Urban Ecosyst (2008) 11:243–255
DOI 10.1007/s11252-008-0060-0

Gray squirrel density, habitat suitability, and behavior in urban parks

Tommy S. Parker · Charles H. Nilon

Published online: 16 May 2008

Abstract Increased density, increased intraspecific aggression, and a reduced fear of humans have been suggested as the more observable and frequently described characteristics of wildlife species undergoing synurbization, the process of becoming urbanized. The relationship among these variables and how they may be related to environmental variables that change with urbanization is poorly understood. In this paper we explore the relationship between density, intraspecific aggression, and reduced fear of humans in urban populations of gray squirrel. In the summer and fall of 2003 and 2004, we studied a park with a documented high density of gray squirrels, Lafayette Park, Washington, DC, and six urban parks in Baltimore, MD with unknown squirrel densities. We used linear regression (SAS Institute, *SAS/STAT user's guide*. SAS Institute, Cary, NC, 2005) to determine if there was a relationship (P<0.05) between squirrel density and intraspecific aggression, squirrel density and reduced fear of humans (wariness), and squirrel density and habitat suitability. We found a positive association between density and intraspecific aggression (R^2=0.81, P<0.00). A negative relationship between density and wariness ($R^2_{adj} = 0.71$, P<0.00). However, no relationship was evident between habitat suitability and squirrel density ($R^2_{adj} = -0.50$, P=0.437).

Keywords Squirrel · Urbanization · Behavior · Aggression · Wariness

T. S. Parker
Department of Biology, University of Louisville, Life Sciences Building, Louisville, KY 40292, USA

C. H. Nilon
Department of Fisheries and Wildlife Sciences, University of Missouri–Columbia,
302 Anheuser Busch Natural Resources Building, Columbia, MO 65211-7240, USA
e-mail: nilonc@missouri.edu

Present address:
T. S. Parker (✉)
USDA Forest Service, Suite 700, 626 East Wisconsin Avenue, Milwaukee, WI 53202-4616, USA
e-mail: tommyparker@yahoo.com

Introduction

The "urban wildlife syndrome", increased density, increased intraspecific aggression, and a reduced fear of humans have been suggested as the more observable and frequently described characteristics of wildlife species undergoing synurbization, the process of becoming urbanized (Warren et al. 2006). This suite of characteristics has been described in urban populations of gray squirrels (*Sciurus carolinensis*; Flyger 1970), rock doves (*Columba livia*; Cooke 1980), coyote (*Canis latrans*; Shargo 1988), striped field mouse (*Apodemus agrarius;* Gliwicz et al. 1994), blackbirds (*Turdus merula*; Gliwicz et al. 1994), raccoons (*Procyon lotor*; Smith and Engeman 2002), and northern water snakes (*Nerodia sipedon*; Burger 2001). These characteristics, while receiving substantial attention across varying species, have not been studied for the affects they may have on each other.

The relationship among these variables and their relationship to environmental variables that change with urbanization is poorly understood. However, evaluating the relationship between organisms and their environment is the fundamental aim of ecology. With urbanization increasing at rates never before seen throughout the world, studies focusing on wildlife in urban areas will have to consider the geographical features in cities and their effects on wildlife.

In this paper we explore the relationship between density and habitat suitability, density and intraspecific aggression, and density and reduced fear of humans in urban populations of a well-studied species, the gray squirrel. The species' history in urban areas, human habituation to their presence, and previous research on the species in this setting, make gray squirrels ideal for population density and behavioral studies in urban habitats.

A study of gray squirrel density in urban parks of Baltimore, MD revealed squirrel densities of 3–10/ha (Flyger 1970, 1974). Manski et al. (1980) showed that the population density of gray squirrels in Lafayette Park, Washington, DC, ranged from 22.75/ha in the spring to 51.5/ha in the fall. Squirrel density in each of these studies was higher than those typically reported for the species in non-urban areas; however, Lafayette Park displayed the highest densities ever reported for the species. In addition to high squirrel density, Manski et al. (1980) also found that gray squirrels in this park were more active throughout the day than were conspecifics in nonurban areas. However, the authors did not evaluate the relationship between squirrel density and their behavior.

