metabolic rate and activity are much reduced; therefore, they may be particularly sensitive to the spatial distribution of food resources in their environment (Tyrrell, 1985; Unwin, 2011). Multiple studies show that hummingbird abundance and/or species composition is correlated with flower availability (Cotton, 2007; Montgomerie & Gass, 1981; Rodrigues & Rodrigues, 2015). Montgomerie and Gass (1981) found that, in both tropical and temperate regions, availability of nectar-producing flowers was a limiting resource for hummingbird populations, and caused hummingbirds to travel within and between habitats to find adequate food resources. Arthropod availability could also influence hummingbird abundance since they are a known food resource; for example, spider abundance has been positively correlated with hummingbird species richness (Cotton, 2007). Excessive dispersion (patch-to-patch distance) of food-resource patches might be detrimental to sustaining local hummingbird populations in some landscapes. A study in Costa Rica found that hummingbird abundance and species richness were positively correlated with the area of the forest fragments in which they were found (Borgella, 2001). Therefore, hummingbirds may be expected to suffer from urbanization due to habitat loss and populations might be unable to survive for long in an area with habitat fragmentation. Landscapes with varying levels of urbanization may influence where hummingbirds travel; inability to move through areas of unsuitable habitat could prevent hummingbirds from reaching areas where resources are available. A study of the critically endangered black-breasted puffleg (*Eriocnemis nigrivestis*) of Ecuador found that these hummingbirds are found more often in habitat that is farthest from the nearest forest border, likely due to the potential consequences of edge effects (Guevara et al., 2014).

However, some studies on hummingbirds suggest otherwise. Urbanization appears, in at least some cases, to benefit hummingbirds by creating environments abundant with artificial nectar feeders and ornithophilous nectar-producing plants used in landscaping. For example, Anna's hummingbird (*Calypte anna*) has undergone a range expansion due to urbanization and has been shown to persist across an urban-rural gradient in California (Blair, 2004; Greig et al., 2017). One subspecies of Allen's hummingbird (*Selasphorus sasin sedentarius*) in California has also undergone a major population expansion in the past forty years that is being driven by food availability--they are often found in urban parks, gardens, and campuses (Clark, 2017). A study in Tucson, Arizona, found that there were significantly more black-chinned hummingbirds

(*Archilochus alexandri*) in urban areas than rural areas, which is attributed to the nectar feeders placed in the yards of local residents (Emlen, 1974). Different intensities of urbanization may be more suitable to hummingbirds than others; for example, a study in Argentina found that White-throated hummingbirds (*Leucochloris albicollis*) were more abundant in periurban areas than suburban or rural areas, suggesting that landscapes near the center of the urban-rural gradient may provide the greatest benefits to hummingbirds (Leveau & Leveau, 2005).

In central Texas, the ruby-throated hummingbird (*Archilochus colubris*) and the black-chinned hummingbird are the only nesting hummingbird species, breeding from about April to October. Ruby-throated hummingbirds have a large breeding range that spans eastern and central North America from Canada to Texas, and a wintering range in Central America. They generally occupy woodland areas, preferably along water features, though they are often seen in more open areas as well (Tyrrell, 1985; Natural Resources Conservation Service, 1999; Tilford, 2008). Black-chinned hummingbirds, on the other hand, have a breeding range that spans the western portion of the United States, and a wintering range in Central America (Baltosser & Russell, 2000). Although they do not have specific habitat requirements and therefore occupy a wide range of habitats, they are most common in riparian groves and shrubland (Tyrrell, 1985; Baltosser and Russell, 2000). Although neither species is characterized as occupying densely-wooded habitat, canopy cover preferences have not been studied in detail (Baltosser, 1989; NRCS, 1999).

