

THE LOCAL AND LANDSCAPE FEATURES ASSOCIATED WITH ROOST
ATTENDANCE AND NESTING SUCCESS IN URBAN BLACK VULTURE (*CORAGYPS*
ATRATUS) AND TURKEY VULTURE (*CATHARTES AURA*) POPULATIONS.

by

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ABSTRACT

HANNAH PARTRIDGE. The local and landscape features associated with roost attendance and nesting success in urban black vulture (*Coragyps atratus*) and turkey vulture (*Cathartes aura*) populations. (Under the direction of DR. SARA GAGNÉ)

Land cover changes that result from increasing urbanization alter habitat type, structure, and resource availability on local and global scales. Vultures provide important ecosystem services including disease management and nutrient cycling, making them an important feature of urban areas. For vultures, urbanization may have both positive and negative impacts, such as increased foraging opportunities due to the presence of roadkill and decreased nesting success due to human presence, complicating our understanding of the effect of urbanization on these essential species. I examined how local and landscape features affect roost attendance and nesting success of black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) in the Charlotte Metropolitan Area, USA. I counted the number of vultures at twenty-nine permanent roost sites once a month between November 2019-March 2020 and November 2020-March 2021 and monitored the nesting activities and periods once a week between March and August 2020 at two rural black vulture nests and one urban black vulture nest. At each roosting site, I characterized vegetation height, roost height, right-of-way corridor width, and weather conditions, and measured land cover, carcass density, and Developed-Forest edge density in the surrounding landscape within radii ranging from 0.4km to 20km. I tested the effects of these variables on the number of vultures at roosts using generalized linear models and multi-model inference. The best model for roost attendance included the date, wind speed, corridor edge vegetation height, carcass density within 15km and 20km of roosts, Developed land cover within 15km of roosts, and Developed-Forest edge density within 15km of roosts. Of these variables,

Developed land cover was associated with higher numbers of vultures while all other variables were associated with lower roost attendance. The two rural black vulture nests each successfully fledged two young whereas the urban nest failed with no eggs hatched. The rural black vulture nests each had much less developed landcover and more forested landcover surrounding the site, potentially representing negative impacts of developed land cover on vulture nesting success.

The negative effect of carcass density on vulture numbers suggests more reliance of vultures on trash and other anthropogenic food sources. The change in urban vulture diets may have important implications for urban systems, altering nutrient cycling within ecosystems and decreasing the reproductive success of urban vultures.

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INTRODUCTION

By 2040, the global human population is projected to be greater than 9 billion, with 68% of people living in urban areas (United Nations, 2019). Populations growing at these rates require more infrastructure, bringing increased levels of traffic, pollution, and disturbance to natural environments and wildlife populations. Land cover changes that result from this increasing urbanization reduce and degrade critical bird habitats on local and global scales (Isaksson, 2018). Many species cannot persist in these altered conditions, leading to decreased diversity and just a few successful species in highly urbanized areas.

Vultures within the Cathartidae family include several of these successful species, to the point that they are often seen as a nuisance in cities (Blackwell, 2007). Cathartid vultures have adapted to cities well, using human-made structures for roosting, nesting, and foraging across North and South America (Avery et al., 2002; Coles, 1944; Hill & Neto, 1991). Wildlife collisions and landfills offer increased foraging opportunities and transmission towers are commonly used by roosting vultures. However, habitat loss and disturbances during the nesting season can drastically affect nest success and improving sanitation in urban areas reduces the opportunity for easy scavenging (Coleman & Fraser, 1989; Houston et al., 2007; Stewart 1974).

Historically, vultures roosted on trees and other natural structures in largely undeveloped areas (Coleman & Fraser, 1989; McVey, 2008; Rabenold & Decker, 1990). Today, urban vulture roosts are commonly found on artificial structures such as transmission towers, cellular towers, and water towers across the United States, representing a dramatic change in behavior over a relatively short time span (Avery et al., 2002; Seamans, 2004). Similarly, in the past, vultures nested in a variety of locations, including steep cliffs, swamps, rocky caves, salt marshes, and tree cavities (Coles, 1944; Houston et al., 2007; Jackson, 1983). Although nests were

occasionally found in abandoned buildings in the past, black and turkey vultures now appear to nest almost exclusively in abandoned buildings when available (Houston et al., 2007; Rabenold & Decker, 1990; Stewart, 1974). However, since nests are often located on the ground in buildings, these locations may be associated with reduced nesting success due to increased disturbance and predation risk from humans and other animals (Beaulieu, 1985; Houston, 2006; Jackson, 1983; Mossman & Hartman, 1992). Finally, vultures also benefit from roadkill, landfills, and residential land cover in cities for foraging (Novaes & Cintra, 2015; Thompson et al., 1990), although foraging opportunities may be dependent on sanitation practices, which can change over time (Coleman & Fraser, 1989; Houston et al., 2007; Stewart, 1974).

In our study area in the southeastern United States, black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) are common sights in highly urbanized areas, despite previous population declines (Robbins et al., 1989) and drastically altered ecological conditions. In previous research, black vultures have been found near foraging sites, such as street markets and garbage dumps, possibly to reduce movement costs in developed landscapes (Novaes & Cintra, 2013). Similarly, Campbell (2014) found that black vulture numbers show strong associations with largely urbanized areas, commonly found in city centers and suburbs across all types of urban land cover (Campbell, 2014). The authors tested the density of vulture species in El Salvador along an urban to forest gradient to find which areas each species is most associated with. Black vultures were found to be much more common in urban areas, with the fundamental landscape factor thought to be food availability (Campbell, 2014). Turkey vultures are also associated with urbanized areas, but to a lesser extent than black vultures as they tend to range farther and forage on less predictable sources (Campbell, 2014). Black and turkey vulture nest sites have clear associations with heavily forested areas and relatively low human disturbance,

even with rising rates of urbanization. Both species historically nested in heavily wooded areas far from buildings and human disturbance (Coleman & Fraser, 1989; Stewart, 1974), but have been more commonly found nesting in areas with much higher rates of urbanization with similar nesting success (Rabenold & Decker, 1990). The vultures still appear to find sites with minimal human disturbance but have more tolerance for urbanization than previously thought. The amount of urban land cover surrounding the nest may be largely dependent on the study area, with even heavily urban, degraded habitats not deterring black and turkey vultures.

Due to negative attitudes towards vultures and the difficulty in studying their breeding biology, black and turkey vulture nesting has not often been studied. Given the private nature of black and turkey vultures during the nesting season, they generally find private, secretive locations to nest. The locating of nesting sites often requires collaboration between researchers, local officials, and landowners and multiple trips searching for a nest. Monitoring the nests over the approximately four-month nesting season requires a similar amount of effort and technology that may be costly, unavailable, or impractical. Even large-scale nest monitoring projects can be done, but they require a significant amount of time, energy, and funding, causing the breeding biology of black and turkey vultures to be understudied and often anecdotal. Some studies have described the nesting behavior of vultures (Coles, 1944; Houston et al., 2007; Rollack et al., 2013; Stewart, 1974) but few have evaluated the nesting success of these species. Of those that have studied the nesting success of black and turkey vultures, it appears to be similar across studies, often averaging 1.7-1.8 young/nest (Houston et al., 2007), although there have been some lower estimates of 0.73 young/nest, potentially caused by human disturbance (Coleman & Fraser, 1989; Rabenold & Decker, 1990).

Vultures are specialized for scavenging, with efficient soaring flight, bald heads, and extremely corrosive stomach acid that allows them to consume carcasses infected with diseases such as rabies, Ebola, and anthrax without becoming infected (Ogada et al., 2011). As such, vultures carry out a vital function in urban ecosystems by disposing of carcasses and organic matter that could otherwise spread deadly diseases to other scavengers and ultimately human populations. For example, from 1992-2006, while vulture populations in India plummeted, in some cases by over 90%, nearly 50,000 additional people died after contracting rabies from feral dog bites, a 17% annual increase (Markandya et al., 2008). By their scavenging, vultures also play an important role in nutrient cycling at the relatively large spatial scales over which they forage (Hill et al., 2018).

Despite the importance of vultures to ecosystem functioning and their increasing prevalence in urban landscapes, we know very little about the factors underlying their success. My objectives for this study were to 1) assess the impact of several local and landscape features on vulture roost attendance, and to 2) assess the impact of surrounding urban land cover on vulture nesting success. In the Charlotte Metropolitan Area, I used vulture roost surveys, habitat surveys, and spatial analysis to evaluate the effects of date, temperature, wind speed, cloud cover, right-of-way corridor width, corridor edge vegetation height, roost height, Developed land cover, open water land cover, carcass density, and Developed-Forest edge density on the roost attendance of black and turkey vultures. Black vulture nests were monitored until young fledged and correlated to the amount of Developed land cover in surrounding landscapes to evaluate the effect of urban land cover on nesting success. Based on previous studies and observations, I expect Developed land cover to positively impact roost attendance as vultures will readily take advantage of anthropogenic structures and resources. However, given the increased disturbance and predation

associated with Developed land cover, I expect greater Developed land cover to negatively impact the nesting success of black vultures.

METHODS

Study area

The Charlotte Metropolitan Area (CMA) is composed of 12 counties in North and South Carolina, USA surrounding the city of Charlotte, North Carolina (35.22° N, 80.86° W) and covering an area of 8,280 km². The CMA human population is estimated at 2.8 million, with rapid growth since 2010 (American Community Survey, 2019). The population of Mecklenburg County alone is expected to grow by over 570,000 between 2010 and 2040 with an annual growth rate of 2.3% (Charlotte Future, 2019). Similar growth rates are seen in the surrounding counties in overall population and commercial and industrial development (Charlotte Future, 2019).

The Charlotte city center consists of large amounts of developed land cover types, but development across the entire CMA is fairly sprawling and dominated by developed open space and single-family housing. Deciduous forest accounts for approximately 25% of land cover across the CMA, with all forest types together accounting for nearly 50% of land cover across the area. Pasture and hayfields also make up a large portion of the CMA, coming in at over 20%. Other land covers such as wetlands, grasslands, and open water do occur but are relatively rare when compared to the overall landscape. Elevations in the region range between 93 and 780 meters and the climate is humid continental, with average summer highs of 32° C, average winter lows of -1° C, and average annual precipitation of 116 cm (US Climate Data).

Roosting attendance

Roosting sites

I identified 15 black vulture (*Coragyps atratus*) and turkey vulture (*Cathartes aura*) roosts within the CMA in 2019 and an additional 14 in 2020 for a total of 29 roosts (Fig 1). Selected roosts were chosen from a larger list compiled in collaboration with Mecklenburg Audubon Society members. Additional roosting sites were found using eBird hotspots and observations of vulture movements at sunrise and sunset. Roosts reported from members of the community are likely those that are more obvious, near major roadways and buildings. Because of this, there may be some bias in this study towards the more noticeable sites. Vulture movements at sunrise and sunset were observed and tracked to find additional roosts which were often less noticeable in the landscape. Prior to being included in the study, all reported and observed roosts were surveyed for vulture presence and type of roost. The active roosts that hosted vultures overnight were included in the study, while temporary roosts used before or after the overnight roost were not chosen for study.

Two roosts from the first year were eliminated from the second year when found to be inactive. Of all roosts, twenty-seven were located on transmission or cellular towers. Roosts on transmission towers (22) were situated in right-of-way corridors with forest on either side, whereas roosts on cellular towers (5) were not located in right-of-way corridors and were adjacent to a variety of land covers. The two roosts not located on towers were on small clusters of deciduous trees within 0.5 km of transmission towers and adjacent to residential development.

Roost surveys

I counted the number of vultures at each roost once a month from November 2019 to March 2020 and from November 2020 to March 2021, for a total of five surveys per roost per year. Thirteen roosts were surveyed in both years and 16 roosts were surveyed for a single year. Survey periods coincided with the annual period during which vultures use roosts most consistently in the non-nesting season, with the vultures more frequently using the same roosts each night in larger numbers (Sweeney, 1984). During each survey, I or a trained volunteer counted vultures at roosts between 30 minutes before and 30 minutes after sunrise when individual vultures could be distinguished as they became more active and spread out on the roosting structure but before they left the structure to forage in the surrounding landscape (Sweeney, 1984). During the second year of surveys, the count period was shortened to only 30 minutes before sunrise as a result of observations the previous year that vultures often left roosts earlier than expected.