Gliwicz et al. (1994) studied density, aggression, and wariness in two taxonomically distant species, striped field mouse and blackbird. Results of the study showed that both species displayed higher densities and intraspecific aggression and a reduced fear of man. Gliwicz et al. (1994) concluded that the effects of urban conditions upon wildlife are so strong that parallel changes in life history characteristics occurred in both taxa.

Williamson (1983) identified the features of urban habitats that are important for gray squirrel abundance. McPherson and Nilon (1987) developed a habitat suitability index model (HSI) to assess urban habitats for factors that may limit gray squirrel abundance. Hein (1997) described population density, Thompson and Thompson (1980) and Bowers and Breland (1996) the food habits, Manski et al. (1980) the activity patterns, and Merwe et al. (2005) gray squirrel distribution over varying landscape types in urban habitats. Substantial work has been conducted on the factors that influence squirrel abundance in urban areas. However, studies of the behaviors exhibited by urban wildlife (i.e., decreased wariness and increased intraspecific aggression) have been limited.

We studied gray squirrel populations in small urban parks. Locations such as these are common in urban areas and play an important role in offering opportunities for human and wildlife interactions (Nilon et al. 1999) and they reflect top down decision making by local governments (Kinzig et al. 2005). We studied a park with a documented high density of gray squirrels, Lafayette Park, Washington, DC, and six urban parks in Baltimore, MD with unknown squirrel densities. The squirrel density in Lafayette Park has been reported to exceed 31.3 individuals per hectare, and has been the subject of several studies regarding their elevated abundance (Manski et al. 1980) and their management needs (Hadidian et al. 1988; Steele and Koprowski 2001). Other studies of gray squirrels in urban parks, including those located in Baltimore, have shown squirrel abundance to be 3–10 individuals per hectare (Flyger 1970, 1974; Koprowski 1994; Steele and Koprowski 2001). Thus, the use of Lafayette Park, in conjunction with the Baltimore parks, allowed us to study the relationship between density and behavior over contrasting levels of squirrel abundance. This study was part of a larger study evaluating how habitat and landscape features influence gray squirrel density and behavior.

In addition to evaluating the relationship between density and behavior of gray squirrels, we were also interested in how squirrel density relates to the habitat suitability of parks. Understanding the relationship between park habitat suitability and gray squirrel density and behavior is important because it may provide insights into the drivers of squirrel abundance in urban habitats. We used the gray squirrel HSI model developed by McPherson and Nilon (1987) to evaluate each park.

In this study we ask the following questions: (1) What is the relationship between gray squirrel density and habitat suitability? (2) What is the relationship between gray squirrel density and wariness of humans? (3) What is the relationship between gray squirrel density and intraspecific aggression? Additionally, we want to know if other gray squirrel density, intraspecific aggression, and wariness are comparable to the population in a well studied park.

Methods

Study area

Lafayette park

Lafayette Park is located adjacent to the White House in downtown Washington, DC. The park has an area of 3.3 ha and is listed on the National Register of Historic Places (Olszweski 1964). Lafayette Park, which is part of the National Park System, has been managed since 1933 with the primary objective being to protect and preserve the historic landscaping themes established in 1853 by Andrew Downing (Olszweski 1964; Hadidian et al. 1988). The park has a canopy cover of 60%, comprised of both native and exotic tree species; the grounds are 50% manicured turf, 34% brick walkways, and 10% flower beds (Hadidian et al. 1988).

Baltimore parks

We obtained a list of municipal parks from the Parks and People Foundation of Baltimore and identified parks approximately the same size as Lafayette Park (2–7 ha). We then visited each park and selected those with canopy cover between 40% and 65%. This amount of canopy cover has been identified as an important habitat component for gray squirrels in urban areas (Williamson 1983). The six parks chosen in Baltimore were: Federal Hill Park, Irvin Luckman Park, Stoney Run Park, Lakeland Park, Burdick Park, and Carroll Park (Table 1).