I examined the effect of varying intensities of urbanization and natural habitat (i.e. preserved habitat) on the relative abundance of hummingbirds (i.e. Ruby-throated and Black-chinned) across an urbanizing landscape in central Texas by using removal rates of sucrose solution from feeders as an indicator of relative hummingbird abundance. To my knowledge, no previous studies have quantified relative hummingbird abundance across urban-rural gradients using resource removal rate as the main response variable. I predicted that, due to intentional landscaping of ornithophilous plants and the use of hummingbird feeders in neighborhoods and parks, landscapes in the middle of the urban-rural spectrum (i.e. periurban and suburban) would have the highest rates of resource removal, particularly because hummingbird populations can sometimes exceed natural carrying capacity where artificial feeders are supplied (Tilford, 2008).

II. METHODS

Study Region

The study was conducted within and around San Marcos, Texas, with some data gathered during the first field season from the Bamberger Ranch Preserve in Johnson City, Texas. San Marcos has a population around 60,000 and is 78.6 km^2 in area (U.S. Census Bureau, 2015). It is one of the fastest-growing cities in the USA, so there are landscapes around San Marcos with varying levels of urban development. There is no spatially-discrete definition for *landscape*; in concept and in practice the term varies contextually. I use the term *landscape* to define an area of land (e.g., 10 km^2) that is relatively homogeneous with regard to development (buildings, houses, pavement, roads) and human activity. Rural landscapes are those that have relatively low levels of development and human activity compared to highly urban landscapes that have substantial development and human activity. Suburban and peri-urban landscapes are in the middle of the continuum from urban to rural.

Field Data Collection

I collected data for this study during two field seasons (Summer 2016 and Spring 2017). During the first season, customized plastic "nectar" feeders were placed at locations around San Marcos, Texas, and Johnson City, Texas. I selected locations that would be accessible throughout the field season, were unlikely to be disturbed by humans or animals (e.g. livestock or pets), and were visible at eye level at least 180˚. Additionally, I selected locations encompassing a wide variety of land use (i.e. neighborhoods, parks, ranches, campuses) so that varying levels of urbanization would be represented. Point counts were conducted between 2 July and 15 August 2016. Since *A. colubris* and *A. alexandri* are fairly difficult to distinguish from one another during field observation, and neither have strict habitat requirements that suggest they would not occupy the same areas in central Texas, *A. colubris* and *A. alexandri* were not examined as separate species. Feeders were filled with 500 mL of 20% sucrose solution (herein "solution"), and were set out for 3-9 days prior to conducting point counts so that hummingbirds would have time to find the feeders. Point counts were 10-minute periods during which an observer stood approximately 15-20 m from the feeder and recorded the greatest number of hummingbirds visually observed at a single instance. Recording the greatest number of hummingbirds simultaneously seen (herein "hummingbirds observed") rather than each time an individual was observed ensured that the observer was not counting the same individual multiple times, and therefore was the best indicator of relative hummingbird abundance. After each point count, the observer measured the amount of solution remaining in the feeder using a graduated cylinder. This value was later converted to the average amount of solution consumed per day at the point in order to make values comparable despite being set out for differing numbers of days. There were 2-4 point counts performed at each point throughout the course of the summer, with the feeder always being deployed for 3-9 days prior to obtaining the point count. A Pearson correlation was used to determine the strength of the relationship between hummingbirds observed and the average amount of solution consumed per day.

Data from the first field season revealed a relatively strong relationship between hummingbirds observed and solution consumption, so I determined that solution consumption was a reliable indicator of relative hummingbird abundance. Therefore, I discontinued point counts and only measured solution consumption during the second year of fieldwork, which enabled me to collect data at more feeders with a greater number of replications. That is, the time saved on a given day by not conducting point counts allowed for a greater sample size to be obtained. I did not once observe non-hummingbird visitors (e.g. finches, orioles) at or near the feeders, so the possibility of such birds consuming solution from any of the feeders was unlikely.

