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Landscape and Urban Planning 71 (2005) 277–293

LANDSCAPE AND URBAN PLANNING

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Mammalian nest predators respond to greenway width, landscape context and habitat structure

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Received 21 October 2003; received in revised form 5 April 2004; accepted 8 April 2004

Abstract

Birds of conservation concern breed in suburban greenways, yet abundant populations of mammals that depredate bird nests might reduce nest success. We evaluated how three factors influenced the abundance of mammalian nest predators in thirty-four 300-m long forested greenway segments in Raleigh and Cary, North Carolina, USA: (1) the width of the forested corridor containing the greenway, (2) the land-use adjacent to the forested corridor, and (3) the habitat structure within the greenway. Forest corridor width and adjacent land-use were measured using aerial photographs. Attributes of adjacent land use included categorical measures of development intensity (low-density residential, high-density residential, office/institutional), and the proportions of forest canopy, grass, buildings, and pavement. Several measures of habitat structure within the greenway were collected in the field, including trail width and surface type, and percentage of mature forest. We measured the relative abundance of mammalian nest predators with scent-station transects, operated for five nights during the 2002 breeding bird season.

Total abundance of mammalian nest predators increased significantly as forest corridor width decreased. We found no relationship between categorical measures of land-use and total abundance of mammalian nest predators. Specific attributes of the landscape adjacent to the greenway, however, did have an effect. Greenways adjacent to landscapes with fewer buildings had a higher abundance of mammalian nest predators. The abundance of individual species varied with the amount of canopy, lawn, and pavement in the adjacent landscape. Some measures of habitat structure of greenways also were correlated with the abundance of mammalian nest predators. Greenway segments with wider trails had a higher abundance of mammalian nest predators, as did segments with a higher percentage of mature forest. No habitat structure variables were significant for all species.

To reduce the overall risk of avian nest predation by mammals, forested greenways should be designed with wider forest corridors and narrower, unpaved trails. Some greenway characteristics that favor high-nest predator populations also favor birds of conservation concern. Similarly, some characteristics correlated with lower predator occurrence are also correlated with lower abundance of birds of conservation concern. Thus, management of greenways and the surrounding landscape must balance reduction of predator communities with the promotion of desired bird communities and other conservation goals.

Keywords: Corridor; Greenway; Landscape context; Mammal; Nest predator

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doi:10.1016/j.landurbplan.2004.04.001

1. Introduction

A major threat to wildlife worldwide is the ongoing loss and fragmentation of habitat to suburban and urban development. One important method of habitat conservation within urbanizing regions is the designation of areas of semi-natural vegetation as protected open space, including parks and greenways (Hess et al., 2000; Miller and Hobbs, 2000). Greenways can be identified by two basic characteristics: (1) they are linear open spaces; and (2) they are corridors composed of natural vegetation, or at least vegetation that is more natural than in surrounding areas (Smith, 1993). Greenways require less land than traditional non-linear parks and they fulfill a variety of community needs, such as protecting floodplains and watersheds, providing recreational areas and transportation routes, and enhancing regional economics (Binford and Buchenau, 1993; Cooper et al., 1987; Hopey, 1999; Long, 2002; Miller et al., 1998; National Park Service, 1995).

Goals for wildlife conservation often are stated or implied in many urban greenway plans, but the contribution of greenways to wildlife conservation is unclear (Schiller and Horn, 1997). Ecologists have been called upon to strengthen greenway design and management for the benefit of wildlife, and continued research investigating the ecological properties of greenways is an integral step towards accomplishing these goals (Adams and Dove, 1989; Fabos, 1995; Miller and Hobbs, 2000; Schiller and Horn, 1997).

Greenways provide breeding habitat for some birds (Hull, 2003; Manifold, 2001). The quality of a greenway as avian habitat depends partially on the reproductive success of birds within them (VanHorne, 1983), and greenways containing abundant populations of nest predators will have less value for avian conservation than those with fewer predators. Nest predation, including that by mammals, is the most significant cause of nest failure (Ricklefs, 1969). Several factors are known to influence the distribution of mammals within forest patches and corridors. These include forest patch size and corridor width (Downes et al., 1997; Lomolino and Perault, 2001; Schiller and Horn, 1997), the nature of the surrounding landscape (Chalfoun et al., 2002; Dijak and Thompson, 2000; Sorace, 2002) and habitat characteristics, such as water availability and vegetation structure (e.g. Gabor et al., 1994; Hall et al., 2000; Schiller and Horn, 1997; Williamson, 1983).

Although the results of nest predation studies vary with the species and the type of landscape being studied (Flashpohler et al., 2001; Paton, 1994), nest predation attributed to mammals is generally higher at habitat edges than in interior habitat (Donovan et al., 1997; King et al., 1998; Zegers et al., 2000), higher in small habitat fragments than large habitat fragments (Small and Hunter, 1988; Wilcove, 1985), and higher in suburban woodlots compared to rural woodlots (Wilcove, 1985). One explanation for higher levels of nest predation is a higher abundance of mammalian nest predators (Anthony et al., 1991; Beauchamp et al., 1996; Jackson-Digger, 2001; Small and Hunter, 1988; Wilcove, 1985).

Greenways could be more effectively designed and managed to reduce the risk of avian nest predation by mammals if the factors affecting the distribution of mammalian nest predators in greenways were known. Research efforts should focus mainly upon features of greenways and the surrounding landscape that can be controlled by greenway and city planners and managers, facilitating the implementation of research findings at current and future greenway sites. Greenway corridor width, the amount of development permitted in the land adjacent to the greenway corridor, and the habitat within the greenway are obvious candidates for planning and management.

1.1. Objective

Our study was designed to determine if the relative abundance of mammalian predators in greenways is influenced by:

(1) the width of the forested corridor containing the greenway,
(2) the land use directly adjacent to the greenway (landscape context), or
(3) the structure of the habitat within the greenway.