Explanatory variables

Local variables

I measured the local habitat variables at each roost that may be important predictors of vulture presence including date, temperature, wind speed, cloud cover, roost height, surrounding vegetation height, and corridor width (Table 1). The date and the time of year is very important in vulture roosting numbers, with roosting numbers peaking in December and dropping off very quickly in February-April with the lowest roosting numbers in the summer months (Sweeney & Fraser, 1986). The same trend appears with weather – vultures will generally remain at or near the roost longer during colder temperatures or inclement weather (Sweeney & Fraser, 1986). The

exception to this generality is wind speed. On windy mornings, vultures may be more likely to leave the roost earlier, perhaps to take advantage of the wind currents to aid in early-morning foraging flights (Davis, 1989). Many of the vultures roosting site habitat features may aid in arrival, departure, and flight. Open fields or corridors surrounding roosts allow unobstructed arrival and departure and may provide upward air currents (Coleman & Fraser, 1989; Davis, 1989). The same benefits may be provided by the height of the roosting structure, with structures above the tree level providing ease of access.

Most of the roosts studied were located on transmission towers and were surrounded by a right-of-way (ROW) corridor. I measured the width of the ROW corridor using Google Earth and confirmed the distance with a Nikon Aculon rangefinder, measuring the distance from one side of the corridor to the opposite side. As cellular towers and trees are not surrounded by utility corridors, these sites were assigned a value representing the average width of open space surrounding the site. This distance was measured in the same way, using Google Earth and confirming the distance with a rangefinder.

I measured the height of each roosting structure and surrounding vegetation using a Suunto PM-5/360 clinometer and Nikon Aculon rangefinder. Using the clinometer, I measured the angle of elevation from the viewpoint to the top of the roost. With the rangefinder, I measured the distance from the viewpoint to the bottom of the roost. The height of the roosting structures was measured at the point of the highest roosting vulture, often at the top of transmission and cellular towers and near the top of the trees. The corridor width and height of roost and vegetation was measured in January 2020 for the first-year sites and in January 2021 for sites added in the second year.

To gather accurate weather conditions during the time of each survey, I collected data on temperature and wind speed for each survey from Weather Underground Personal Weather Stations (PWS) located near survey sites. I chose the PWS located closest to each roost site and collected the temperature and wind speed for the beginning of the survey time. During each survey, I also recorded the percent cloud cover as a measure of the weather conditions using visual estimates.

Landscape variables

I measured several landscape variables surrounding each roost that could be predictors of vulture presence – Developed land cover, Open Water, carcass density, and Developed-Forest edge density. Developed land cover provides roosting and nesting structures and food sources that appear to attract larger vulture roosting populations (Novaes & Cintra, 2015; Campbell, 2014; Thompson, 1990). Especially attractive to vultures may be roads as they provide a food source by way of roadkill (Thompson, 1990). Carcass and other food availability is an important factor in vulture presence with food availability appearing to be a main predictor of vulture roosting sites (Novaes & Cintra, 2015; Campbell, 2014). The habitat preference of black and turkey vultures changes depending on the time of year, but they have been found to frequently use the edge habitat between open and forested habitats, perhaps to benefit from the safety and foraging opportunities available in both landscapes (Coleman & Fraser, 1989; Novaes & Cintra, 2015).

Each landscape variable was measured in landscapes with radii of 0.4, 0.5, 1, 2, 3, 4, 5, 10, 15, and 20km centered on roosts. Holland (2015) found that the annual home range size of black and turkey vultures is as large as 75-100 km² during the winter when the landscape use is at its largest, while the core area size is only around 1.5 km² at the largest (Holland, 2015). These results equate to radii of 0.7km for the core area to 5.6km for the annual home range. Houston, et

al. (2011) however, has recorded turkey vulture home ranges with areas over 900 km² (Houston, et al., 2011), which is a radius of over 17km. Per Jackson and Fahrig (2015), it is recommended to evaluate multiple scales that are relevant to the species biology to best estimate importance of the landscape variables (Jackson & Fahrig, 2015). Given the extremes found in core and home range size, I chose the ten radii listed to evaluate the vulture landscape use at scales ranging from the daily area used to the annual home range.

I measured the Developed land cover and Open Water land cover as proportions of each landscape covered by the Developed classes or the Open Water class of the 2016 National Land Cover Database (Wickham et al., 2014). I used 2018 Tiger/Line road data (US Census Bureau, 2018) and 2018 deer collision data (NCDOT, 2018; SCDPS, 2018) to estimate the carcass availability by roadway density within each radii. I calculated the number of deer collisions and the kilometers of roadway within landscapes surrounding roosts. Roadway data was filtered to include only those roadways on which deer collisions were recorded. The number of deer collisions was divided by kilometers of roadway, which was then divided by square kilometers of total area within the landscapes, producing a measure of carcass density across the landscapes. The South Carolina Department of Transportation tracks only the number of deer collisions in each county (SCDPS, 2018) and I scaled the number of deer collisions in each county to the size of each buffer by area. With the scaled deer collisions and roadway data, the same method was used to calculate the final carcass density as stated above.

Finally, I measured the Developed-Forest edge density of each landscape as the length of edge between any Developed class (Open space, Low intensity, Medium intensity, and High intensity) and any Forest class (Deciduous forest, Evergreen forest, Mixed forest) of the 2016 National Land Cover Database divided by the total landscape area. Landscape variables for land cover,

carcass density, and edge density were calculated using ArcGIS Pro, v2.5.0 (ESRI, 2020) and FRAGSTATS, v4.2.1.603 (McGarigal et al, 2015).

Analyses

Roost count adjustment

During the 2019-2020 roost survey season, I noticed that the vultures often left the roost earlier than expected, with most of the roost gone by 30 minutes after sunrise. Starting in March of 2020, I began conducting the surveys within only the 30 minutes before sunrise to ensure an accurate count of the roosting vultures.

To adjust previously surveyed roosts, I conducted detailed observations of roosts on fifteen different days. I counted the number of vultures roosting every minute from 60 minutes prior to sunrise to 60 minutes after sunrise to get an approximation of the rate that vultures leave the roost with relation to the time of sunrise. After removing outliers, these observations yielded a total of 1,049 data points. Using a 6th order polynomial regression, the formula below represents the proportion of the roost remaining with respect to the minutes after sunrise (Fig A1, Table A1). All the surveys from 2019-2020 and from 2020-2021 have been adjusted using this formula to account for any vultures that had already left the roost. This model accounts for approximately 60% of the variation in the data.

To adjust the roost counts, I used the minutes after sunrise to calculate the proportion of the roost remaining with the calculation below:

Proportion remaining

$$\begin{aligned}
 &= (1.429e^{-10} * \text{minutes after sunrise}^6) - (1.212e^{-8} * \text{minutes after sunrise}^5) \\
 &- (1.233e^{-7} * \text{minutes after sunrise}^4) + (2.489e^{-5} * \text{minutes after sunrise}^3) \\
 &- (2.993e^{-5} * \text{minutes after sunrise}^2) - (2.426e^{-2} * \text{minutes after sunrise}) \\
 &+ 0.6835
 \end{aligned}$$

Using the calculated proportion remaining, I divided the count by the proportion remaining to get the count when the proportion remaining is equal to 1.

Statistical analysis

I identified the habitat and landscape features associated with the number of vultures at roosts using a repeated measures, linear mixed model and multi-model inference. All models included a fixed effect to account for the non-independence of observations from the same roost site. To avoid correlation between variables, I analyzed each landscape scale separately, for a total of ten different datasets including the same habitat and landscape features at different scales. The variance inflation factor (VIF) was calculated to test for collinearity between variables, with collinearity values under five acceptable (Table B2). Within pairwise correlation matrices, all correlation values were less than 0.7 with the exception of the correlation between Developed land cover and Developed-Forest edge density at the 15km and 20km scales, with values of 0.766 and 0.724, respectively (Tables B3-B12). The response variable was log-transformed to address heteroskedasticity in the dataset.

Using RStudio v1.3.1073 (RStudio Team, 2020), each dataset was analyzed to create models using every possible combination of explanatory variables with the adjusted count. I ranked each model by the AIC_c value using the ‘dredge’ function from the MuMIn v1.43.17 package (Barton, 2020). Prior to averaging the models, I combined the top models ($\Delta\text{AIC}_c < 2$) from all scales.

From these models, I calculated model-averaged parameters using all new top models ($\Delta AIC_c < 2$) with standard errors and confidence intervals.

Nesting success

Site selection

In late 2019, Mecklenburg Audubon Society members and Mecklenburg County officials reported nest sites of black and turkey vultures to me. Prior to the start of the 2020 nesting season in February, I had fifteen potential nesting sites. During February and March of 2020, I observed each nesting site weekly for activity such as fresh fecal matter, feathers, disturbed surfaces, or eggs. Weekly observations continued until each site was declared active or inactive in early April. There were two active nesting sites in 2020, with one additional active nest reported to me later in the nesting season (Fig 2). The same fifteen potential nesting sites were observed in 2021 for nesting activity, with the addition of two new nesting sites reported. In total, there were four active nests studied in 2021.

Nest surveys

I conducted weekly observations of active nests during daylight hours from March 2020 to August 2020. The observations were conducted from a reasonable distance with Vortex Diamondback 12X50 binoculars to reduce disturbances to the nesting vultures.

The observations included the approximate date that eggs were laid, the number of eggs laid and those hatched or unhatched, any nest or juvenile predation, activity of the young, parental care, and the number of young fledged (Table 2). Additionally, one active nesting site in 2020 was observed with a Victure HC200 trail camera to gather more accurate estimates of behavior and

nesting activity dates. Nesting observations for the 2021 season began in mid-February and are ongoing. All active nests are being observed using a Victure HC200 trail camera.

Landscape variables

I measured the Developed land cover, Forested land cover, and Open Water land cover within landscapes within radii of 0.4km and 15km buffers around each site to estimate the impact of urban land cover on the black vulture nesting success. Landscape features directly surrounding the nesting site likely have more impact on the success of the nest, given the core area sizes found in previous work (Holland, 2015). The small landscape size of 0.4km was chosen as an estimate of these localized features, and the 15km radius was chosen to investigate the features at this scale found to be an important predictor size of roost attendance. While developed land cover may offer more foraging potential, it also increases disturbance from humans and domestic animals and the risk of predation from urban predators (Rollack et al., 2013). These measurements were collected using the same methods as described above within “Landscape variables” for the vulture roosting attendance study.

Analyses

As there was not enough data to analyze the effect of land cover features on nesting success, no major statistical analyses were completed. The proportion of Forested, Developed, and Open Water land cover within 4km buffers was compared between the sites without any statistical tests run. Nesting activities and periods were quantified using the trail camera footage. With additional data, I will identify the land cover features that are associated with vulture nesting success using general linear models and multi-model inference.

RESULTS

Roost attendance

The average number of vultures counted at roosts was 36.47 ± 3.63 SE (Table B1). The corridor width and corridor edge vegetation height had high variability, averaging $37.43\text{m} \pm 22.26$ SE and $33.79\text{m} \pm 16.20$ SE, respectfully. The height of roosts also varied widely with an average of $58.05\text{m} \pm 42.04$ SE. While the landscape variables were similar at most scales, the 0.4 km radii had much greater variability than the larger scales. For example, the Developed-Forest edge density within 0.4 km radii averaged 0.29 ± 0.30 SE while the same variable averaged 0.32 ± 0.04 within 20 km radii (Table B1).

Five models qualified as the best models ($\Delta\text{AIC}_c < 2$) describing vulture roost attendance (Table 3). Models included survey date, corridor edge vegetation height, wind speed, carcass density within 15km and 20km of roosts, Developed land cover within 15km of roosts, and Developed-Forest edge density within 15km of roosts. The number of vultures was larger at roosts situated in corridors bordered by lower vegetation, with less wind, and surrounded by lower carcass density, lower Developed-Forest edge density, and more Developed land cover (Figure 3).