The second field season began in 18 April 2017, around the time that most *A. colubris* and *A. alexandri* had returned from overwintering, and ended 9 June 2017. For logistical reasons, I discontinued research in Johnson City and opted to focus specifically on research in San Marcos. Twenty-seven feeder locations around San Marcos were selected using the same parameters as the 2016 field season (Figure 1). Each feeder was outfitted with a plastic "hat" to reduce measurement error due to evaporation and precipitation, as well as an ant moat filled with water to prevent ants from invading the feeder and contaminating the solution. Each feeder was filled with 500 mL of a 20% sucrose solution and hung with wire from a tree branch, and ranged from 76 to 180 cm from the ground, depending on the height of the most suitable branch. After 3-7 days, I measured the amount of solution remaining to determine the rate at which solution was consumed. Consumption of the solution was converted to mL per daylight hour because hummingbirds are only active during the day. Each feeder point had 3-5 replicates (trials) with the exception of one point that became inaccessible after one observation. For all feeders, the replicated trials were conducted with at least 8 days between trials.

Resource availability at each feeder location was measured by surveying all ornithophilous plants within approximately 15 m of the feeder. To ensure that the surveys were accurate, I photographed all flowers within the 15 m area, identified them, and then ran a literature search to determine if ruby-throated and/or black-chinned hummingbirds use those flowers as resources. Resource availability was scored as either 0 (absence of flowers) or 1 (presence of flowers); given that most feeder locations lacked ornithophilous flowers there was no reason to measure this variable with any greater precision. Precipitation and temperature data were derived from the National Oceanic and Atmospheric Administration's online climate data (https://www.ncdc.noaa.gov/cdo-web/); the nearest weather station to each feeder location was determined, which ranged from 277 to 5,885 m away, and those data were used accordingly. Precipitation during each trial was converted to centimeters per daylight hour since precipitation would only realistically affect a hummingbird's feeding behavior during the day. For temperature, the high for each day during each trial was averaged to determine the average high during each trial. I also recorded the Julian date on the final day of each trial.

NLCD as a Resource for Quantifying Urbanization

The National Land Cover Database (NLCD 2011), created by the Multi-Resolution Land Characteristics Consortium (https://www.mrlc.gov), provides maps of the United States associated with land cover, including one that provides impervious surface data (NLCD 2011 Percent Developed Imperviousness) and one that provides canopy cover data (NLCD 2011 USFS Tree Canopy Cartographic). The maps have a spatial resolution of 30 meters. Each 30 x 30 m pixel has a value between 1 and 100 that refers to the percentage of that area covered in impervious surface or canopy cover for each of those layers, respectively. I used NLCD data and the Zonal Statistics tools from the Spatial Analyst Toolbox in ArcGIS 10.4 to determine the percent of impervious surfaces (herein "imperviousness") and canopy cover within a 100-meter radius buffer (approximately 35 pixels) centered on each feeder location. I also used buffer sizes of 200- and 400-meter radii (approximately 139 and 558 pixels respectively) to characterize imperviousness and canopy cover at an even greater spatial extent and to test for scaling effects. Since impervious surfaces (i.e. concrete, asphalt) are associated with land development, these data should accurately represent the level of urbanization for each feeder location. Canopy cover, although not directly related to imperviousness, was tested to determine whether it affects relative hummingbird abundance (using sucrose consumption as an indicator).

Analysis

As a preliminary examination of the data, an ANOVA was used to determine whether there was more variation in solution consumption within or between feeder sites. The effect of Julian date, resource availability, precipitation, and temperature on solution consumption were analyzed using multiple regression to control for these extraneous variables during subsequent regressions examining the effects of imperviousness and canopy cover. Standardized residuals were obtained from that multiple regression. The relative effects of imperviousness and canopy cover at each spatial scale (100 m, 200 m, 400 m) were analyzed using multiple regressions at each spatial scale on both the standardized residuals and the raw response variable at each feeder location. These regressions were applied to averages of the trials (replicates) at each feeder location (N=27) rather than all trials (N=106) to avoid temporal pseudoreplication (i.e. incorrectly using temporal replicates as unique and independent spatial replicates). All analyses were performed using R Studio Version 1.0.136.