1.2. Study area

The Triangle Region of North Carolina, USA, consists of seven counties clustered around the cities of Raleigh, Durham, and Chapel Hill (Fig. 1). This region comprises 972,000 hectares within the larger

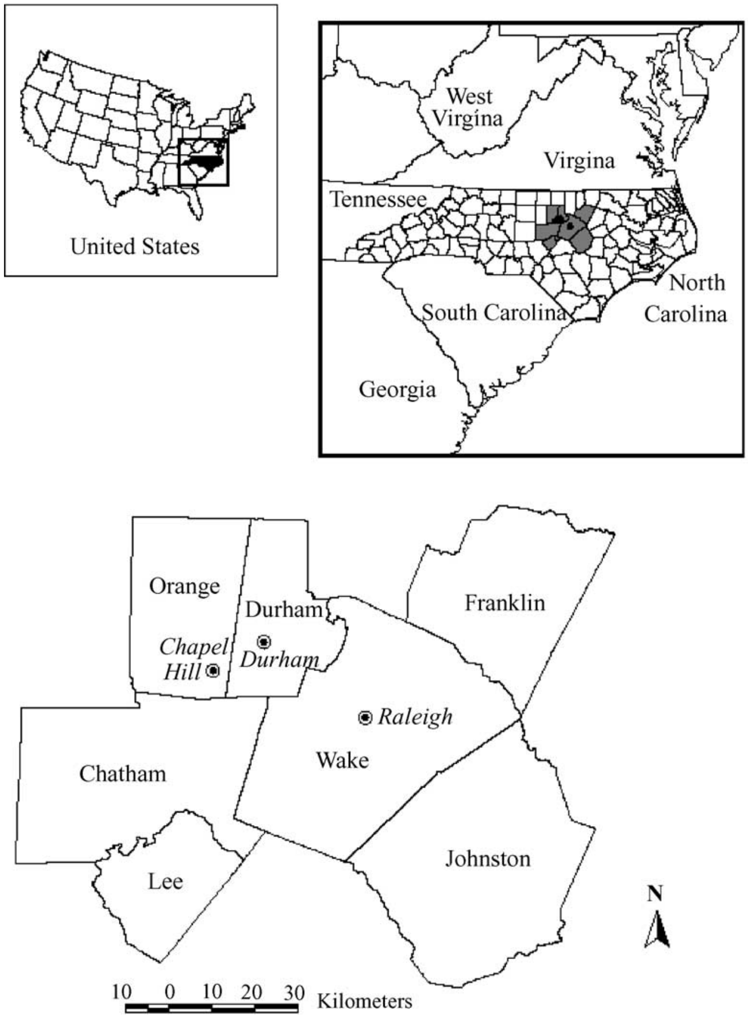

Fig. 1. The triangle region of North Carolina, USA.

physiographic region of the Central Appalachian Piedmont (Rubino and Hess, 2003). Agricultural development began during the mid-18th century and peaked during the early 20th century, resulting in severe regional deforestation. Forest cover increased during the first half of the 20th century, as secondary forests replaced abandoned cultivated lands. Forest cover in Wake County was estimated at 75% in the 1960s (United States Department of Agriculture, 1970).

A more recent phenomenon associated with rapid regional population growth is the conversion of forest to developed land, including housing, shopping areas, business parks and roads. Between 1987 and 1997, the amount of developed land in the Triangle region increased by 70%. Forests provided 68% of the source land for this development, resulting in the loss of 8% of the region's forested land (Hess et al., 2000). Forest now covers approximately 45% of the region and is continuing to decline. This phenomenon is not unique to the Triangle, and the effect of continued urbanization on native ecosystems and wildlife is likely to become more pronounced worldwide.

Our research was conducted on greenways within the City of Raleigh and the Town of Cary, located in the Triangle Region. Both have nationally-recognized greenway systems incorporating more than 130 kilometers of trails (City of Raleigh, 2004; Town of Cary, 2004). Several birds of conservation concern have been recorded in these greenways during the breeding season, including the brown-headed nuthatch (*Sitta pusilla*), ovenbird (*Seiurus aurocapillus*), Acadian flycatcher (*Empidonax virescens*), wood thrush (*Hylocichla mustelina*), and red-headed woodpecker (*Melanerpes erythrocephalus*) (Hull, 2003).

2. Methods

2.1. Study site selection

We defined our sampling units as 300-meter long greenway segments, at which we measured both predictor and response variables. We selected this length to allow our experimental units to be relatively homogenous for forest corridor width, landscape context and habitat, while still being long enough to allow adequate sampling of mammals. To select segments, we used aerial orthophotographs (1999, 1:40,000 scale) from the Wake County GIS Department; digital land-use maps obtained from the Town of Cary; and digital zoning maps obtained from the City of Raleigh.

We selected 34 study sites well distributed over a range of corridor widths and landscape contexts (Table 1) using the following rules:

(1) The forest corridor was of relatively uniform width for the entire length of the segment.
(2) The land use adjacent to the segment was relatively consistent along each side.
(3) No two segments were less than 75 m apart on the same greenway.
(4) The segment followed a riparian corridor.

We treated all greenway segments as independent samples regardless of their location. Segments within one greenway usually did not have identical landscape and habitat characteristics due to high land-use variability within our study area. One exception to this variability was trail width, which was usually identical for all segments located on the same greenway. No more than three segments were located on a single greenway (at least 75 m apart).