Nesting success

In 2020, I gathered 18.3 hours of video and 3,800 photos from the trail camera stationed at one black vulture nest and I visually observed two other nests (Fig 4-5). Two nests each fledged two young successfully and one failed with zero of two eggs hatched and no fledglings produced. Across the three nests observed, each had two eggs laid between mid-February and mid-March and hatched between March 21-29 (Table 4). At the camera-trapped nest, the brooding period ended at 35-37 days post hatching, although the adults were regularly absent from the nest for

several daylight hours at this time. The period between hatching and fledging for both successful nests was 96-102 days (Table 4).

At the nest monitored by an infrared camera, both adult black vultures participated in the care of the young, including incubation, brooding, and feeding. Using the recorded footage and audio, the young are estimated to have been fed 3.2 ± 0.17 SE times per day throughout the nesting season. The adults were observed to frequently feed the other adult at the nest as well, often before feeding the juveniles. The adults were also recorded performing courtship behavior on three occurrences. No successful mating attempt was recorded. At the camera-trapped nest, the chicks began standing and flapping their wings at only 14 days post hatching, almost immediately after the adults began leaving the nest unattended for short periods of time. They developed their first flight feathers at 30 days post hatching.

Neither the adult nor juvenile black vultures showed a reaction to nonpredatory species such as the groundhog (*Marmota monax*), eastern grey squirrel (*Sciurus carolinensis*), Carolina wren (*Thryothorus ludovicianus*), common five-lined skink (*Plestiodon fasciatus*), or various mouse species within the nest building. Potential predators such as humans and domestic dogs (*Canis lupus familiaris*) near or within the nest building caused the adult to abandon the nest briefly, while the adult guarded the nest against gray foxes (*Urocyon cinereoargenteus*). Few predators were recorded within the building during the nesting period, but coyotes (*Canis latrans*) and gray foxes were recorded within the building soon after the vultures fledged. Before the vultures fledged, there were four recorded predators at the nest site, for a frequency of 0.04 visits/day. In the seven days of footage recorded after the vultures fledged, there were two predators recorded at the site, averaging 0.29 visits/day. Wildlife presence as a whole also increased quickly, rising from 0.11 recorded wildlife occurrences/day pre-fledging to 0.57 occurrences/day post-fledging.

Nest context

Successful nests had slightly less Forest land cover within 0.4 km of their locations and less Developed land cover and more Forest land cover within 15km of their locations compared to the failed nest (Table 5).

DISCUSSION

My results demonstrate that vulture roost attendance is affected by the date, wind speed, corridor edge vegetation height, carcass density within 15 km and 20 km radii, Developed-Forest edge density within 15 km radii, and Developed land cover within 15 km radii. This shows that the most important predictor variables of vulture roost attendance are at the larger spatial scales and at the very small spatial scales, indicating that vultures may congregate in areas with favorable site-specific features within a much larger favorable landscape, potentially with significant impacts by other features such as food availability at sites that are not captured within this study. Although vultures readily use human-made structures, they still show preferences for natural features such as shorter corridor edge vegetation height and will select higher quality human-made roost sites across landscapes. Corridor edge vegetation height had a predicted negative effect on roost attendance, as shorter vegetation surrounding a roost may allow easier entry and departure for the vultures.

The positive effect of Developed land cover and the negative effect of carcass density seen at large scales implies that vultures are relying less on roadkill and more on trash found in urban areas. A negative effect was also found from Developed-Forest edge density, indicating that these populations will use primarily developed land cover during the winter months and do not rely on forested areas or the resources they provide. While this relationship will be different during the nesting season, it implies a similar heavy reliance of vultures on urban resources and trash. This change in urban vulture diets likely has important implications for urban systems, with the source and magnitude of nutrient cycling altered (Ballejo et al., 2021). The diet composition of urban vultures may also have broader effects on urban ecosystems as vultures are

spreading anthropogenic materials and foods across the environment, creating plastic islands in otherwise natural areas (Ballejo et al., 2021).

Roost sites varied greatly in the species use. Turkey vultures would commonly roost with black vultures in small numbers, but they tended to prefer to roost in natural sites. As such, both natural tree roosts studied were dominated by turkey vultures. Black vultures would also roost in the natural sites, but in very small numbers. They greatly preferred the nearby transmission towers over trees and the highest numbers of black vultures were found on towers. I noticed similar differences between the species in terms of their departure times. The black vultures would frequently leave the roost very soon after first light while turkey vultures were more commonly seen at the roost sunning for hours after sunrise. Finally, the species also differ greatly in their foraging preferences. Black vultures are more commonly seen foraging in dumpsters near their roosting site, but turkey vultures were not spotted at dumpsters throughout this study. Turkey vultures tend to range farther and eat smaller, more sporadic food items, and thus, are much less likely to consume trash and other anthropogenic materials. These observations also show that the two species may be studied more accurately separate as they exhibit very different behaviors and preferences.

Nesting success

The trail camera footage revealed brooding and fledging periods that differed from previous research. The brooding period at Site 1 ended 35-37 days post hatching which is slightly shorter than the brooding period of 43 days reported in previous research (Stewart, 1974). While the black vulture fledging period may fluctuate with weather and resources, the observed fledging dates were quite a bit later than what has previously been noted. Juveniles from Site 1 and 2 fledged between 96-102 days post hatch, compared to 80 days post hatch in Stewart (1974) and

81-83 days post hatch in McHargue (1981). Vultures are likely consuming more trash and plastic in urban areas with less nutritional content, perhaps leading to a longer nesting period (Ballejo et al., 2021).

Reviewing trail camera footage showed that the juveniles are fed 3.2 times/day on average, with more feedings early in the brooding phase and fewer as they grow. This matches estimates of 3-4 feedings/day from Stewart (Stewart, 1974). The adults were frequently observed feeding each other before feeding the juveniles, which has not been recorded previously. The adults were also observed performing courtship behavior on three instances during the last week of April near the end of the brooding period. There are reports of second mating attempts for turkey vultures if the first nest fails (Kirk & Mossman, 1998) and black vultures will likely attempt a second nest after a failed nest as well. However, the courtship behavior observed was at an active nest with two apparently healthy young. As black vulture nests appear to be limited by food availability (Buckley, 1999), one pair of black vultures likely could not support two active nests at the same time. No successful mating attempt was observed, and the courtship behavior may serve to strengthen the bond between the two mates, although the true purpose is unclear.

There was a considerable difference in Developed and Forested land cover within 15km radii of the nesting sites, with the successful nests surrounded by less Developed and more Forested land cover. All nests were surrounded by similar amounts of Forested land cover within 0.4km radii although Developed land cover at this scale was variable. While black vultures do have a clear preference for forested land cover at nesting sites (Buckley, 1999), the more important factor is likely human presence and disturbance. Site 1 experienced minimal human disturbance during the nesting season. Other than my weekly observations, the only human disturbance caught on the trail camera was the presence of a domestic dog twice during the season. Site 3 however, had

significant human presence and disturbance, likely leading to the failure of the nest. During weekly observations, new trash and food items were seen at the site nearly every week. As these items were within feet of the nest, the adult would not have remained with the human presence. It is likely that the frequent disturbances led to the prolonged incubation period and to the failure of the nest.

Future directions

Several roosts were abandoned after the survey season began, resulting in many zero counts. The overdispersion and heteroskedasticity present in this dataset can be accounted for by using a negative binomial distribution rather than a normal distribution (O'Hara & Kotze, 2010). The top models at each scale ($\Delta AIC_c < 2$) also show strong spatial autocorrelation after adjustment using the Bonferroni correction ($p < 3.14e-17$, Fig B1-B7) and can be re-run using a simultaneous autoregressive model and Bonferroni correction to account for spatial autocorrelation after the models are reanalyzed using a negative binomial distribution.

These results are likely more representative of black vultures. While I did not track the two species separately with this study, the large majority of vultures at each roost were black vultures, often with only a few turkey vultures in the group. Given the evidence that black vultures are more associated with urban areas and turkey vultures are more associated with forest fragments (Novaes & Cintra, 2015), we may see different results if the two species were studied separately. These results are also only based on winter roost attendance, which could be very different than summer roost attendance and overall landscape use. As with most species, vultures use different habitats and landscapes throughout the year. While the resident vultures of the Charlotte Metropolitan Area use the same broad landscape throughout the year, their favorable sites may change depending on the season and the resource usage. I studied the habitat and

landscape features that impact the vulture roost attendance in the winter months and likely missed the effect of the same variables during the nesting season. Given the susceptibility of vultures to disturbance and predation during the nesting season (Houston, 2006), this warrants further research. However, the difficulty of studying the effects of these local and landscape features during the nesting season comes with the dispersed nature of the birds during this time. As the temperatures warm, the vultures disperse and begin nesting, leading to fewer birds congregating at roosts and an inaccurate idea of the number of vultures using the area (Sweeney & Fraser, 1986). Further, the birds that continue using common roosting sites during the nesting season when compared to the winter season are more likely to be immature individuals that may not accurately represent the nesting season habitat and landscape use (Rabenold, 1987).

The nesting success study was limited in scope due to the availability of accessible nests and the minimal observations that can be gathered while reducing disturbance to the nesting birds. Given the extended nesting periods observed and the potential impacts of development and human disturbance, more research is needed to better understand how urban land cover and changing climates are affecting the nesting success of black vultures in the southeastern United States. Of special interest is the altered vulture diet composition in urban areas (Ballejo et al., 2021) and its impact on reproductive success and the ecosystem as a whole. Vulture populations are increasing and may be more reliant on anthropogenic food sources in urban systems, a change that could impact nutrient cycling over large scales and decrease the vulture reproductive output of urban areas.

CONCLUSION

As urban areas continue growing in size and population, it is important to understand how these areas impact local wildlife populations. By testing the impacts of multiple local and landscape features on vulture roost attendance, this study showed that the corridor edge vegetation height, date, wind speed, carcass density, and Developed-Forest edge density led to lower roosting attendance while Developed land cover has a positive effect on the number of roosting vultures. Developed land cover may have a negative effect on nesting success as well, but vultures appear to be fairly adaptive and tolerate heavily urban areas for nesting activities, although excessive disturbance can reduce their success. While neither black or turkey vultures are threatened species, they provide essential ecosystem services and are a valuable part of an urban ecosystem. However, they also lead to conflicts with human populations. Future research on vulture roosting attendance should focus on the site-specific features that attract vultures, how to better manage the roosting vulture populations to reduce human-wildlife conflicts, and the ecosystem level impacts of altered vulture diet composition. Given the results seen on nesting success here, the effect of developed land cover on nesting success and the overall reproductive output of urban areas warrants additional research as well. With the behavioral differences between the two species, they may provide more clear associations and management applications if studied separately.

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Table 1 – Variables measured to investigate black vulture (*Coragyps atratus*) and turkey vulture (*Cathartes aura*) roost attendance in the Charlotte Metropolitan Area, USA. Developed land cover, Open water land cover, carcass density, and Developed-Forest edge density measured within landscapes with radii of 0.4, 0.5, 1, 2, 3, 4, 5, 10, 15, and 20km.

Variable	Type	Spatial scale	Data source
Number of vultures	Response	NA	Sunrise roost surveys
Date	Explanatory	NA	NA
Temperature	Explanatory	Local	Weather Underground Personal Weather Station (PWS) (Weather Underground, 2021)
Wind speed	Explanatory	Local	Weather Underground Personal Weather Station (PWS) (Weather Underground, 2021)
Cloud cover	Explanatory	Local	Visual estimate of percent cloud coverage
Corridor width	Explanatory	Local	Google Earth and rangefinder measurements
Height of roost	Explanatory	Local	Clinometer and rangefinder measurements
Height of corridor edges	Explanatory	Local	Clinometer and rangefinder measurements
Developed land cover	Explanatory	Landscape	MRLC National Land Cover Database (Wickham, et al., 2014)
Open water land cover	Explanatory	Landscape	MRLC National Land Cover Database (Wickham, et al., 2014)
Carcass density	Explanatory	Landscape	North Carolina Department of Transportation and Wildlife Resources Commission (NCDOT, 2018), TigerLine roadway density (US Census Bureau, 2018)
Developed-Forest land cover edge density	Explanatory	Landscape	MRLC National Land cover Database (Wickham, et al., 2014), Fragstats (McGarigal, et al., 2015)

Table 2 – Variables measured to study the black vulture (*Coragyps atratus*) nesting success across urban landscapes within the Charlotte Metropolitan Area, USA. Developed land cover, Forested land cover, and Open Water land cover measured within landscapes with radii of 0.4km and 15km.