Table 1 Habitat characteristics of Lafayette Park located in Washington, DC, USA, and six urban parks located in Baltimore, MD, used to study the influence of squirrel density on squirrel wariness and intraspecific aggression

Location	Park size (ha)	Canopy cover (%)
Lafayette park	3.3	60
Baltimore parks		
Federal Hill	3.9	60
Irving Luckman	2.2	65
Stoney Run	2.7	45
Lakeland	4.9	50
Burdick	4.2	45
Carroll	6.9	40

Squirrel habitat suitability index (HSI)

Each park's ability to provide food and cover resources was assessed using the gray squirrel HSI model developed by McPherson and Nilon (1987). This HSI model is designed to measure the quality of habitat for gray squirrels at a given point in time using the average tree diameter and tree canopy closure as indicators of food availability or quantity and the number of preferred and supplemental plant species as indicators of food quality (McPherson and Nilon 1987). The limiting factors, for urban gray squirrel populations, can be the availability of preferred winter food species or the amount of tree cover. Preferred winter food species are those that produce hard mast: oak, hickory, walnut, pecan, beech, maple, pine, and horse chestnut (Table 2). Supplemental food species are dogwood, spruce, hemlock, and Douglas-fir (Table 2).

HSI scores were calculated by adding the scores from the preferred winter food trees (possible score=1–10), percent canopy closure (possible score=1–5), number of preferred food plants (possible score=1–5), number of supplemental food plants (possible score=1–5), and average DBH of park trees (possible score=1–10). Scores for each category were summed, divided by the maximum score possible (35), and multiplied by 100 (McPherson and Nilon 1987). The resulting number is the HSI score for the park.

Scores for winter foods were determined by summing the scores for preferred winter food trees, percent canopy closure, number of preferred food plants, and number of supplemental food plants, then dividing the resulting number by the maximum score possible (35), and multiplying by 100. Scores for tree cover were calculated by dividing the score for average DBH of park trees by the maximum score possible for the category (10) and multiplying by 100. The category with the lowest score, winter food or tree cover, is the limiting factor for the park.

Squirrel density

Time area counts, as defined below, were used to determine an index of abundance for each park during four sampling periods: summer, July–August 2003 and 2004, and fall, October–November 2003 and 2004 (Flyger 1959). This method is considered ideal for urban areas because it eliminates the use of traps in areas of high human activity and may be conducted rather inconspicuously to the public (Hein 1997; Steele and Koprowski 2001).

We divided each park into equal sized quadrants, established two vantage points within each quadrant, and recorded the distance from the vantage points to the outer edge of the park. Two vantage points were selected so that one would be available if a park visitor occupied the other. The distance from the vantage points to the edge of the park was used to estimate the distance from the vantage point to each squirrel counted. A random numbers generator was used to predetermine the sampling order of parks and quadrants within each park.

Table 2 Gray squirrel habitat suitability index (HSI) model

Characteristic	Possible score
I. Winter food	
A. Average tree diameter of preferred food plant species (cm dbh)	
1. >25.0	10
2. 15.1–25.0	7–9
3. 7.6–15.0	3–6
4. <7.6	1–2
B. Percentage of canopy closure	
1. 40–60	5
2. 60–70, 30–40	2–4
3. >70, <30	1
C. Number of preferred food plant species	
1. >10	5
2. 6–9	3–4
3. 5	2
4. <5	1
D. Number of supplemental food plant species	
1. >5	5
2. 3–5	3–4
3. 2	2
4. <2	1
II. Tree cover	
A. Average tree diameter (cm dbh)	
1. >45.7	10
2. 38.1–45.7	8–9
3. 25.4–38.0	6–7
4. 15.0–25.3	2–5
5. <15.0	1
HSI calculation	
1. Maximum score	35
2. Actual score	—
3. (2)/(1)×100	—
Limiting factors	
A. Winter food	
1. Maximum score=A+B+C+D	25
2. Actual score=A+B+C+D	—
3. (2)/(1)×100	— Food suitability
B. Tree cover	
1. Maximum score: A	10
2. Actual score: A	—
3. (2)/(1)×100	— Cover suitability