2.2. Measuring forest corridor width

The forest corridor associated with the greenway segment was defined by measuring the width of the

Table 1
Distribution of greenway segments among the forested corridor width and land-use context categories

Forest corridor width	Landscape context			
	All contexts	Low-density residential (≤7.5 lots/hectare)	High-density residential (>7.5 lots/hectare)	Office/institutional
Narrow (<150 m)				
Number of segments	17	4	6	7
Minimum width (m)	32. 5	50	35	32.5
Maximum width (m)	137.5	100	137.5	135
Mean width (m)	76.5	72.5	91.7	65.7
Standard error (m)	9.2	12	19	13.8
Medium (150–300 m)				
Number of segments	11	4	4	3
Minimum width (m)	150.0	150	150	200
Maximum width (m)	225.0	182.5	160	225
Mean width (m)	173.0	163.8	153.1	211.7
Standard Error (m)	8.2	6.8	2.4	7.3
Wide (>300 m)				
Number of segments	6	2	1	3
Minimum width (m)	400.0	600	500	400
Maximum width (m)	1300.0	1300	500	650
Mean width (m)	642.5	950	500	485
Standard error (m)	137.8	350	0	82.5

forested, undeveloped area visible on the aerial photographs. We included all forest along the greenway, even if it extended beyond the legal right of way for the greenway. The forest corridor width was measured for each segment by averaging the narrowest and widest widths within the segment.

2.3. Measuring landscape context

We used simple categorical variables to assign greenway segments to a land use context class, to ensure equitable sample distribution and to use for preliminary analyses. Categories of landscape context were low-density residential (≤7.5 lots/hectare), high-density residential (>7.5 lots/hectare) or office/institutional. Our land use categories were defined solely by built structures, and each category varied with respect to other attributes such as the amount of canopy and shrubs within yards, and the area occupied by lawns and parking lots.

We developed continuous measures of landscape context to quantify variation among segments that was not reflected by our simple categorical variables. A 300-m × 300-m box was drawn on each side of the forest corridor and filled with 100 sampling points on a systematic grid, for a total of 200 points per segment (Fig. 2). The aerial photographs we used for this analysis were taken during the winter when deciduous trees are leafless, allowing us to determine land-cover underneath the forest canopy. Each sampling point was assigned one of the following six land-cover types: water, agriculture, lawn, bare earth, pavement, or building. We also recorded whether each sampling point included tree canopy. Because the photographs were leaf-off, we assumed canopy was present in hardwood forests if the point intersected a tree bole or branches. The proportions of each of the land-cover types and tree canopy were calculated for a segment as the number of points assigned that cover-type in the two adjacent boxes divided by 200.

2.4. Mammal surveys

We used scent stations to measure the relative abundance of mammals within each greenway segment (Leburg and Kennedy, 1987; Linhart and Knowlton, 1975). Scent stations contain scented bait at the center of a tracking medium on which one can observe the footprints of animals that approach the bait. Scent stations offer a cost-effective and reliable method of sampling mammals to obtain relative population indices (Leburg and Kennedy, 1987; Linscombe et al., 1983). They are low impact and non-toxic, so they are appropriate for use in public greenways.

Five scent stations spaced 50 m apart were placed along a transect through the center of the forest corridor in each greenway segment (Fig. 2). The scent-station transect was oriented parallel to the predominant direction of the greenway path in the segment. We used a global positioning unit (GeoExplorer II, Trimble Navigation Unlimited) to locate the center point in each segment and placed a scent station as close to this point as possible. A compass and tape measure were used to space the remaining four stations at 50-m intervals along the transect, two on each side of scent station at the central point.

Stations were placed on soil from which we had removed all vegetation and duff. Stations consisted of a smoothed 1-m circle of completely dry fine-grained sand spread 3–5 cm thick and mixed with approximately 50 ml of mineral oil (350 viscosity/heavy, white technical grade; STE Oil Company, Corpus Christi, TX) for improved tracking. Stations were baited with a cotton ball glued to a Popsicle stick and saturated with fox urine. We assumed an equal detection probability of all mammal species at scent-stations using fox urine as an attractant, although it is possible that different species respond differently to this scent (Andelt and Woolley, 1996). Stations were created before noon and tracks were identified and recorded the following morning (Murie, 1975) (Fig. 3).

Each segment was sampled for two consecutive nights in May, two consecutive nights in June, and a single night in July on a rotating schedule so that measurements were obtained approximately once every four weeks. Stations that had been rained upon or disturbed by people were considered inoperable and not included in our analysis. The presence of any tracks of a particular species at a scent-station was counted as one observation of that species. Therefore, for a five-station transect at any given segment, the maximum number of observations of one species during a single night was five.

We assumed that tracks of the same species at different scent stations within a segment, or between segments on the same greenway, were from different