Variable	Type	Spatial scale	Date source
Feedings/day	Response	NA	Weekly observations, trail camera footage
Young fledged/nest	Response	NA	Weekly observations, trail camera footage
Brooding period length	Response	NA	Weekly observations, trail camera footage
Days to fledging	Response	NA	Weekly observations, trail camera footage
Developed land cover	Explanatory	Landscape	MRLC National Land cover Database data (Wickham, et al., 2014)
Forested land cover	Explanatory	Landscape	MRLC National Land cover Database data (Wickham, et al., 2014)
Open water land cover	Explanatory	Landscape	MRLC National Land cover Database data (Wickham, et al., 2014)

Table 3 – The top models ($\Delta AIC_c < 2$) describing black vulture (*Coragyps atratus*) and turkey vulture (*Cathartes aura*) roost attendance in the Charlotte Metropolitan Area. Variables include survey date (DATE), corridor edge vegetation height (VEG), wind speed (WIND), Developed land cover within 15 km radii surrounding roosts (DEV_15), Developed-Forest edge density within 15 km radii surrounding roosts (EDGE_15), carcass density within 15 km radii surrounding roosts (CARC_15), and carcass density in 20 km radii surrounding roosts (CARC_20).

Model	df	logLik	AICc	ΔAIC_c	weight
VEG+CARC_20	5	-265.06	540.4	0	0.23
VEG+EDGE_15	5	-265.36	541.0	0.59	0.17
VEG+DATE+CARC_20	6	-264.33	541.1	0.65	0.17
VEG+DATE+EDGE_15	6	-264.70	541.8	1.39	0.12
VEG+WIND+CARC_20	6	-264.72	541.8	1.43	0.11
VEG+CARC_15+EDGE_15	6	-264.78	542.0	1.56	0.11
VEG+DEV_15+EDGE_15	6	-264.98	542.4	1.96	0.09

Table 4 – Reproductive measures for three black vulture (*Coragyps atratus*) nests monitored in the Charlotte Metropolitan Area in 2020.

	Site 1	Site 2	Site 3
Number of eggs laid	2	2	2
Lay date	February 15-17 ¹	February 12-20 ¹	Before March 19 ²
Number of eggs hatched	2	2	0
Hatching date	March 24-26	March 21-29 ³	NA
Period between hatching and standing/flapping behavior (days)	14	Unknown	NA
Period between hatching and flight feather development (days)	30	Unknown	NA
Brooding period (days)	35-37	Unknown	NA
Number of young fledged	2	2	0
Period between hatching and fledgling (days)	97-101	96-102	NA
Number of feedings per day	3.2 ± 0.17	Unknown	NA

¹Estimated using incubation periods from equations in McHargue (1981) and Stewart (1974).

²Date monitoring initiated. More precise estimate of lay date was not possible due to egg mortality, prolonged incubation time, and nest disturbance.

³Estimated based on juvenile development when compared to Site 1 and reports from landowner.

Table 5 – The proportion of landscapes surrounding black vulture (*Coragyps atratus*) nests monitored in 2020 in the Charlotte Metropolitan Area covered by Developed, Forested, and Open Water land covers (Wickham, et al., 2014). Landscapes had radii of 0.4 km or 15 km, chosen to estimate the features within the core home range of nesting vultures (Holland, 2015) and at the 15 km scale found to be an important predictor of roost attendance.

	Site 1	Site 2	Site 3
Number of young fledged	2	2	0
Developed within 0.4 km (%)	18	57	29
Forested within 0.4 km (%)	42	43	55
Open water within 0.4 km (%)	4	0	1
Developed within 15 km (%)	24	24	63
Forested within 15 km (%)	45	72	26
Open water within 15 km (%)	13	0	1

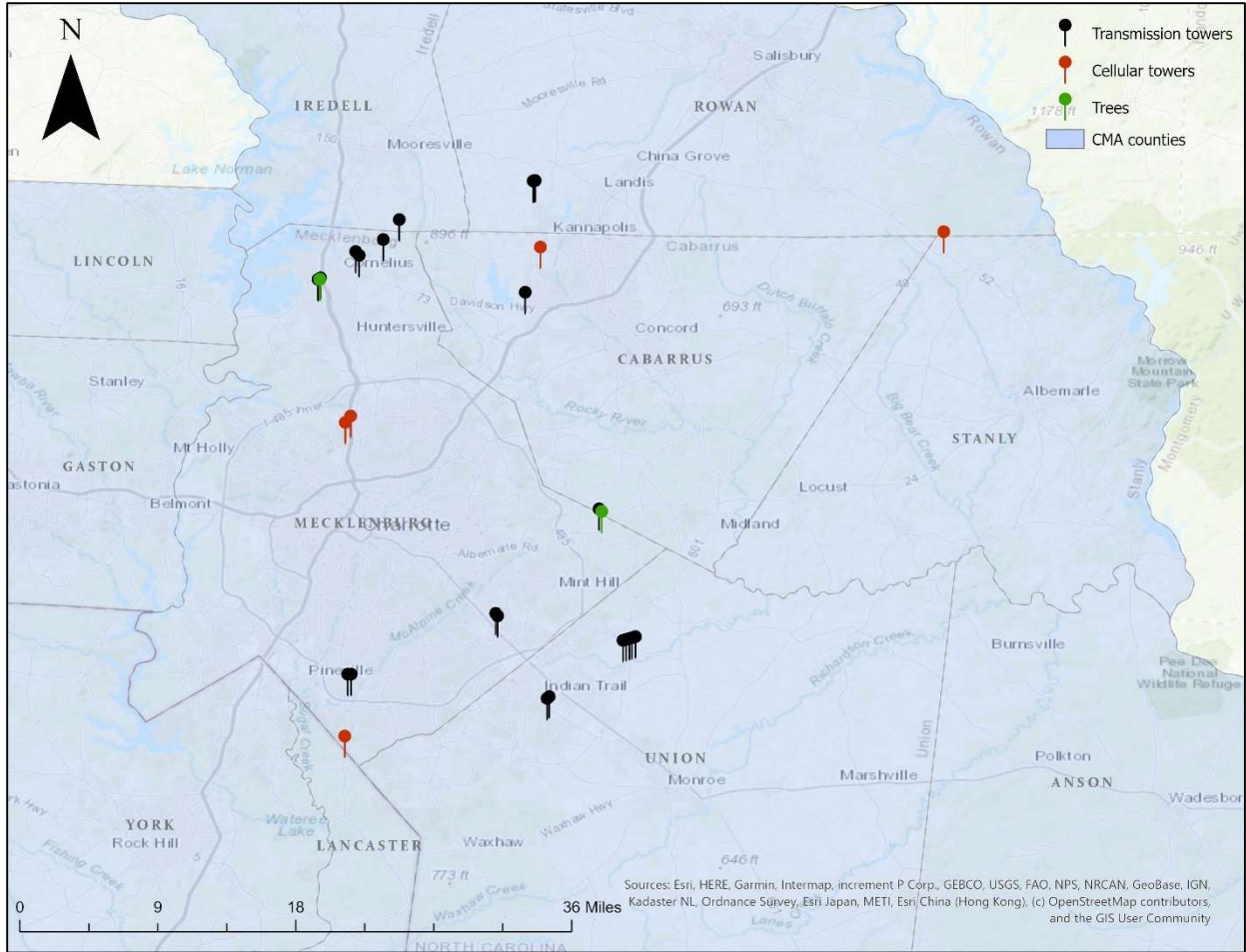


Figure 1 – All roosting sites (29) within the Charlotte Metropolitan Area, USA, labelled by roost structure type.

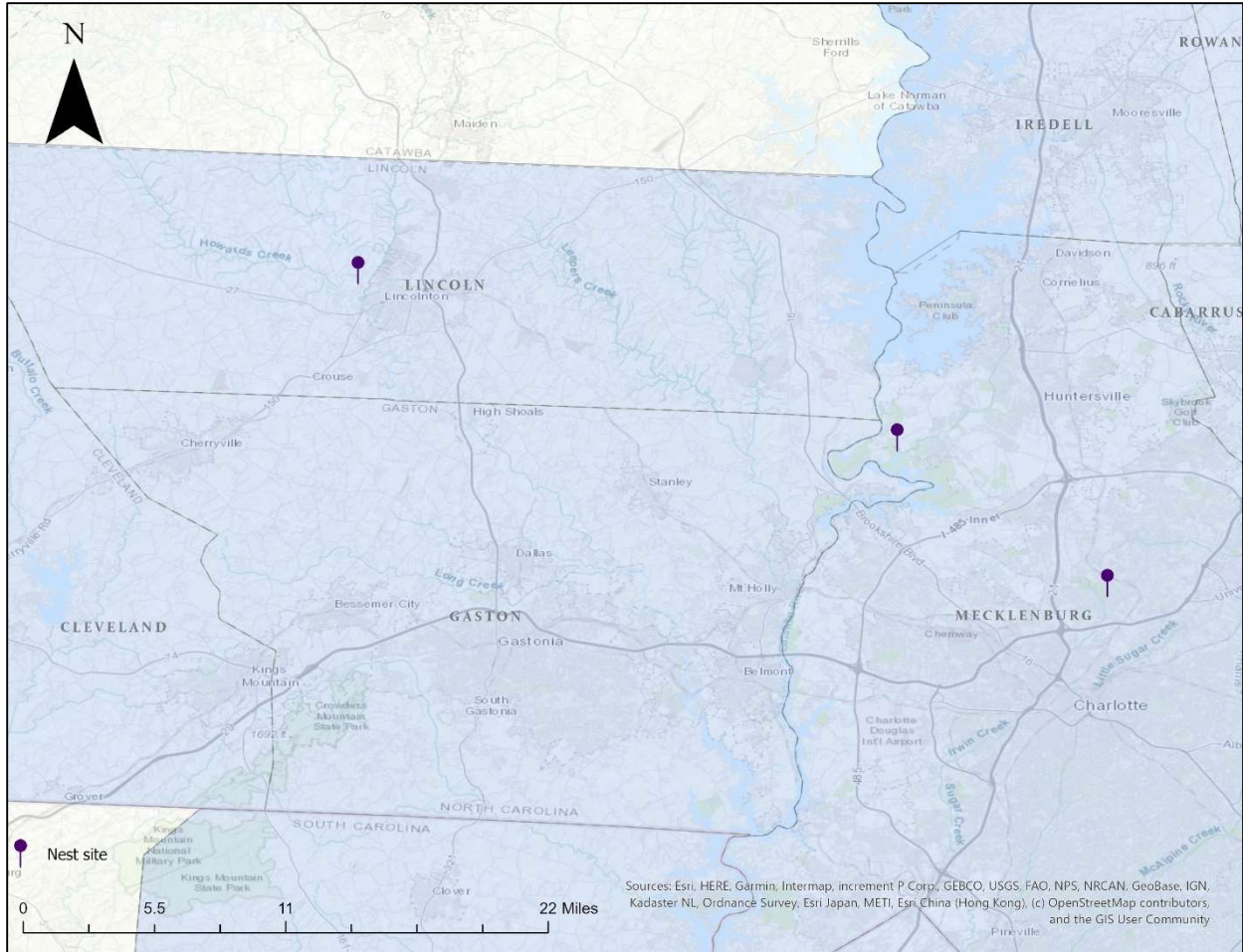


Figure 2 – All active nest sites (3) within the Charlotte Metropolitan Area, USA studied in 2020.