Limiting factor is the lowest suitability value. Taken from (McPherson and Nilon 1987)

Time area counts lasted 15 min and the number of squirrels visible within the quadrant, the average distance to each squirrel counted, and the percentage of the quadrant that was observable was recorded. The index of abundance was determined for each location using the equation:

$$P = \frac{AZ}{(v)\pi S y^2}$$

where, P is squirrel population, A is total area of park, Z is number of squirrels counted, v is percent of quadrant visible, S is number of 15 min observational periods, and y is the average distance to the counted squirrels. This method estimates abundance based on the number of observational periods conducted at each location, and thereby provides an index of abundance for each season the location was sampled. Counts were conducted from sunrise to four hours after sunrise and four hours prior to sunset until sunset. These are the times when urban squirrels are most active, and thus provide the best opportunities to count all the squirrels present in each quadrant (Manski et al. 1980; Gustafson and VanDruff 1990).

Wariness

Wariness was quantified using a standardized threat stimulus. An observer approaching an individual gray squirrel on the ground, directly at a constant pace while observing the animal without making any deliberate auditory stimulation, was used as the threat stimulus (Gustafson and VanDruff 1990). The same observer was used throughout the study to avoid bias resulting from observer height, size, and walking pace variation. The distance between the squirrel and the approaching threat stimulus at the instant the squirrel fled was measured with a rolling tape measure and recorded as the startle distance.

A random numbers generator predetermined the order in which the quadrants within each park were sampled for squirrel wariness. Once a quadrant was selected, the third squirrel visible within that quadrant was sampled. This eliminated squirrels that were atypically bold, and thus more visible. To avoid conditioning squirrels to our presence, no quadrant was sampled in consecutive order.

Intraspecific aggression

Gray squirrels were observed for acts of aggression continuously throughout each sampling day, sunrise to sunset, by listening for chatter and watching for squirrel chases either on the ground or through the tree canopy. Intraspecific encounters that involved an agonistic action (chasing, biting, chattering, or rapid tail flicking); or that elicited an agonistic or submissive response (fleeing, dropping of head or tail) were counted as an aggressive act (Gustafson and VanDruff 1990). Repeat encounters between the same individuals were excluded because they constituted nonindependent observations. If a role reversal occurred in instances that involved the same set of individuals, it was considered as a new act of aggression and was recorded as such (Gustafson and VanDruff 1990).

Adults are dominant in the social system of the gray squirrel; therefore, only acts of aggression between adult squirrels were recorded. Adult squirrels were distinguished from juveniles by the size and coloration of their tails. Quadrant and time of occurrence were recorded for each act of aggression. The average number of aggressive acts per hour was calculated for each location seasonally by dividing the total number of aggressive acts by the total number of hours observed.

Data analysis

A linear regression analysis (SAS Institute 2005) was used to determine if a relationship ($P<0.05$) exist between habitat suitability and squirrel abundance. We used the mean of the four seasonal density estimates as an index of abundance for each location then performed a linear regression, with all parks combined, with the index of abundance as the dependent variable and HSI score as the independent variable.

We used linear regression to determine if there was a relationship ($P<0.05$) between wariness and squirrel abundance. Data were grouped by locations with density, wariness, and intraspecific aggression averaged across seasons. We then analyzed the data using abundance as the independent variable and wariness and aggression as dependent variables (in separate analyses) to evaluate the relationship between abundance and these behaviors. Analyses were conducted for each park across the four sample seasons, all of the Baltimore parks combined, and the Baltimore parks combined with Lafayette Park. We reviewed the R^2_{adj} and P-values to determine how efficiently density performed as a predictor for each behavior.

Results

Squirrel habitat suitability index (HSI)

Lafayette Park scored an HSI=57. Among Baltimore parks, HSI scores ranged from HSI=51 (Federal Hill) to HSI=71 (Irving Luckman). Cover suitability was the limiting factor at all parks except Lakeland Park (Table 3).