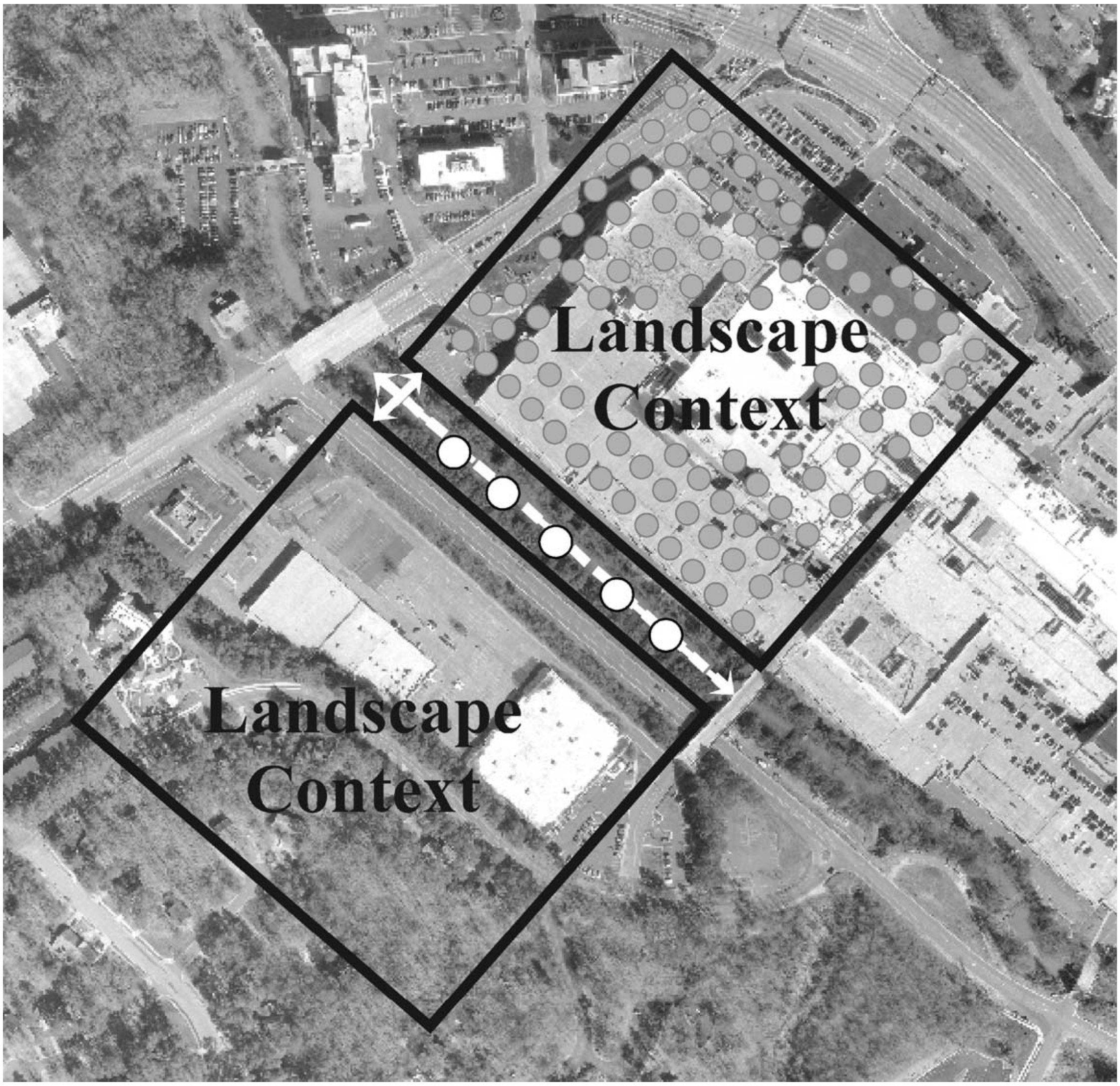

Fig. 2. Aerial photograph demonstrating 300 m greenway segment (dashed white arrow), forested corridor width (solid white arrow), landscape context measurement (gray circles) and scent station transect placement along the segment (white circles).

individuals. It is possible that one animal was recorded more than once within a segment or greenway, because we did not identify individual animals by their tracks. However, we followed a sampling procedure similar to Dijak and Thompson (2000), who found no evidence of the same individual visiting scent stations 50 m apart. Patterns in our data also supported our assumption: a scent station was rarely visited by a species within 50 m of another scent station visited by the same species, and visits by the same species two nights in a row at the same scent station were rare.

2.5. Measuring habitat structure

We measured greenway habitat structure variables in a 20-m radius circle around each scent station during September 2002 (Table 2). Data gathered included most factors thought to affect mammal distributions, such as the width and type of trail within a greenway,

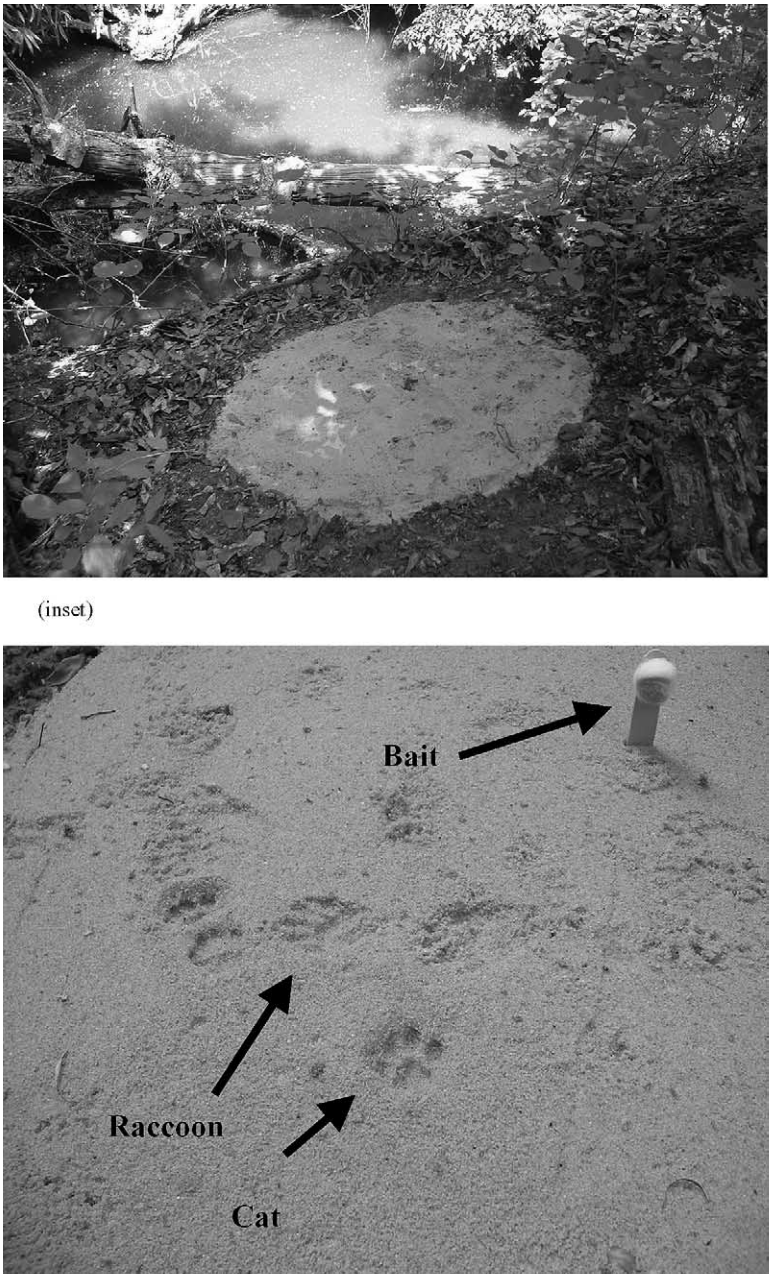

Fig. 3. Photograph of a 1-m diameter scent station with bait in the center and tracks.

distance to water, forest type and structure, and quantification of any non-forest areas within or adjacent to the greenway. We considered trails to be any purposefully cleared, walkable linear areas within the segment, including power line right-of-ways and other mowed paths. The widest trails in our study were unpaved grassy mowed areas between 5 and 12 m wide. Paved paths were approximately 2.5 m wide. The narrowest trails were dirt footpaths approximately 1 m wide.