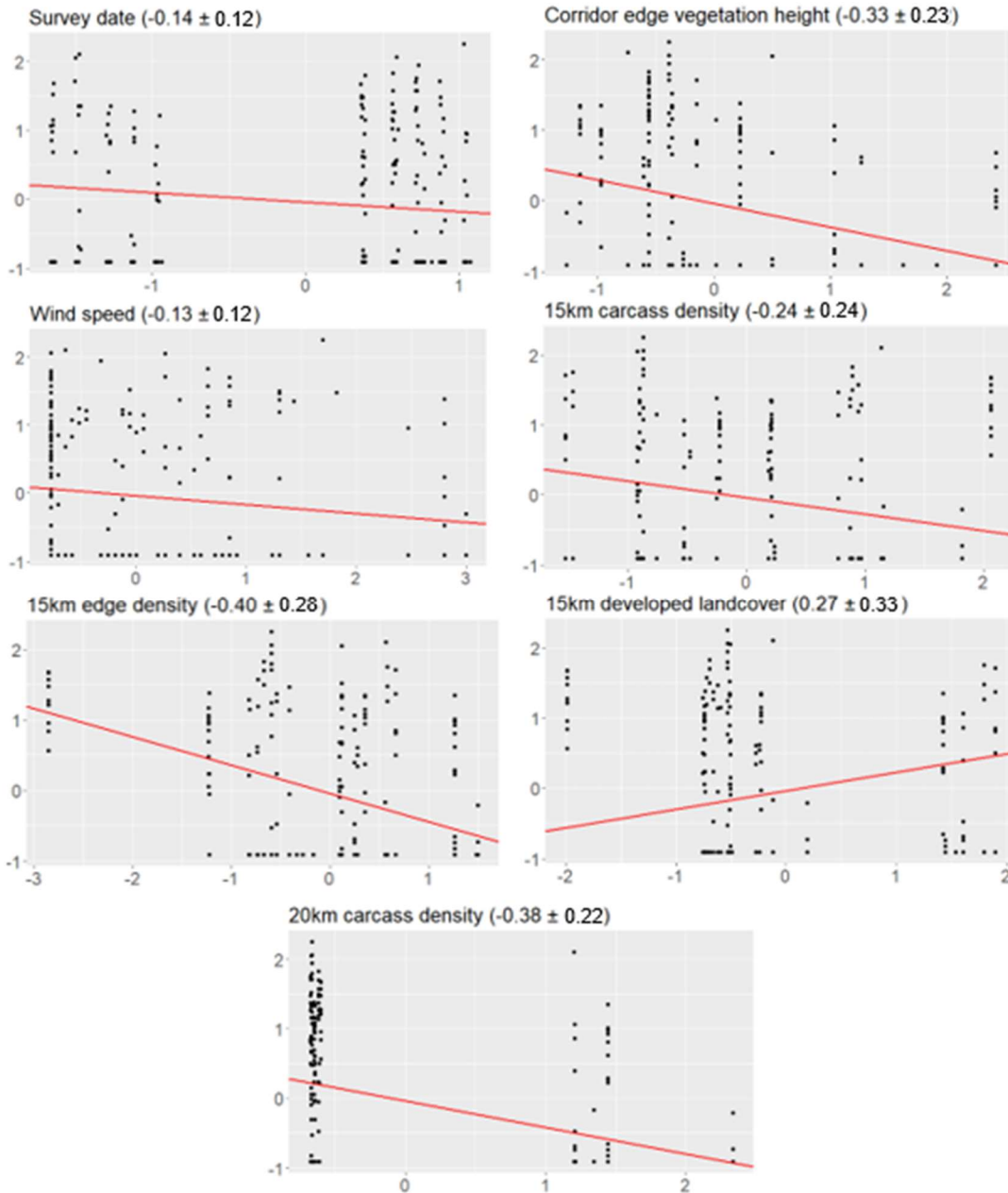


Figure 3 – The effects of predictors in the top models ($\Delta AIC_c < 2$) describing black vulture (*Coragyps atratus*) and turkey vulture (*Cathartes aura*) roost attendance in the Charlotte Metropolitan Area. Standardized coefficients ± 2 SE are shown for each predictor variable with the standardized roost attendance. Corridor edge vegetation height was measured as the height of vegetation on the edges of open right-of-way corridors surrounding roosts. Carcass density was measured as the number of deer-automobile collisions/km roadway/km² landscape area in landscapes with radii of 15km or 20km surrounding roosts. Edge density was measured as the length of edge between Forested and Developed land covers (Wickham, et al., 2014) within 15 km radii landscapes surrounding roosts. Developed land cover was measured as the proportion of Developed land cover (open space, low intensity, medium intensity, and high intensity) within the total landscape (Wickham, et al., 2014).



Figure 4 – Two adult black vultures (*Coragyps atratus*) brooding at a nest in the Charlotte Metropolitan Area in March 2020, 5-6 days after the chicks hatched.



Figure 5 – One adult black vulture (*Coragyps atratus*) and two chicks approximately six weeks post-hatching (in the background, seen just above the adult's head) at a nest site in the Charlotte Metropolitan Area in May 2020.

APPENDIX A – ROOST ADJUSTMENT

Table A1 – A 6th order polynomial regression representing the proportion of vulture roosts remaining with respect to the time of sunrise. Roost attendance data for 15 days from 60 minutes pre-sunrise to 60 minutes post-sunrise was analyzed and fitted with a polynomial approximator describing the expected proportion of the roost remaining with regards to the time of sunrise. The generated equation was used to adjust the roost counts from the first survey season for accurate counts.

Call: lm(formula = poly(Time, 6, raw = T), data = departure)					
Residuals:					
Min	1Q	Median	3Q	Max	
-0.86	-0.13	0.01	0.13	0.67	
Coefficients:					
(Intercept)	Estimate	Std. Error	T value	Pr(> t)	
Poly(Time, 6, raw = T)1	6.84e-01	1.46e-02	46.97	<2e-16 ***	
Poly(Time, 6, raw = T)2	-2.43e-02	1.50e-03	-16.18	<2e-16 ***	
Poly(Time, 6, raw = T)3	-2.99e-05	8.12e-05	-0.37	0.71	
Poly(Time, 6, raw = T)4	2.49e-05	4.86e-06	5.12	3.61e-07 ***	
Poly(Time, 6, raw = T)5	-1.23e-07	7.86e-08	-1.57	0.12	
Poly(Time, 6, raw = T)6	-1.21e-08	4.16e-09	-2.92	0.00 **	
Poly(Time, 6, raw = T)6	1.43e-10	4.92e-11	2.90	0.00 **	
Signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					
Residual standard error: 0.238 on 1042 degrees of freedom					
Multiple R-squared: 0.60, Adjusted R-squared: 0.60					
F-statistic: 262.3 on 6 and 1042 DF, p-value: < 2.2e-16					

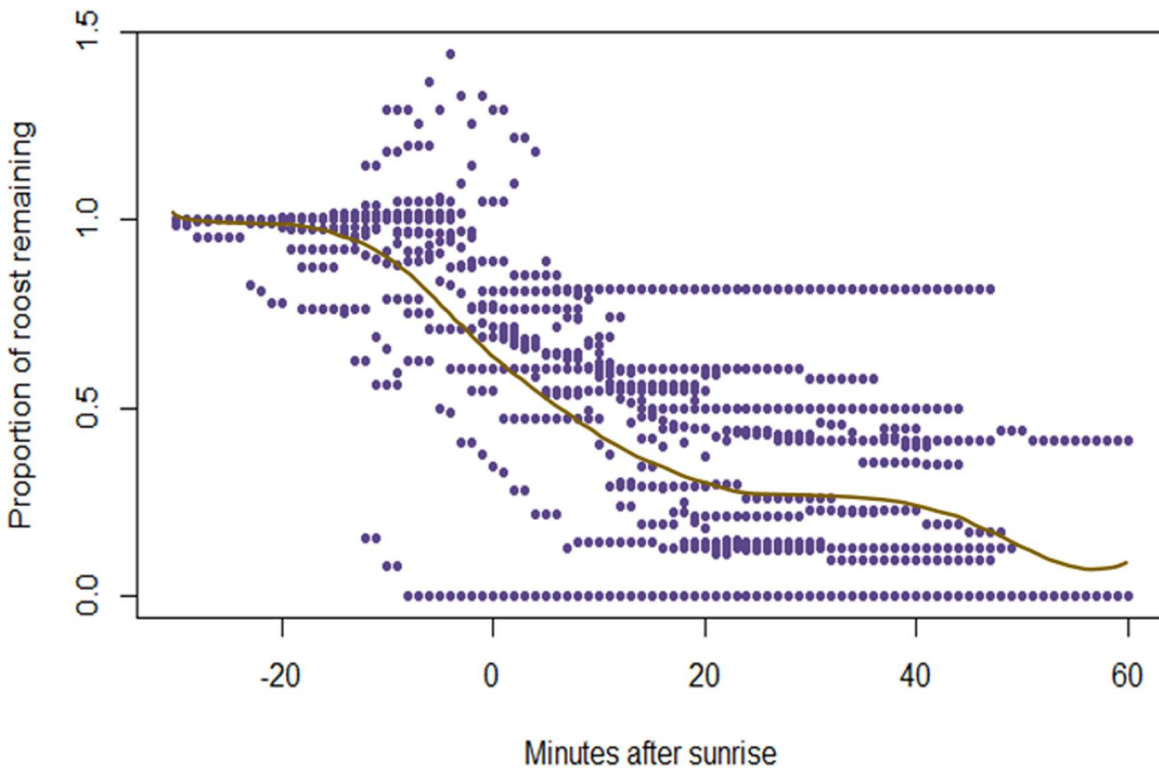


Figure A1 – The proportion of roost remaining with respect to the minutes after sunrise. The data was fit with a 6th order polynomial regression. Roost attendance data for 15 days from 60 minutes pre-sunrise to 60 minutes post-sunrise was analyzed and fitted with a polynomial approximator describing the expected proportion of the roost remaining with regards to the time of sunrise.

APPENDIX B – DATA AND CORRELATION VALUES

Table B1 – The averages and standard errors for all variables measured for roost attendance.

Date	Count	Temperature (C)	Wind speed (mph)	Cloud cover (%)	Corridor width (m)	Roost height (m)	Corridor edge vegetation height (m)
Average	36.47	4.16	1.19	44.05	37.43	58.05	33.79
SE	3.63	0.40	0.11	3.08	22.26	42.04	16.20
0.4km							
Developed land cover	0.4km Open Water land cover	0.4km carcass density	0.4km edge density	0.5km Developed land cover	0.5km Open Water land cover	0.5km carcass density	0.5km edge density
Average	0.01	0.03	0.29	0.40	4.43e-3	0.03	0.29
SE	0.01	0.13	0.30	0.35	0.01	0.11	0.27
1km							
Developed land cover	1km Open Water land cover	1km carcass density	1km edge density	2km Developed land cover	2km Open Water land cover	2km carcass density	2km edge density
Average	2.28e-3	8.25e-3	0.29	0.35	2.59e-3	2.81e-3	0.29
SE	2.60e-3	0.01	0.22	0.28	3.31e-3	2.82e-3	0.13
3km							
Developed land cover	3km Open Water land cover	3km carcass density	3km edge density	4km Developed land cover	4km Open Water land cover	4km carcass density	4km edge density
Average	1.23e-2	1.43e-3	0.30	0.35	1.85e-2	6.25e-4	0.32
SE	2.27e-2	1.35e-3	0.12	0.22	3.37e-2	5.02e-4	0.12
5km							
Developed land cover	5km Open Water land cover	5km carcass density	5km edge density	10km Developed land cover	10km Open Water land cover	10km carcass density	10km edge density
Average	2.04e-2	3.45e-4	0.32	0.33	3.98e-2	7.85e-05	0.32
SE	3.46e-2	2.07e-4	0.11	0.16	6.04e-2	4.25e-05	7.84e-2
15km							
Developed land cover	15km Open Water land cover	15km carcass density	15km edge density	20km Developed land cover	20km Open Water land cover	20km carcass density	20km edge density
Average	3.62e-2	3.42E-05	0.32	0.32	3.39e-2	2.21e-4	0.32
SE	4.93e-2	1.65E-05	0.04	9.73e-2	3.70e-2	3.74e-4	3.78e-2

Table B2 – Variance inflation factor (VIF) values for all roost attendance variables. Values less than five were considered acceptable, high values are highlighted in red.

Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height
0.4 km	1.12	1.05	1.09	2.40	1.25	1.32	1.81	1.51	2.13	1.44
0.5 km	1.12	1.05	1.09	2.68	1.37	1.57	1.90	1.59	2.34	1.41
1 km	1.12	1.05	1.09	2.13	2.12	2.14	1.90	1.44	2.64	1.40
2 km	1.12	1.09	1.10	1.72	1.21	1.78	1.84	1.38	2.01	1.20
3 km	1.12	1.09	1.10	1.71	1.41	2.19	2.01	1.10	1.88	1.24
4 km	1.13	1.09	1.10	1.87	1.50	2.07	2.05	1.04	1.81	1.32
5 km	1.13	1.08	1.10	2.28	1.49	2.05	2.17	1.05	1.70	1.37
10 km	1.13	1.08	1.10	4.31	2.81	2.41	4.46	1.16	2.15	1.70
15 km	1.13	1.09	1.10	6.69	3.58	3.71	3.77	1.07	1.54	1.52
20 km	1.13	1.10	1.10	5.35	4.98	2.80	6.73	1.06	2.00	1.25

Table B3 – The pairwise correlation matrix for all data at the 0.4km landscape scale. Correlation values less than 0.7 were considered acceptable.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.464	0.401	-0.274	-0.108	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.193	0.167	-0.070	0.015	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	0.036	-0.089	0.024	0.110	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.257	0.022	-0.100	-0.036	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.022	-0.051	-0.035	0.050	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.464	-0.193	0.036	-0.257	-0.022	1	-0.321	0.335	-0.393	-0.126	-0.526	0.436	-0.075
Open water land cover	0.401	0.167	-0.089	0.022	-0.051	-0.321	1	-0.112	0.134	0.127	0.260	-0.296	0.029
Carcass density	-0.274	-0.070	0.024	-0.100	-0.035	0.335	-0.112	1	-0.200	0.117	-0.113	0.422	-0.215
Edge density	-0.108	0.015	0.110	-0.036	0.050	-0.393	0.134	-0.200	1	-0.287	0.006	-0.390	0.219
Corridor width	-0.024	-0.063	0.018	0.015	0.006	-0.126	0.127	0.117	-0.287	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.526	0.260	-0.113	0.006	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.436	-0.296	0.422	-0.390	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.075	0.029	-0.215	0.219	-0.161	0.112	-0.266	1

Table B4 – The pairwise correlation matrix for all data at the 0.5km landscape scale. Correlation values less than 0.7 were considered acceptable.

Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
1	0.435	-0.142	0.234	-0.027	-0.432	0.420	-0.376	-0.082	-0.024	0.528	-0.235	-0.089
0.435	1	-0.178	0.165	-0.057	-0.187	0.216	-0.100	0.019	-0.063	0.361	-0.141	-0.036
-0.142	-0.178	1	-0.008	0.297	0.028	-0.102	0.034	0.094	0.018	-0.182	-0.047	-0.033
0.234	0.165	-0.008	1	0.078	-0.264	0.056	-0.14	-0.021	0.015	0.288	-0.144	-0.002
-0.027	-0.057	0.297	0.078	1	-0.031	-0.073	-0.051	0.052	0.006	-0.019	-0.021	-0.004
-0.432	-0.187	0.028	-0.264	-0.031	1	-0.298	0.480	-0.426	-0.093	-0.543	0.428	-0.082
0.420	0.216	-0.102	0.056	-0.073	-0.298	1	-0.170	0.130	0.131	0.359	-0.286	-0.009
-0.376	-0.100	0.034	-0.14	-0.051	0.480	-0.170	1	-0.319	0.181	-0.238	0.468	-0.208
-0.082	0.019	0.094	-0.021	0.052	-0.426	0.130	-0.319	1	-0.299	0.037	-0.395	0.210
-0.024	-0.063	0.018	0.015	0.006	-0.093	0.131	0.181	-0.299	1	-0.124	-0.033	-0.161
0.528	0.361	-0.182	0.288	-0.019	-0.543	0.359	-0.238	0.037	-0.124	1	-0.217	0.112
-0.235	-0.141	-0.047	-0.144	-0.021	0.428	-0.286	0.468	-0.395	-0.033	-0.217	1	-0.266
-0.089	-0.036	-0.033	-0.002	-0.004	-0.082	-0.009	-0.208	0.210	-0.161	0.112	-0.266	1

Table B5 – The pairwise correlation matrix for all data at the 1km landscape scale. Correlation values less than 0.7 were considered acceptable.

Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
1	0.435	-0.142	0.234	-0.027	-0.328	0.065	-0.364	-0.128	-0.024	0.528	-0.235	-0.089
0.435	1	-0.178	0.165	-0.057	-0.164	0.168	-0.129	0.001	-0.063	0.361	-0.141	-0.036
-0.142	-0.178	1	-0.008	0.297	-0.005	-0.054	-0.008	0.158	0.018	-0.182	-0.047	-0.033
0.234	0.165	-0.008	1	0.078	-0.284	0.083	-0.162	-0.039	0.015	0.288	-0.144	-0.002
-0.027	-0.057	0.297	0.078	1	-0.051	-0.030	-0.055	0.038	0.006	-0.019	-0.021	-0.004
-0.328	-0.164	-0.005	-0.284	-0.051	1	-0.435	0.609	-0.209	-0.003	-0.568	0.454	-0.104
0.065	0.168	-0.054	0.083	-0.030	-0.435	1	-0.509	0.367	0.055	0.504	-0.435	0.247
-0.364	-0.129	-0.008	-0.162	-0.055	0.609	-0.509	1	-0.380	0.171	-0.421	0.531	-0.253
-0.128	0.001	0.158	-0.039	0.038	-0.209	0.367	-0.380	1	-0.331	-0.034	-0.264	0.133
-0.024	-0.063	0.018	0.015	0.006	-0.003	0.055	0.171	-0.331	1	-0.124	-0.033	-0.161
0.528	0.361	-0.182	0.288	-0.019	-0.568	0.504	-0.421	-0.034	-0.124	1	-0.217	0.112
-0.235	-0.141	-0.047	-0.144	-0.021	0.454	-0.435	0.531	-0.264	-0.033	-0.217	1	-0.266
-0.089	-0.036	-0.033	-0.002	-0.004	-0.104	0.247	-0.253	0.133	-0.161	0.112	-0.266	1

Table B6 – The pairwise correlation matrix for all data at the 2km landscape scale. Correlation values less than 0.7 were considered acceptable.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.252	-0.072	0.251	-0.247	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.155	0.050	0.169	-0.026	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	-0.012	-0.045	-0.183	0.132	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.320	-0.097	0.322	-0.247	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.064	-0.067	-0.025	-0.043	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.252	-0.155	-0.012	-0.320	-0.064	1	-0.021	0.020	0.188	0.042	-0.539	0.411	-0.122
Open water land cover	-0.072	0.050	-0.045	-0.097	-0.067	-0.021	1	0.058	0.083	0.142	0.201	-0.148	-0.132
Carcass density	0.251	0.169	-0.183	0.322	-0.025	0.020	0.058	1	-0.390	-0.004	0.391	0.137	-0.086
Edge density	-0.247	-0.026	0.132	-0.247	-0.043	0.188	0.083	-0.390	1	-0.364	-0.165	-0.112	-0.009
Corridor width	-0.024	-0.063	0.018	0.015	0.006	0.042	0.142	-0.004	-0.364	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.539	0.201	0.391	-0.165	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.411	-0.148	0.137	-0.112	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.122	-0.132	-0.086	-0.009	-0.161	0.112	-0.266	1

Table B7 – The pairwise correlation matrix for all data at the 3km landscape scale. Correlation values less than 0.7 were considered acceptable.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.209	-0.081	0.342	-0.446	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.163	-0.041	0.207	-0.163	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	-0.005	-0.123	-0.177	0.172	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.343	-0.082	0.45	-0.344	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.076	-0.015	-0.007	-0.052	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.209	-0.164	-0.005	-0.343	-0.076	1	0.277	-0.455	0.391	0.074	-0.508	0.395	-0.164
Open water land cover	-0.081	-0.041	-0.123	-0.082	-0.015	0.277	1	-0.138	-0.309	0.112	-0.164	0.302	-0.056
Carcass density	0.342	0.207	-0.177	0.450	-0.007	-0.455	-0.138	1	-0.420	-0.075	0.627	-0.125	0.012
Edge density	-0.446	-0.163	0.172	-0.344	-0.052	0.391	-0.309	-0.420	1	-0.181	-0.358	0.220	-0.168
Corridor width	-0.024	-0.063	0.018	0.015	0.006	0.074	0.112	-0.075	-0.181	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.508	-0.164	0.627	-0.358	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.395	0.302	-0.125	0.220	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.164	-0.056	0.012	-0.168	-0.161	0.112	-0.266	1

Table B8 – The pairwise correlation matrix for all data at the 4km landscape scale. Correlation values less than 0.7 were considered acceptable.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.186	-0.091	0.265	-0.418	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.167	-0.060	0.147	-0.183	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	0.010	-0.124	-0.152	0.171	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.35	-0.085	0.422	-0.327	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.083	-0.010	-0.004	-0.066	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.186	-0.167	0.010	-0.35	-0.083	1	0.201	-0.523	0.517	0.104	-0.496	0.379	-0.195
Open water land cover	-0.091	-0.060	-0.124	-0.085	-0.010	0.201	1	-0.245	-0.253	0.103	-0.196	0.362	-0.053
Carcass density	0.265	0.147	-0.152	0.422	-0.004	-0.523	-0.245	1	-0.382	-0.091	0.601	-0.150	-0.013
Edge density	-0.418	-0.183	0.171	-0.327	-0.066	0.517	-0.253	-0.382	1	-0.018	-0.451	0.240	-0.256
Corridor width	-0.024	-0.063	0.018	0.015	0.006	0.104	0.103	-0.091	-0.018	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.496	-0.196	0.601	-0.451	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.379	0.362	-0.150	0.240	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.195	-0.053	-0.013	-0.256	-0.161	0.112	-0.266	1

Table B9 – The pairwise correlation matrix for all data at the 5km landscape scale. Correlation values less than 0.7 were considered acceptable.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.166	-0.124	0.193	-0.425	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.164	-0.088	0.138	-0.171	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	0.015	-0.110	-0.162	0.165	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.352	-0.093	0.359	-0.332	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.089	-0.005	-0.009	-0.063	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.166	-0.164	0.015	-0.352	-0.089	1	0.171	-0.628	0.589	0.091	-0.496	0.376	-0.208
Open water land cover	-0.124	-0.088	-0.110	-0.093	-0.005	0.171	1	-0.210	-0.213	0.131	-0.191	0.403	-0.062
Carcass density	0.193	0.138	-0.162	0.359	-0.009	-0.628	-0.210	1	-0.401	-0.153	0.529	-0.199	-0.002
Edge density	-0.425	-0.171	0.165	-0.332	-0.063	0.589	-0.213	-0.401	1	0.021	-0.497	0.237	-0.265
Corridor width	-0.024	-0.063	0.018	0.015	0.006	0.091	0.131	-0.153	0.021	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.496	-0.191	0.529	-0.497	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.376	0.403	-0.199	0.237	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.208	-0.062	-0.002	-0.265	-0.161	0.112	-0.266	1

Table B10 – The pairwise correlation matrix for all data at the 10km landscape scale. Correlation values less than 0.7 were considered acceptable.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.066	-0.216	0.146	-0.255	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.036	-0.236	0.031	-0.106	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	0.046	0.003	-0.030	0.151	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.314	-0.075	0.238	-0.247	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.104	0.078	0.024	-0.059	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.066	-0.066	0.046	-0.314	-0.104	1	-0.288	-0.492	0.790	0.010	-0.292	0.186	-0.177
Open water land cover	-0.216	-0.236	0.003	-0.075	0.078	-0.288	1	-0.375	-0.384	0.165	-0.341	0.467	-0.045
Carcass density	0.146	0.031	-0.030	0.238	0.024	-0.492	-0.375	1	-0.224	-0.151	0.378	-0.480	-0.022
Edge density	-0.255	-0.106	0.151	-0.247	-0.059	0.790	-0.384	-0.224	1	0.131	-0.410	0.090	-0.269
Corridor width	-0.024	-0.063	0.018	0.015	0.006	0.010	0.165	-0.151	0.131	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.292	-0.341	0.378	-0.410	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.186	0.467	-0.480	0.090	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.177	-0.045	-0.022	-0.269	-0.161	0.112	-0.266	1