Squirrel density

Squirrel density ranged from 38.2/ha (summer 2003) to 49.1/ha (fall 2003) in Lafayette Park and 2.0/ha (Carroll Park, fall 2003) to 13.1/ha (Federal Hill, summer 2003) in Baltimore (Table 4). There was no relationship between habitat suitability and mean squirrel abundance values ($R^2_{adj} = -0.50$, P=0.437, df=6).

Wariness

The average startle distance for gray squirrels in Lafayette Park was 2.25±0.04 m. Distances varied at this location from 1.82±0.05 m (fall 2004) to 2.77±0.30 m (summer

Table 3 Habitat suitability scores of Lafayette Park and six urban parks located in Baltimore, MD

	Location						
Characteristic	Lafayette	Federal Hill	Irving Luckman	Stoney Run	Lakeland	Burdick	Carroll
Food							
Average diameter	6	9	8	9	9	9	8
Canopy closure	5	5	4	5	5	5	5
Preferred spp.	5	1	3	3	2	3	2
Supplemental spp.	2	1	4	1	1	1	1
Food total	18	16	19	18	17	18	16
Food suitability	72	64	76	72	68	72	64
Cover							
DBH	2	2	6	5	7	6	5
Cover total	2	2	6	5	7	6	5
Cover suitability	20	20	60	50	70	60	50
Actual score	20	18	25	23	24	24	21
HSI	57	51	71	66	69	69	60

Table 4 Summer and fall index of abundance (individuals/ha) for gray squirrels located in Lafayette Park, Washington, DC, and six urban parks located in Baltimore, MD

	2003		2004	
Location	Summer	Fall	Summer	Fall
Lafayette park	38.2	49.1	44.3	46.3
Baltimore parks				
Federal Hill	13.1	11.9	8.5	10.4
Irvin Luckman	2.9	2.7	5.2	8.9
Stoney Run	3.7	2.9	2.2	3.0
Lakeland	3.2	7.2	9.5	11.6
Burdick	5.6	5.2	6.1	7.9
Carroll	2.4	2.0	4.8	6.7

2003). The startle distances for Baltimore parks ranged 4.64±0.174 m (Federal Hill) to 12.50±0.441 m (Stoney Run, Table 5).

There was a negative association between squirrel abundance and mean startle distance for Lafayette Park and five of six Baltimore parks (Table 6). All regressions returned significant *P*-values, with the exception of Stoney Run Park, (Table 6). There was a negative relationship between density and startle distance in Baltimore parks across seasons ($R^2_{adj} = 0.71$, $P<0.00$, $df=23$, Fig. 1).

Intraspecific aggression

Lafayette Park was observed for 100 hours for acts of intraspecific aggression among gray squirrels. Mean values ranged from 11.75/h±0.31(summer 2003) to 27.40/h±0.43 (fall 2004) at this location. In Baltimore a total of 608 hours of observations were completed with means ranging from 2.20/h±1.30 (Carroll Park) to 6.40/h±1.35 (Lakeland Park).

There was no evidence of a relationship between gray squirrel density and aggression in Lafayette Park (Table 6). There was a positive relationship between density and aggression in four of six Baltimore parks. There was a positive relationship between density and intraspecific aggression in Baltimore parks across seasons. ($R^2_{adj} = 0.68$, $P<0.00$, $df=23$, Fig. 2).

Discussion

Gray squirrel abundances in Lafayette Park were similar to those previously reported for this location. Manski et al. (1980) and Hadidian et al. (1988) suggested that the high squirrel abundance in this park was a consequence of the availability of supplemental foods of anthropogenic origin, which comprised 35% of these squirrels' diets. Results of the HSI model for Lafayette Park and all the Baltimore parks suggest that the available natural food and cover resources in these parks are insufficient to support such high abundance of squirrels. This lack of a relationship between habitat suitability and squirrel abundance may suggest that urban gray squirrel populations are void from bottom-up effects. In the case of Lafayette park, with current landscaping features remaining similar to that during the Manski et al. (1980) study and without the addition of any natural food resources, it appears that foods provided by humans continue to sustain the population.