Table 2
Greenway habitat data collected as covariables for each scent-station

Variable	Description
Measured at closest point to scent station	
Trail surface type	Classified as paved, natural dirt, gravel, boardwalk, clearcut, grass
Trail width	Width of trail (measured in m)
Managed width[a]	Width of trail plus any additional maintenance past edges of trail (measured in m)
Stream width[a]	Width of stream (measured in m)
Distance to trail	Distance from scent station edge to trail edge (measured in m)
Distance to stream	Distance from scent station edge to stream edge (measured in m)
Estimated within 20 m radius around scent station	
Percent mature forest	Amount occupied by canopy >6 m tall
Percent young forest[a]	Amount occupied by canopy <6 m tall
Percent trail[a]	Amount occupied by trail
Percent grass[a]	Amount occupied by grass (included managed areas adjacent to trail)
Percent park[a]	Amount occupied by playground, picnic tables over mulch
Percent backyard	Amount occupied by fenced in areas behind houses
Percent paved	Amount occupied by pavement that was not trail (parking lot, road)
Percent water	Amount occupied by water (streams, ponds, etc.)
Percent playing field	Amount occupied by soccer field or baseball diamond
Percent cleared[a]	Amount occupied by power-line right-of-way or development area
Percent wetland	Amount occupied by saturated earth containing aquatic plants
Dead wood index[a]	Percent dead wood cover in deciles (0: none, 1: 0–10%, 2: 10–20%, 3: 20–30%, 4: 30–40%, 5: 40–50%)
Leaf litter index[a]	Percent litter cover (0: none, 1: 0–20%, 2: 20–40%, 3: 40–60%, 4: 60–80%, 5: 80–100%)
Ground cover index	Percent ground cover (0: none, 1: 0–20%, 2: 20–40%, 3: 40–60%, 4: 60–80%, 5: 80–100%) Ground cover is woody or non-woody stems < 0.5 m tall
Shrub index[a]	Percent shrub cover (0: none, 1: 0–20%, 2: 20–40%, 3: 40–60%, 4: 60–80%, 5: 80–100%) Shrubs were defined as woody vegetation >0.5 m tall, <3″ DBH
Vine index	Percent vine cover (0: none, 1: 0–20%, 2: 20–40%, 3: 40–60%, 4: 60–80%, 5: 80–100%) Vines were defined as climbing or trailing plants requiring support, present on either the ground or the vertical structure of the plot
Number of snags[a]	The number of snags within the plot. Snags were defined as dead trees > 3″ DBH, > 2 m tall, standing at an angle >45°

Continuous covariables were averaged across segments to provide a single value for each segment. For categorical covariables, the segment was assigned the most frequent value.

[a] Covariables removed from the full model after correlation analysis.

On the whole, the vegetational composition of our study sites was similar; therefore we did not collect data on individual plant species. We would describe these greenways as mixed hardwood-pine forests adjacent to streams. We initially considered the amount of hardwood versus pine forest, but there did not appear to be an important effect on our results, therefore we focused our data collecting efforts on those variables listed in Table 2.

2.6. Data analysis

For each greenway segment, we calculated the mean relative abundance of each species observed and the community of mammalian nest predators. We pooled data for each segment across the entire sampling period, because we found no evidence of seasonal variation in visitation during the sampling period for any species. The following formula was used:

$$\text{Mean relative abundance (species)} = \frac{\text{Number of observations of species at segment}}{\text{Total number of operable stations at segment}}$$

We defined the community of mammalian nest predators to be the sum of all mammalian nest predators observed, which were raccoon (*Procyon lotor*), virginia opossum (*Didelphus virginiana*), gray squirrel

(*Sciurus carolinensis*), domestic cat (*Felis catus*), striped skunk (*Mephitis mephitis*), rats (*Rattus* sp.), mice (unidentified), gray fox (*Urocyon cinereoargentus*) and red fox (*Vulpes vulpes*). Evaluating mammalian nest predators provided a relative measure of the total nest predator pressure in the greenway segment. We calculated this as:

$$\text{Mean relative abundance (total)} = \frac{\text{Total number of predator observations at segment}}{\text{Total number of operable stations at segment}}$$

We averaged the greenway habitat measurements collected at each of the five stations in each segment to obtain a representative measurement of each variable at that segment. For the categorical variable of trail surface type, the most frequent surface type within the segment was used.

We conducted a correlation analysis (PROC CORR; SAS Institute, 1996) on all predictor variables and habitat covariables to identify variables that were correlated. We dropped one of any two variables with a correlation coefficient greater than 0.55. If correlation occurred between a major predictor variable and a covariable, the covariable was dropped. Variables selected to remain in the models were those that were thought to be most under the control of greenway planners. Variables dropped were managed width, stream width, percent park, percent young forest, shrub index, leaf litter index, dead wood index, sum of snags, percent grass and percent cleared (Table 2).

Preliminary analyses indicated that simple categorical measurements of landscape context did not explain observed patterns in mammal relative abundance among segments, therefore continuous measurements of landscape context were used for all subsequent analyses. We developed multiple regression models to estimate the relative abundance of the community of mammalian nest predators (raccoon, opossum, domestic cat, rats and mice, and gray squirrel) based on forest corridor width, continuous measurements of landscape context, and habitat variables. All rats and mice were treated as a single group for regression analysis because species identification was difficult for very small tracks. We did not combine building and pavement in the landscape context for a measure of impervious surface, because preliminary analyses indicated that these factors had different influences on the abundance of mammalian nest predators.