III. RESULTS

A Pearson correlation on the data from the first field season (Summer 2016) revealed a moderately strong relationship between hummingbirds observed and the average amount of solution consumed per day ($r = 0.59$, $N = 61$, $P < 0.0001$). This gave support to using solution consumption as a response variable to analyze data from the second field season (Summer 2017). The ANOVA applied to the 2017 data revealed that there was more variation in solution consumption among feeder locations than within temporal replicates at each location, $F(26,79) = 4.33$, $P < 0.001$. Although expected, this result provided initial support for subsequent testing (regression models) to determine whether imperviousness and canopy cover was the source of differences among the feeder locations.

The multiple regression used to determine the relative effects of Julian date, resource availability, precipitation, and temperature indicated that those four extraneous variables together explained 9.3% of the variation in solution consumption, although none of them individually had a significant regression coefficient ($P > 0.05$) (Table 1). However, resource availability was marginally significant ($0.05 < P < 0.1$) (Table 1). Their combined effect on the response variable was relatively small, nonetheless it seemed appropriate to remove the effect in subsequent regression models testing the effects of imperviousness and canopy cover. I accomplished this by using the standardized residuals as a "new" response variable. However, for comparison, I also conducted the same set of regression models on the raw response variable.

The multiple regressions testing the relative effects of imperviousness and canopy cover on solution consumption (standardized residuals of the response variable, N=27) revealed that imperviousness had a stronger effect than did canopy cover as evidenced by the consistently larger regression coefficients for the latter (Table 2). The effect of imperviousness was negative at the 100 and 200 m spatial extents although only marginally significant ($0.05 < P < 0.1$) and non-significant at 400 m, whereas the effect of canopy cover was non-significant ($P > 0.1$) at all extents (Table 2, Figure 2). The multiple regressions testing the relative effects of imperviousness and canopy cover on the raw response variable (N=27) revealed that imperviousness again had a negative and significant effect ($P \leq 0.05$) on solution consumption, and the effect of canopy cover was still non-significant (Table 3, Figure 3).

IV. DISCUSSION

Contrary to my hypothesis, landscapes in the middle of the urban-rural spectrum did not have the highest rate of resource consumption and hence presumably did not have the greatest hummingbird abundance. Visual inspection of the data clearly reveals the lack of a negative quadratic (hump-shaped) relationship between imperviousness and solution consumption (Figure 2). However, there does appear to be a negative linear relationship between imperviousness and solution consumption, indicating that hummingbirds tend to have the highest abundance in landscapes with very little urbanization and the lowest abundance in highly urbanized landscapes (e.g. imperviousness > 50%). This relationship appears to be scale-independent (at least up to 400 m). The fact that the regression models using the raw response variable and the standardized residuals were both statistically significant shows that the relationship persists without the effects from the extraneous variables.

The non-significant effect of canopy cover supports the idea that *A. colubris* and *A. alexandri* do not have particularly specific habitat requirements with regard to vegetation structure. As mentioned previously, ruby-throats occupy woodland habitat, which is characterized by a low density of trees spaced such that there is little or no canopy overlap of adjacent trees. However, they are also commonly seen in more open areas; in fact, some studies indicate that ruby-throats prefer primarily open habitats to primarily forested ones (Tyrrell, 1985; Tilford, 2008; Rousseau et al., 2014). Dense canopy cover is not a characteristic of black-chin habitat either, but they tend to occupy a wide range of habitats, so their presence in areas of denser forest would not be unusual. More so than canopy cover, water features may be a key habitat requirement for both species; *A. colubris* and *A. alexandri* are often found near water due to the greater abundance of insects in those areas (Tyrrell, 1985; NRCS, 1999). Given the numerous creeks, rivers, and lakes in and around San Marcos, all of the feeders in this study were quite close to a water feature.