Table 5 Results of gray squirrel wariness and aggression in Lafayette Park, Washington, DC and six urban parks in Baltimore, MD

	2003		2004		
Location	Summer	Fall	Summer	Fall	Location total
Lafayette park					
Wariness	2.77±0.30 (n=31)	2.21±0.11 (n=32)	2.18±0.08 (n=31)	1.82±0.05 (n=30)	2.25±0.04 (n=124)
Aggression	11.75±0.31 (hrs=29)	15.40±0.09 (hrs=24)	16.20±0.13 (hrs=22)	27.40±0.43 (hrs=25)	17.69±0.22 (hrs=100)
Federal Hill					
Wariness	5.05±0.34 (n=32)	4.96±0.31 (n=38)	4.55±0.39 (n=35)	4.00±0.35 (n=30)	4.64±0.17 (n=135)
Aggression	7.10±1.06 (hrs=28)	5.30±0.87 (hrs=24)	3.20±0.52 (hrs=30)	5.40±0.83 (hrs=25)	5.25±0.80 (hrs=107)
Irvin Luckman					
Wariness	10.08±0.82 (n=30)	11.14±0.64 (n=37)	7.03±0.40 (n=37)	5.42±0.24 (n=31)	8.40±0.36 (n=135)
Aggression	2.30±0.25 (hrs=27)	2.10±0.21 (hrs=22)	5.40±0.90 (hrs=29)	4.90±0.88 (hrs=23)	3.70±0.86 (hrs=101)
Stoney Run					
Wariness	14.48±0.88 (n=34)	10.05±0.21 (n=39)	12.84±0.33 (n=37)	12.66±0.22 (n=32)	12.50±0.44 (n=142)
Aggression	2.50±0.20 (hrs=28)	1.80±0.19 (hrs=23)	2.10±0.34 (hrs=27)	2.70±0.12 (hrs=22)	2.30±0.20 (hrs=100)
Lakeland					
Wariness	13.94±0.65 (n=35)	11.36±0.52 (n=36)	6.79±0.64 (n=37)	4.40±0.20 (n=30)	9.12±0.43 (n=138)
Aggression	3.50±0.47 (hrs=27)	5.00±0.62 (hrs=20)	7.20±1.01 (hrs=26)	9.70±1.23 (hrs=21)	6.40±1.35 (hrs=94)
Burdick					
Wariness	12.35±1.21 (n=35)	11.89±0.92 (n=34)	9.01±0.84 (n=38)	8.25±0.66 (n=30)	10.37±0.48 (n=137)
Aggression	6.00±1.02 (hrs=29)	4.00±0.79 (hrs=22)	5.30±0.98 (hrs=27)	3.60±0.82 (hrs=22)	4.70±0.56 (hrs=100)
Carroll					
Wariness	16.65±1.18 (n=35)	13.10±0.71 (n=38)	10.95±0.57 (n=33)	8.63±0.45 (n=31)	12.33±0.46 (n=137)
Aggression	0.00±0.00 (hrs=28)	0.00±0.00 (hrs=24)	4.20±0.90 (hrs=29)	4.80±0.92 (hrs=20)	2.20±1.30 (hrs=101)

Wariness (=startle distance) expressed in meters, followed by the SE, and (n) represents the number of animals sampled. Aggression data is expressed in number of aggressive acts per hour, followed by the SE, and (hrs) which represents the total number of daylight hours observed

Table 6 Results of linear regression analyses of gray squirrel density and wariness, and density and aggression for Lafayette Park, located in Washington, DC, USA and six urban parks of Baltimore, MD, USA