Models were constructed using backwards and stepwise selection (PROC GLM; SAS Institute, 1996). We set alpha = 0.05 for inclusion of variables in the final models. Potential multicolinearity was investigated for each final model using the variance inflation factor (VIF) option in SAS. We considered a maximum VIF greater than 10 to signal multicolinearity, and determined that no final models fit this criteria.

3. Results

At least nine species of mammals were observed in the greenway segments, and a majority of these species are known to prey on bird nests (Table 3). Raccoons, opossums, rats and mice, gray squirrels and domestic cats were detected in a high percentage of the segments; striped skunk, red fox and gray fox were rarely detected. We detected at least one mammalian nest predator within every greenway segment. Individual species relative abundances were generally low, but the mean relative abundance of the mammalian nest predator community was high (0.41) across segments. Raccoon and domestic cat were the most abundant species in the greenway segments. Final multiple regression models for the abundance of mammalian nest predators and individual species are summarized in Table 4.

3.1. Forest corridor width

The total abundance of mammalian nest predators was significantly higher in greenways with narrower forest corridors (Table 4). The abundance of mammalian nest predators was lowest in greenways wider than 200 meters, and continued to decline as forest corridor width increased (Fig. 4). Forest corridor width was significant for raccoon but not in other individual species models.

To verify that raccoon, the most abundant individual species, did not overly influence the total predator model, we removed the data for raccoon from the total predator count and re-ran our model. With raccoon removed, the adjusted R^2 for the total predator model decreased to 0.291, but all relationships remained

Table 3
Abundance of mammalian nest predators in Raleigh and Cary, NC greenway segments

Mammalian nest predators	Across greenway segments					References documenting species as nest predator
	Percent of segments where detected	Mean abundance	Standard error of the mean	Minimum abundance	Maximum abundance	
Raccoon (*Procyon lotor*)	85	0.158	0.026	0.000	0.625	Thompson et al. (1999), Miller and Hobbs (2000), Picman and Schriml (1994), Donovan et al. (1997), Small and Hunter (1988), Heske et al. (1999), Zegers et al. (2000)
Domestic cat (*Felis catus*)	68	0.088	0.017	0.000	0.333	Courchamp et al. (1999), Heske et al. (1999), Hall et al. (2000)
Gray squirrel (*Sciurus carolinensis*)	68	0.068	0.012	0.000	0.280	Miller and Hobbs (2000), Farnsworth and Simons (2000)
Opossum (*Didelphus virginiana*)	65	0.048	0.008	0.000	0.160	Donovan et al. (1997), Heske et al. (1999), Zegers et al. (2000)
Rats and Mice (combined in analyses) (*Peromyscus* sp.) (*Rattus* sp.)	47	0.035	0.012	0.000	0.400	Thompson et al. (1999), Miller and Hobbs (2000), Farnsworth and Simons (2000), Zegers et al. (2000), Courchamp et al. (1999)
Striped skunk (*Mephitis mephitis*)	6	0.002	0.002	0.000	0.042	Picman and Schriml (1994), Donovan et al. (1997), Small and Hunter (1988), Heske et al. (1999)
Red fox (*Vulpes vulpes*)	3	0.001	0.001	0.000	0.040	Heske et al. (1999), Miller and Hobbs (2000)
Gray fox (*Urocyon cinereoargentus*)	3	0.001	0.001	0.000	0.040	
Mammalian predator community	100	0.412	0.037	0.053	0.792	

Mean abundance across greenway segments is the mean relative abundance calculated for each segment averaged across all segments. Minimum abundance is the lowest mean relative abundance calculated for any single greenway segment, maximum abundance is the highest mean relative abundance calculated for any single greenway segment. References included provide evidence of each species as a nest predator.

Table 4
Final models with regression coefficients and partial F-statistic significance levels for included variables

Model	Adj R^2	Intercept	Corridor width	Landscape context				
				Canopy	Paved	Building	Bare earth	Lawn
Total predators	0.578	0.3436	−0.0003 $P = 0.0025$			−1.98 $P = 0.0004$		
Raccoon	0.634	0.0060	−0.0001 $P = 0.0272$	+0.31 $P = 0.0005$				
Opossum	0.448	0.1479		−0.14 $P = 0.0053$	−0.27 $P = 0.0064$		−1.69 $P = 0.0073$	+0.14 $P = 0.0173$
Gray squirrel	0.280	0.4831						
Mice and rats	0.485	−0.0725			+0.44 $P < 0.0001$			
Domestic cat	0.220	0.0152						

Model	Microhabitat									
	Trail width	% Mature forest	Distance to stream	% Paved	% Trail	% Playing field	% Backyard	% Water	Ground cover index	Vine index
Total predators	+0.05 $P < 0.0001$	+0.011 $P = 0.0290$			+0.022 $P = 0.0007$				+0.11 $P = 0.0103$	−0.152 $P = 0.0017$
Raccoon	+0.02 $P < 0.0001$			−0.01 $P = 0.0003$		−0.006 $P = 0.0090$	−0.01 $P = 0.0351$			
Opossum					+0.003 $P = 0.0083$			+0.003 $P = 0.0028$	−0.02 $P = 0.0145$	
Gray squirrel							+0.01 $P = 0.0008$			
Mice and rats										
Domestic cat		+0.002 $P = 0.0182$	−0.003 $P = 0.0151$	+0.0057 $P = 0.0260$						

No entry in a column means that the corresponding factor did not have a statistically significant effect. *Example:* For total predators, the best reduced model (adjusted $R^2 = 0.578$, $n = 34$) was $Y = 0.3436 - 0.0003$ (corridor width) $-$ 1.98 (landscape building) + 0.05 (trail width) + 0.011 (% mature forest) + 0.022 (% trail) + 0.11 (ground cover index) $-$ 0.152 (vine index). Based on partial F-statistics, trail width ($P < 0.0001$) was the most significant variable in this model.