Resource availability had a marginally significant negative effect on solution consumption, which is contrary to my prediction that relative hummingbird abundance would be higher at locations with more resources (such as ornithophilous flowers in residential areas). Admittedly, resource availability was only surveyed within a 10-15 m radius around each feeder location, so future studies should survey larger areas of land surrounding each feeder location to gain a better idea of resource availability within the greater landscape. Given that territory size for hummingbirds is largely a function of resource density and can be thousands of square meters in area (Kodric-Brown & Brown, 1978; Carpenter et al., 1983; Hixon et al., 1983), I may have put feeders within hummingbird territories without observing the extent of the resources within those territories.

The presence of feeders in urban and suburban areas has served as an effective way to attract hummingbirds that do move through those areas. Feeders are often deployed by people who enjoy observing hummingbirds. The effect that feeders have on the pollination success of neighboring ornithophilous flowers is currently contested. In a study by Sonne et al. (2016), feeders increased hummingbird abundance at a relatively small spatial scale (75 m), and resulted in increased visitation to flowers within a slightly larger spatial scale (125 m). However, a study by Arizmendi (2007), flowers located near feeders were visited less frequently than those that were not, resulting in decreased seed set for those flowers. Therefore, there is a possibility that feeders, while a valuable resource to hummingbirds, can affect their efficiency as pollinators.

Functional connectivity has been described as "the degree to which the landscape facilitates or impedes movement along resource patches" (Belisle, 2005). Cities with a mosaic of urban development, such as San Marcos, can present a challenge for wildlife that have specific habitat requirements or that find more urbanized areas to be unsuitable as habitat. Fragmented habitat can impede hummingbird movement; for example, a study on green hermits (*Phaethornis guy*), a particularly vagile species of hummingbird, revealed that they will take longer homing routes in order to move through the most forested areas (their preferred habitat) within agricultural landscapes (Hadley & Betts, 2009). Consistent with my results, *A. colubris* and *A. alexandri* may suffer from habitat fragmentation in the form of taking longer routes across landscapes in order to avoid more urbanized areas. Future studies should include tracking the movements of these hummingbirds using radio telemetry to determine whether they take longer routes across landscapes (rather than flying straight-line distances) to avoid less suitable (more urbanized) areas.

To conclude and summarize, the results of my study suggest that urbanizing landscapes may have a negative effect on hummingbird populations in the form of decreased use of such landscapes. Additionally, canopy cover does not appear to be an indicator of habitat suitability for ruby-throated and black-chinned hummingbirds. Another important finding that emerged from this study is that consumption of sucrose solution from feeders can be effectively used as a reliable proxy variable for measuring relative hummingbird abundance. Hummingbirds are difficult to record in traditional survey methods, and the methods I used resulted in an effective way of indirectly measuring relative hummingbird abundance. To my knowledge, this is the first study to use sucrose solution consumption as a reliable indicator of relative hummingbird abundance. Because various species of hummingbirds across spatially different landscapes are affected by urbanization in unique ways, using easily deployable and cost-effective methods can further elucidate how urbanization affects these birds.

Table 1. Results of the multiple regression testing the relative effects of extraneous variables on solution consumption ($R^2 = 0.093$, $F_{4,101} = 2.6$, $P = 0.041$).

Variable	*ß*	SE *ß*	*P*
Julian Date	0.018	0.022	0.419
Precipitation per DH	31.70	30.82	0.306
Resource Index	-0.598	0.359	0.099
High Temperature	0.058	0.080	0.470

Table 2. Comparison of the multiple regressions testing the relative effects of imperviousness and canopy cover at three spatial scales (100, 200, and 400 m) on solution consumption using standardized residuals of the response variable (*N*=27).

	100 m Model			200 m Model			400 m Model		
	ß	SE *ß*	*P*	*ß*	SE *ß*	*P*	*ß*	SE *ß*	*P*
Imperviousness	-0.015	0.008	0.072	-0.016	0.009	0.072	-0.019	0.012	0.127
Canopy Cover	-0.007	0.007	0.327	-0.013	0.009	0.166	-0.010	0.013	0.445
R^2	0.132			0.130			0.117		
F	1.82			1.79			1.59		
df	2,24			2,24			2,24		
P	0.1837			0.1883			0.2247		

Table 3. Comparison of the multiple regressions testing the relative effects of imperviousness and canopy cover at three spatial scales (100, 200, and 400 m) on solution consumption using the raw response variable (*N*=27).