	Wariness				Aggression			
Location	R^2_{adj}	*df*	*P*	Linear model	R^2_{adj}	*df*	*P*	Linear model
Lafayette park	0.78	3	0.02*	5.21−0.06 density	0.48	3	0.52	13.98+0.71 density
Baltimore parks								
Federal Hill	0.62	3	0.04*	3.00−0.15 density	0.84	3	0.05*	3.55+0.78 density
Irving Luckman	0.85	3	0.05*	12.76−0.88 density	0.41	3	0.22	1.35+0.47 density
Stoney Run	0.40	3	0.59	8.96+1.20 density	0.46	3	0.54	1.37+0.31 density
Lakeland park	0.93	3	0.03*	18.38−1.17 density	0.89	3	0.04*	0.62+0.73 density
Burdick park	0.57	3	0.05*	19.36−1.45 density	0.50	3	0.05*	7.65+0.47 density
Carroll park	0.64	3	0.01*	19.37−1.45 density	0.89	3	0.04*	7.65+0.47 density
Baltimore parks combined	0.72	23	<0.01*	15.21−0.92 density	0.60	23	<0.01*	0.84+0.52 density
All parks combined	0.75	27	<0.01*	11.14−0.23 density	0.81	27	<0.01*	1.71+0.37 density

Significant *P*-values at the 0.05 level are indicated with an asterisk

Foods provided by humans may be fed directly to squirrels, which is the case in Lafayette Park (Hadidian et al. 1988), or provided indirectly from bird feeders, flowers, or trees located throughout the yards of homes located in close proximity to the park (Williamson 1983). The latter, being the likely anthropogenic food source for squirrels in many neighborhood parks such as the Baltimore parks used in this study. Regardless of the

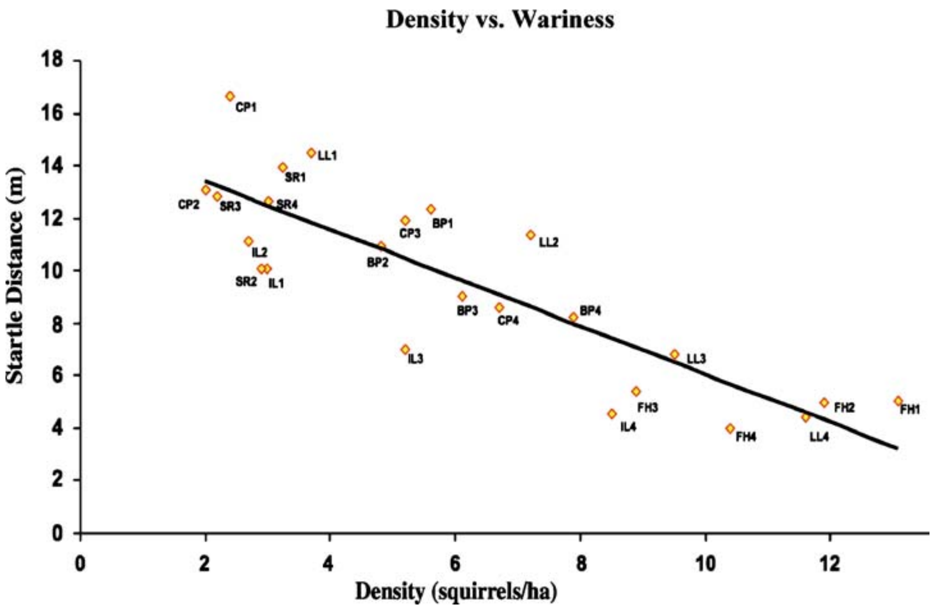

Fig. 1 Results of linear regression analysis of gray squirrel density and wariness. Location abbreviation (*FH* Federal Hill Park, *IL* Irvin Luckman Park, *SR* Stoney Run Park, *LL* Lakeland Park, *BP* Burdick Park, *CP* Carroll Park) is followed by sample seasons (*1* summer 2003, *2* fall 2003, *3* summer 2004, *4* fall 2004). $R^2_{adj} = 0.71$, $P<0.00$, $n=24$, and $df=23$