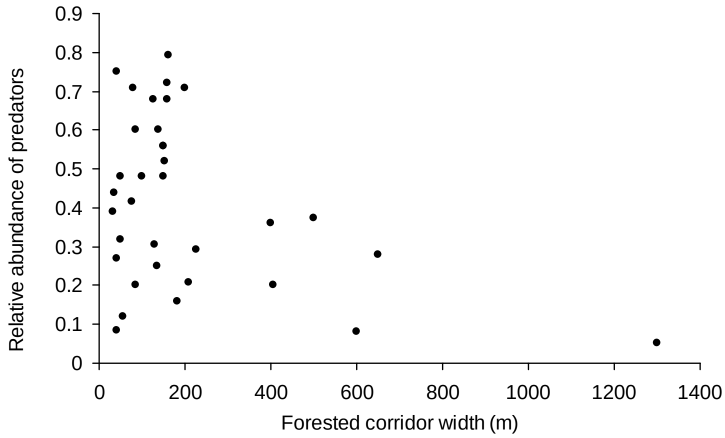

Fig. 4. Scatterplot of forest corridor width and relative abundance of predators in Raleigh and Cary greenways.

statistically significant ($P \leq 0.05$) with the exception of trail width ($P = 0.1247$).

3.2. Landscape context

Mammalian nest predators were significantly less abundant in greenways with more buildings in the surrounding landscape. Raccoons were more abundant in segments with more canopy in the landscape context, and opossums were more abundant in segments with more lawn in the landscape context, but less pavement, bare earth and canopy. Mice and rats were more abundant in segments with more pavement in the landscape context. Domestic cat and gray squirrel abundance showed no significant relationship with landscape context.

3.3. Habitat structure of the greenway

Mammalian nest predators were more abundant in segments with wider trails and a greater percentage of mature forest, ground cover, and trail. Total abundance of mammalian nest predators was lower in segments with a greater percentage of vine cover.

No habitat covariables were significant across all species models. Raccoon abundance was higher in segments with wider trails, and lower in segments with a greater percentage of parking lots or roads, playing fields, and backyards. Opossum abundance was higher in segments with a greater percentage of trail and water in the segment, and lower in segments with a higher percentage of ground cover. Gray squirrel abundance was higher in segments with a higher percentage of backyard. Domestic cat abundance was higher in segments with a higher percentage of mature forest and parking lots or roads, and lower with increased distance from a stream.

4. Discussion

4.1. Forest corridor width

Mammalian nest predators were more abundant in greenways with narrow forest corridors. Based on this result, we would expect nest predation in narrow greenways to be higher than in wide greenways. In a landscape similar to our study area, Wilcove (1985) determined that nest predation rates were higher in smaller woodlots than in large tracts of forest, and suggested that the density of small predators might be greater in small woodlots than in larger forest fragments. One explanation for our pattern is that the edge of the forested corridor was farther away from the sampling transect as forest corridor width increased. Mammalian nest predators, especially raccoon, have been suggested to be attracted to habitat edges because of better foraging opportunities (Dijak and Thompson, 2000). Narrower greenways might harbor a higher density of mammalian nest predators, because there is less distance to an edge from all points in the greenway; this could also be described as a higher edge to interior habitat ratio. Mammalian nest predators' preference for edge habitat might also explain increased nest predation rates near habitat edges in some landscapes (Donovan et al., 1997; King et al., 1998; Zegers et al., 2000).

Mesopredator release is a likely cause of increased nest predation in fragmented systems, which contain smaller habitat patches unable to support top carnivores (Crooks and Soulé, 1999; Schmidt, 2003; Wilcove, 1985). In the absence of top carnivores, populations of smaller mammals are "released" and increase, and nest success of locally breeding songbirds declines (Schmidt, 2003). The mesopredator release hypothesis might also explain why small and medium sized mammalian nest predators are more abundant in greenways with narrow forest corridors. Schiller and Horn's (1997) research on greenways supports the mesopredator release hypothesis. They found that foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*) were present only in wide greenways. The only top carnivores we detected were these two species of fox, and we detected them each once and only in greenways more than 100 m wide.

4.2. Landscape context

Mammalian nest predators were more abundant in greenways with fewer buildings in the adjacent landscape; however, the proportion of building cover in the adjacent landscape was not extremely variable across segments. In one greenway segment with a high proportion of building cover we recorded low predator abundance, suggesting that mammalian nest predators might be averse to greenways in highly developed areas. Sorace (2002) found a higher density of mammalian predators, including rats, mice, cats, and foxes, in urban parks than in open-land habitats in the nearby countryside. Although our result for total predator abundance does not support this finding, rat and mouse abundance was higher in segments with more pavement in the landscape context, which is one indication of increased urbanization.

We found no significant relationship between categorical measures of land-use context and the abundance of mammalian nest predators. Thus, simply restricting the land-use around greenways to one type of development without further management of the habitat within the development is unlikely to have a significant impact upon the abundance of mammalian nest predators. This is consistent with the research of Hostetler and Knowles-Yanez (2003), who suggested that variations within land-use categories have a significant impact upon species abundance.

Greenway segments with higher amounts of canopy cover in the adjacent landscape had higher raccoon abundance. In other studies, raccoon abundance was strongly associated with wooded habitats, including older residential neighborhoods, where raccoons favored dens in mature trees with hollow trunks or cavities over other den types (Hadidian et al., 1991; Hoffman and Gottschang, 1977; Rosatte et al., 1991).

Opossums were more abundant in segments with increasing lawn in the adjacent landscape and less abundant in segments with increasing pavement, bare earth and canopy in the adjacent landscape. Greater amounts of lawn are usually associated with suburbs, which presumably offer unique and beneficial food resources to opossums.