	100 m Model			200 m Model			400 m Model		
	ß	SE *ß*	*P*	*ß*	SE *ß*	*P*	*ß*	SE *ß*	*P*
Imperviousness	-0.035	0.013	0.014	-0.038	0.015	0.016	-0.047	0.020	0.029
Canopy Cover	-0.014	0.012	0.260	-0.023	0.015	0.140	-0.022	0.022	0.322
R^2	0.240			0.221			0.235		
F	3.789			3.412			3.688		
df	2,24			2,24			2,24		
P	0.037			0.050			0.040		

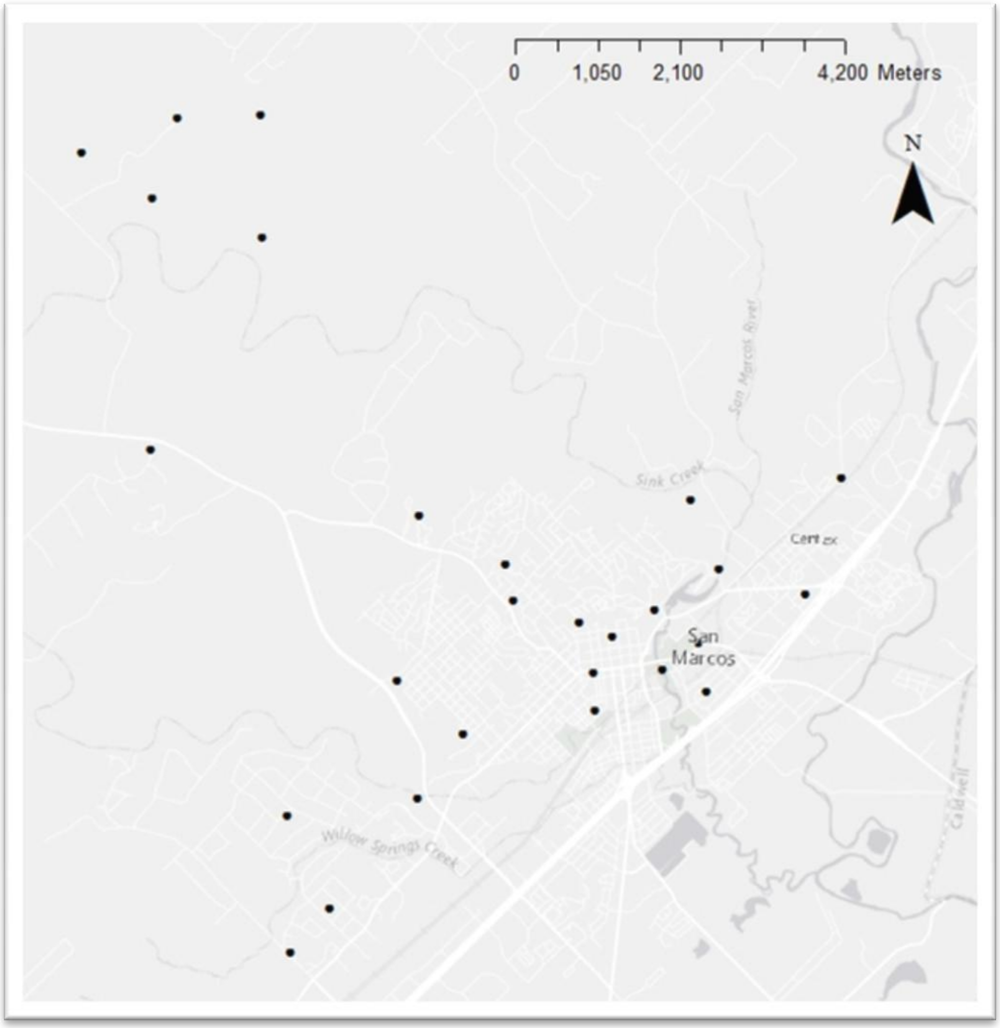

Figure 1 Map of San Marcos, Texas, USA, with points showing the feeder locations (N=27) used in this study.