Table B11 – The pairwise correlation matrix for all data at the 15km landscape scale. Correlation values less than 0.7 were considered acceptable, high correlation is seen between developed land cover and edge density, highlighted in red.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.081	-0.218	0.128	-0.058	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.055	-0.236	0.067	-0.139	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	0.088	0.054	-0.057	0.122	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.287	-0.079	0.183	-0.228	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.085	0.108	-0.010	-0.039	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.081	-0.055	0.088	-0.287	-0.085	1	-0.338	-0.393	0.766	-0.015	-0.317	0.118	-0.196
Open water land cover	-0.218	-0.236	0.054	-0.079	0.108	-0.338	1	-0.512	-0.160	0.173	-0.325	0.415	0.005
Carcass density	0.128	0.067	-0.057	0.183	-0.010	-0.393	-0.512	1	-0.177	-0.152	0.354	-0.525	0.014
Edge density	-0.058	-0.139	0.122	-0.228	-0.039	0.766	-0.160	-0.177	1	0.070	-0.406	0.029	-0.364
Corridor width	-0.024	-0.063	0.018	0.015	0.006	-0.015	0.173	-0.152	0.070	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.317	-0.325	0.354	-0.406	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.118	0.415	-0.525	0.029	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.196	0.005	0.014	-0.364	-0.161	0.112	-0.266	1

Table B12 – The pairwise correlation matrix for all data at the 20km landscape scale. Correlation values less than 0.7 were considered acceptable, high correlation is seen between developed land cover and edge density, highlighted in red.

	Site ID	Date	Temperature	Wind speed	Cloud cover	Developed land cover	Open water land cover	Carcass density	Edge density	Corridor width	Roost height	Corridor edge vegetation height	Count
Site ID	1	0.435	-0.142	0.234	-0.027	-0.097	-0.217	-0.073	-0.055	-0.024	0.528	-0.235	-0.089
Date	0.435	1	-0.178	0.165	-0.057	-0.073	-0.237	-0.132	-0.200	-0.063	0.361	-0.141	-0.036
Temperature	-0.142	-0.178	1	-0.008	0.297	0.127	0.061	0.065	0.106	0.018	-0.182	-0.047	-0.033
Wind speed	0.234	0.165	-0.008	1	0.078	-0.285	-0.129	-0.224	-0.280	0.015	0.288	-0.144	-0.002
Cloud cover	-0.027	-0.057	0.297	0.078	1	-0.059	0.106	-0.066	-0.002	0.006	-0.019	-0.021	-0.004
Developed land cover	-0.097	-0.073	0.127	-0.285	-0.059	1	-0.259	0.470	0.724	-0.045	-0.360	0.077	-0.193
Open water land cover	-0.217	-0.237	0.061	-0.129	0.106	-0.259	1	-0.408	0.264	0.093	-0.320	0.351	0.065
Carcass density	-0.073	-0.132	0.065	-0.224	-0.066	0.470	-0.408	1	0.434	0.092	-0.323	-0.125	-0.341
Edge density	-0.055	-0.200	0.106	-0.280	-0.002	0.724	0.264	0.434	1	0.061	-0.440	0.156	-0.279
Corridor width	-0.024	-0.063	0.018	0.015	0.006	-0.045	0.093	0.092	0.061	1	-0.124	-0.033	-0.161
Roost height	0.528	0.361	-0.182	0.288	-0.019	-0.360	-0.320	-0.323	-0.440	-0.124	1	-0.217	0.112
Corridor edge vegetation height	-0.235	-0.141	-0.047	-0.144	-0.021	0.077	0.351	-0.125	0.156	-0.033	-0.217	1	-0.266
Count	-0.089	-0.036	-0.033	-0.002	-0.004	-0.193	0.065	-0.341	-0.279	-0.161	0.112	-0.266	1

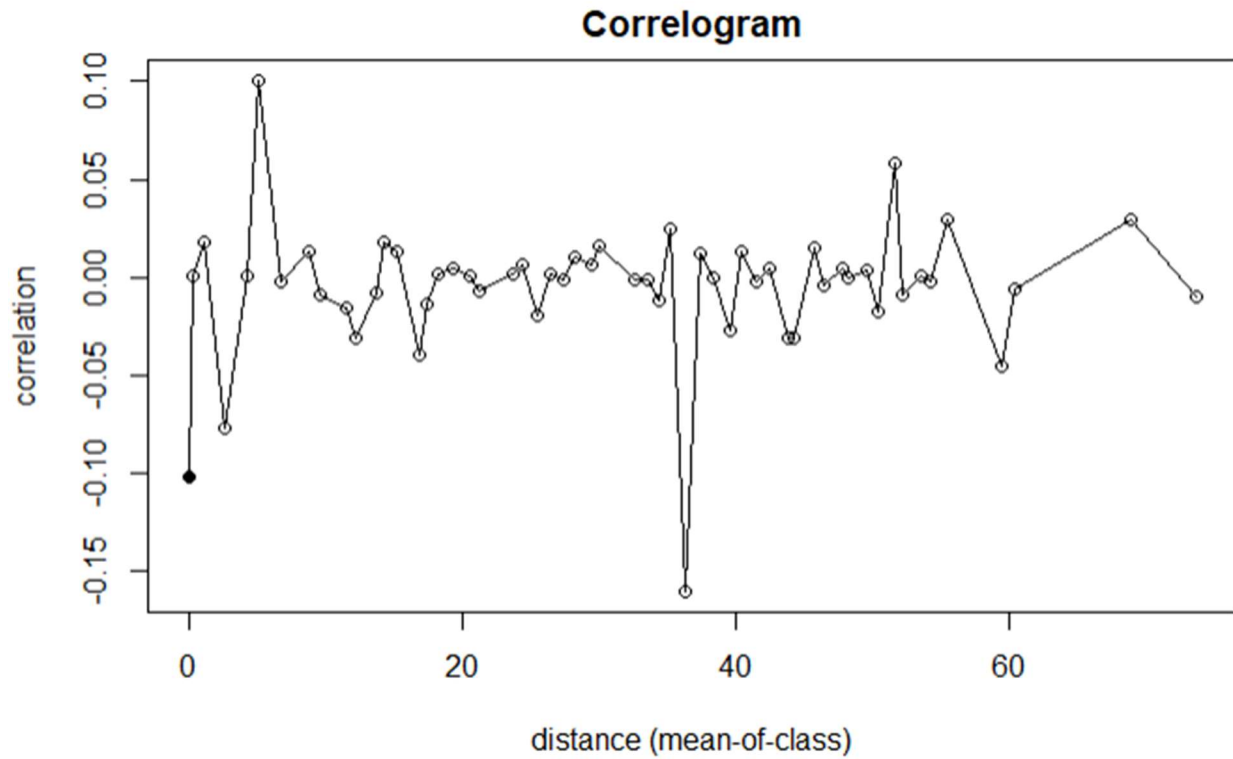


Figure B1 – Correlogram for Model 1 (Table 5) with significant spatial autocorrelation ($p < 3.14e-17$). The model includes the corridor edge vegetation height and the carcass density within 20 km radii surrounding roosts.

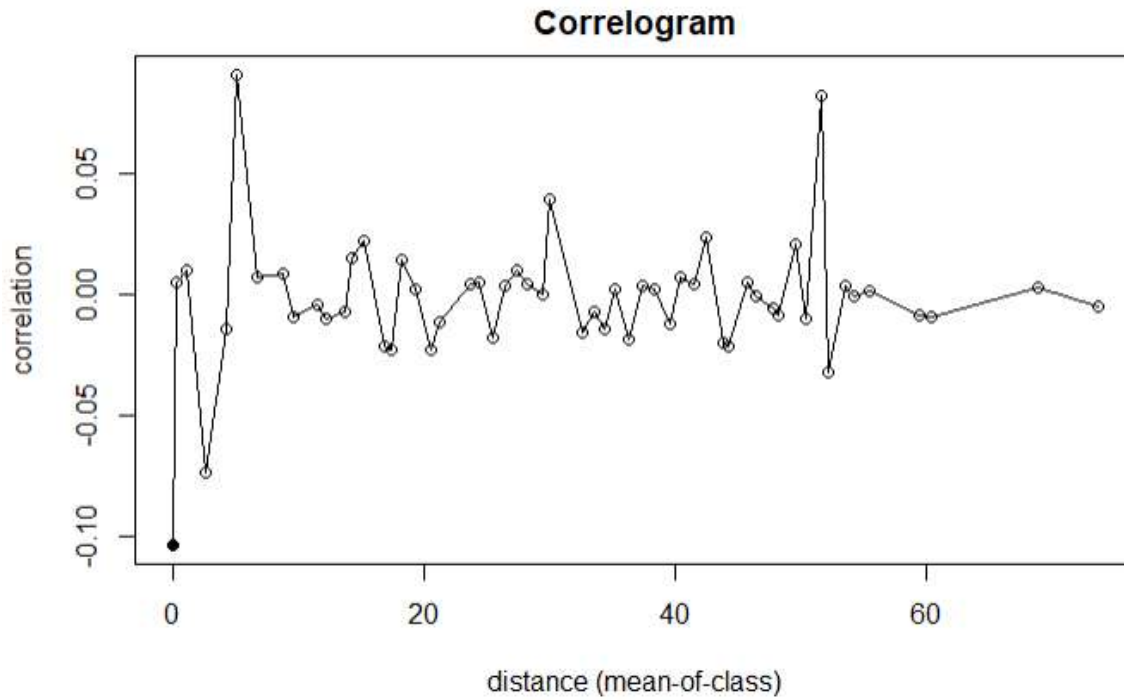


Figure B2 – Correlogram for Model 2 (Table 5) with significant spatial autocorrelation ($p < 3.14 \times 10^{-17}$). The model includes the corridor edge vegetation height and the Developed-Forest edge density within 15 km radii surrounding roosts.

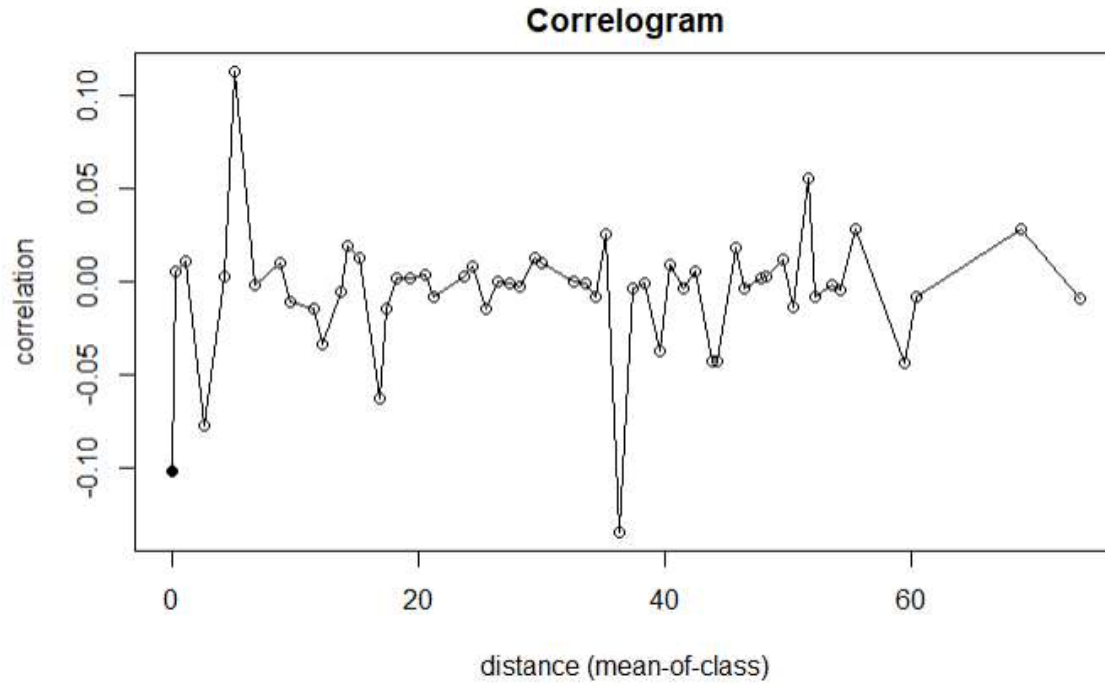


Figure B3 – Correlogram for Model 3 (Table 5) with significant spatial autocorrelation ($p < 3.14 \times 10^{-17}$). The model includes the survey date, corridor edge vegetation height, and carcass density within 20 km radii surrounding roosts.