Gray squirrel and domestic cat abundances were not significantly associated with any of the landscape context measurements. We expected domestic cat to be more abundant in segments with more lawn or building in the adjacent landscape, as an indication of increased housing density (Haskell et al., 2001). Cat ownership levels and the decision to allow cats outdoors, which we did not measure, might be more important determinants of cat abundance than landscape context.

4.3. Habitat structure within the greenway

Segments containing wider trails had a higher abundance of mammalian nest predators. We also recorded higher abundances of mammalian nest predators at segments with a greater percentage of trail near the sampling area. These results suggest that mammalian predators are attracted to trails, possibly because they act as travel corridors. Miller et al. (1998) found elevated rates of nest predation near trails, although mammals have been found to avoid nests near trails in other studies (Miller and Hobbs, 2000). Although we have no data on nest predation rates by mammals at our study sites, we hypothesize that nest predation by mammals might be higher near wide trails.

Mammalian nest predators were more abundant in greenway segments that contained a greater percentage of mature streamside forest. Mammals seeking aquatic food resources such as fish and shellfish would likely be attracted to these sites. Hall et al. (2000) found that cat abundances were highest in riparian habitats with ample forest cover, and suggested that these habitats provided a rich diversity of prey. Mammals also were more abundant in segments with lower vine cover and higher ground cover. Mammals might avoid segments with dense tangles of vines for reasons of accessibility. There was a wide range of ground cover types across segments (mowed lawns to dense undergrowth) which makes an ecological explanation of the positive association with ground cover difficult, but high ground cover was associated with low amounts of vine cover, which again suggests increased accessibility at those segments.

Although no habitat covariables were significant across all species models, some general conclusions regarding human presence and disturbance can be drawn from the individual models. We found raccoon to be less abundant in segments containing a greater percentage of parking lots or roads, playing fields, and backyards, which are all areas lacking abundant natural vegetation where disturbance by humans, pets, and cars is likely to be high. Not all mammalian nest predators responded negatively to managed areas. Gray squirrels were more common in segments with a higher percentage of backyards, possibly indicating their attraction to food sources at bird feeders. Domestic cats were more abundant in segments with a higher percentage of parking lots or roads, either of which might serve as access points to greenways from neighborhoods or commercial areas that support free-ranging cat populations.

5. Implications for the design and management of greenways in forested regions

To reduce the risk of avian nest predation by mammals, forested greenways should be designed with wider forest corridors and narrower trails, particularly natural dirt footpaths instead of paved or cleared trails. Simply restricting the land-use around greenways to specific development categories, such as low-density residential, without additional habitat management is unlikely to have a significant impact upon the abundance of the mammalian nest predator community.

We studied the distribution of mammalian nest predators in greenways and present "total abundance of mammalian nest predators" as a relative, not exact, risk of predation for a majority of ground-nesting and low-shrub nesting bird species. We believe that the total predation index is useful in many greenway management scenarios, especially in cases where it is not known which mammal species are responsible for a majority of the nest predation or even what bird species are mainly being predated upon. Artificial nest experiments with nests placed on or near the ground (up to 0.5 m in shrubs) have all shown predation by raccoon, mice, squirrels, house cats, striped skunks, opossums, and foxes (Donovan et al., 1997; Thompson et al., 1999; Zegers et al., 2000). The most common mammal that we documented was raccoon. In forested environments, raccoons have been documented as predominate nest predators, especially of nests on or near the ground (Thompson and Burhans, 2003).

Nest predator communities and the relative influence of individual predator species on nest success, however, can vary with environmental factors (e.g. vegetation structure, proximity to edge, landscape context) at multiple scales (Chalfoun et al., 2002; Donovan et al., 1997). Without direct evidence of nest predation by raccoons and other mammals (e.g. video of active nests being depredated), we cannot be sure of the relative importance of mammals, birds or snakes as nest predators. Hull (2003) commonly detected blue jays (*Cyanocitta cristata*), crows (*Corvus* sp.), and common grackles (*Quiscalus quiscula*) in most greenway segments, and these bird species were photographed depredating artificial bird nests located in shrubs 1.5–2 m high in our greenway study sites (Sinclair, unpublished data). To better assess the risk of various predator species to bird nests, research on the success of real nests in greenways is warranted. If one or a few species are responsible for the majority of nest predation in a given region, then species-specific findings will offer useful ways for managers to discourage abundant populations of these species in greenways.

Our results suggest that the abundance of mammalian predators could be reduced in greenways by reducing the amount of mature forest within the greenway and reducing the amount of tree cover in adjacent neighborhoods. High levels of tree cover in the greenway and surrounding landscape, however, are needed to support the birds of conservation concern that inhabit these same greenways (Hull, 2003). Similarly, some characteristics associated with lower predator occurrence are also associated with lower abundance of birds of conservation concern. For example, there were fewer predators and fewer development-sensitive birds (Hull, 2003) in greenway segments with more buildings in the adjacent landscape. Management of greenways and the surrounding landscape must, therefore, balance reduction of predator communities with the promotion of desired bird communities and other conservation goals.

Acknowledgements

We thank North Carolina State University and the U.S. Forest Service for funding our research. We thank the Town of Cary, the City of Raleigh, and Hemlock Bluffs Nature Park for allowing us to conduct our study on their greenways, and their respective GIS departments for providing land-use cover maps. Many thanks to R. Vidra and R. Moore for contributing to the project study design. S. Hagevik and N. Tarr were wonderful summer field technicians who assisted with data collection. M. Gumpertz and J. Bartz assisted with our study design and statistical analyses. The Triangle Greenways Council provided us with maps of regional greenways. H. Cheshire generously loaned us GPS units for locating our study sites. R. Powell, J. Weston, M. Mitchell, and B. Palmer provided assistance with scent station protocols. Partners in Flight provided us with a forum to discuss our experimental results and obtain feedback from wildlife professionals. Finally, thanks to N. Haddad and two anonymous reviewers for providing feedback on an earlier version of this manuscript.

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