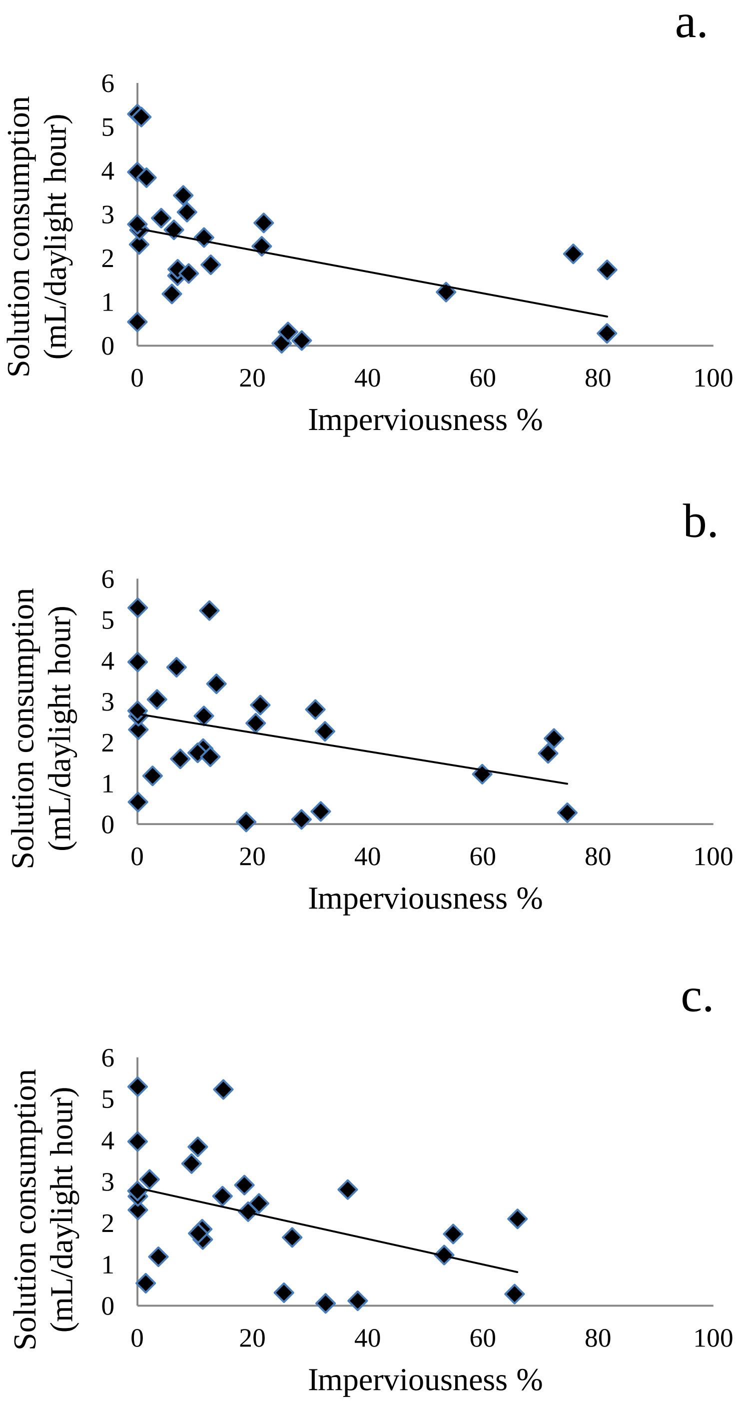

Figure 2 The relationship between imperviousness and solution consumption at each feeder location (N=27) at three spatial scales: 100 m (a), 200 m (b), and 400 m (c). At all three spatial scales, solution consumption tends to decrease as imperviousness increases.