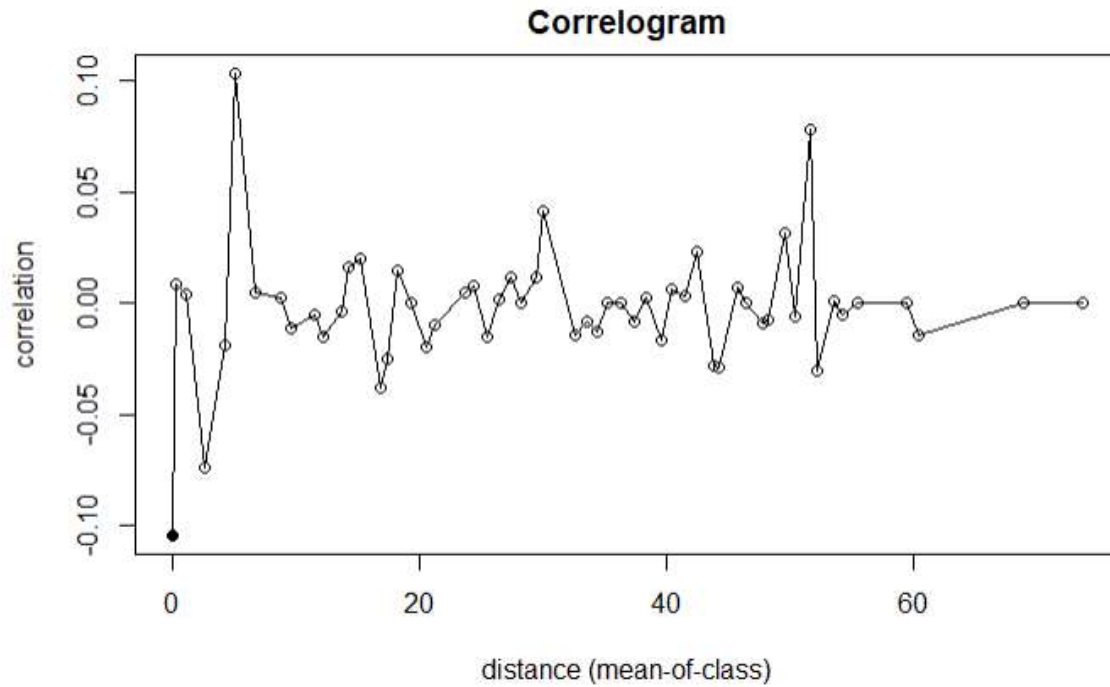


Figure B4 – Correlogram for Model 4 (Table 5) with significant spatial autocorrelation ($p < 3.14 \times 10^{-17}$). The model includes the survey date, corridor edge vegetation height, Developed-Forested edge density within 15 km radii surrounding roosts.

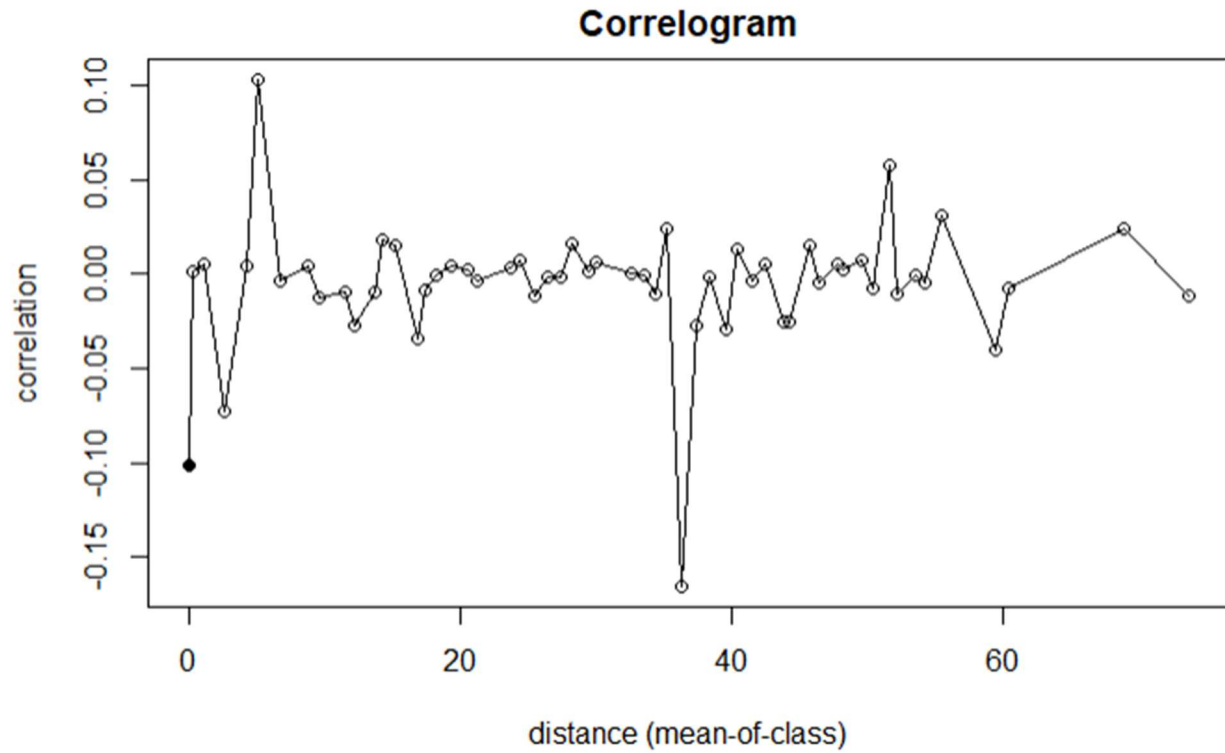


Figure B5 – Correlogram for Model 5 (Table 5) with significant spatial autocorrelation ($p < 3.14 \times 10^{-17}$). The model includes the corridor edge vegetation height, wind speed, and carcass density within 20 km radii surrounding roosts.

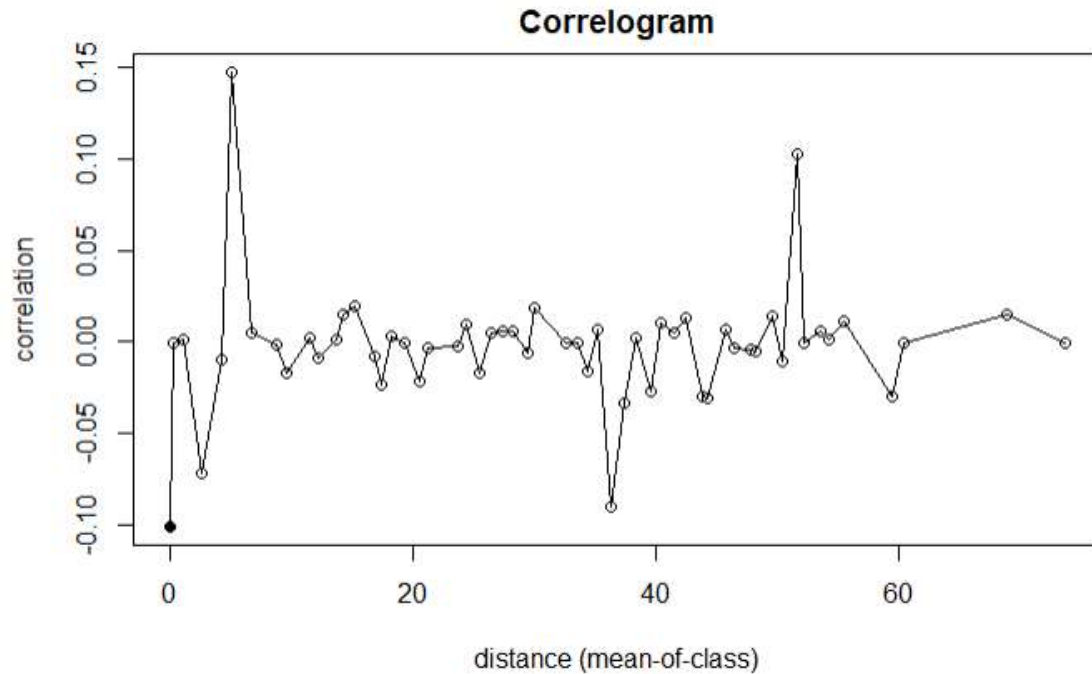


Figure B6 – Correlogram for Model 6 (Table 5) with significant spatial autocorrelation ($p < 3.14 \times 10^{-17}$). The model includes the corridor edge vegetation height, carcass density within 15 km radii surrounding roosts, and Developed-Forest edge density within 15 km radii surrounding roosts.

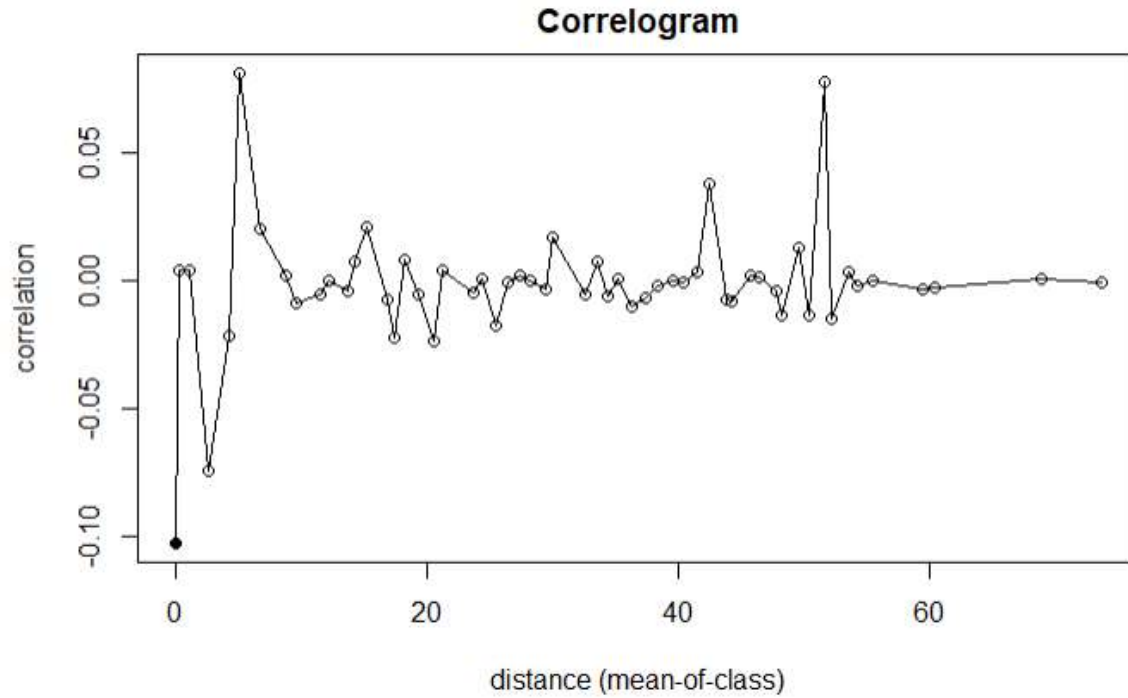


Figure B7 – Correlogram for Model 7 (Table 5) with significant spatial autocorrelation ($p < 3.14e-17$). The model includes the corridor edge vegetation height, Developed land cover within 15 km radii surrounding roosts, and Developed-Forest edge density within 15 km radii surrounding roosts.