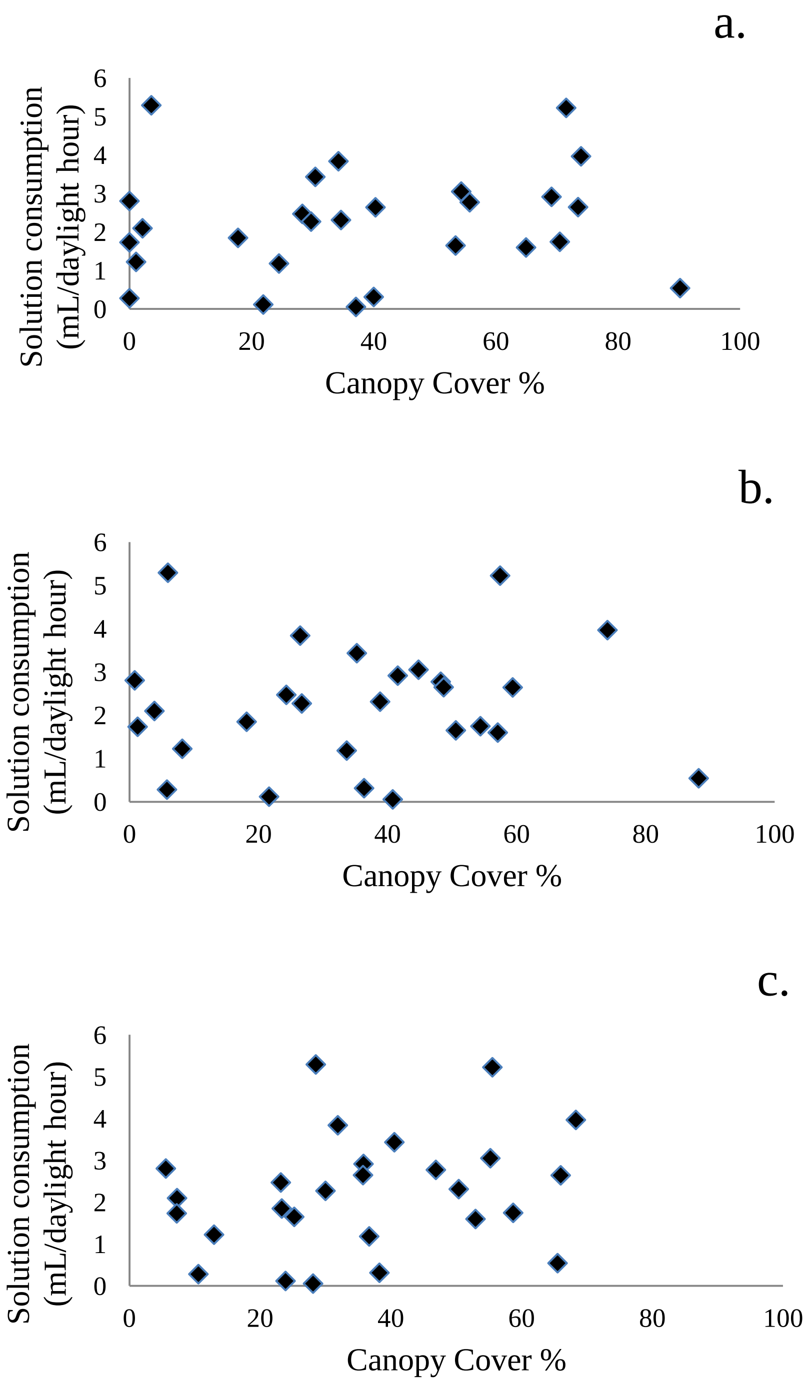

Figure 3 The relationship between canopy cover and solution consumption at each feeder location (N=27) at three spatial scales: 100 m (a), 200 m (b), and 400 m (c). At all three spatial scales, there is no statistically significant relationship.

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