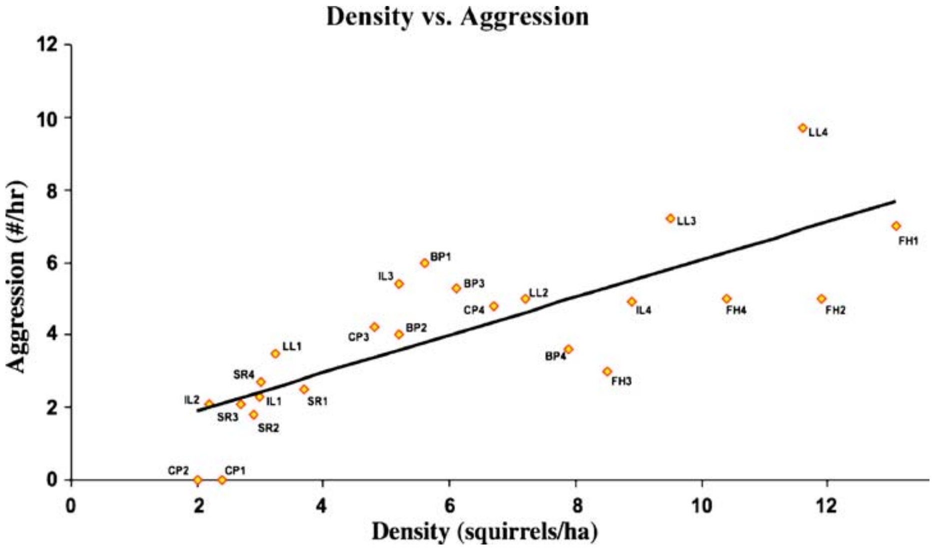

Fig. 2 Results of linear regression analysis of gray squirrel density and intraspecific aggression. Location abbreviation (*FH* Federal Hill Park, *IL* Irvin Luckman Park, *SR* Stoney Run Park, *LL* Lakeland Park, *BP* Burdick Park, *CP* Carroll Park) is followed by sample seasons (*1* summer 2003, *2* fall 2003, *3* summer 2004, *4* fall 2004). $R^2_{\mathrm{adj}} = 0.68$ $P<0.00$, $n=24$, and $df=23$

source, anthropogenic foods provide resources that may help to elevate squirrel densities to levels higher than those without these supplemental foods (Hadidian et al. 1988; Koprowski 1994). This explains the absence of a correlation between habitat suitability and squirrel density; which was further evident in the two locations with the highest population densities, Lafayette Park and Federal Hill Park, also having the two lowest HSI scores. The lack of a relationship between habitat suitability and squirrel density suggests that other factors are contributing to squirrel density in small urban parks.

The results of the linear regression analyses relating abundance to wariness and abundance to aggression demonstrates that as gray squirrel abundance increases, squirrel wariness decreases and intraspecific aggression increases. Gray squirrels in Lafayette Park, which were the least wary of those studied, may be less wary because of the high squirrel abundance. In the social system of gray squirrels, auditory cues are used to warn of predators and other threats (Schwartz and Schwartz 1981; Koprowski 1994); therefore, squirrels in high abundance populations may be less wary because more individuals are present to observe and provide warnings of predators or other threats. This may allow animals to focus more on securing food.

In addition, given the proximity of Lafayette Park to the White House, squirrels in this park are frequently exposed to high numbers of humans and levels of human activities (Manski et al. 1980). In response to this, squirrels may become skillful in determining distances in which humans may approach before they become, or are perceived as, a threat. There were no attempts at quantifying the number of park visitors at each park; however, the Baltimore parks used in this study may have fewer visitors than Lafayette Park. Nonetheless, the squirrels in Baltimore parks also experience humans and human activity which produced similar results. Federal Hill Park, which from personal observations, seemed to have a high number of visitors throughout daylight hours, also had low numbers for squirrel wariness.

Increased abundance, while providing more individuals to warn of threats, may also create increased intraspecific competition for food resources. This may influence individual squirrels to not only be less wary of threats, but also exhibit more aggressiveness. Williamson (1983) found that the more aggressive squirrels in urban habitats were able to secure more food resources than less aggressive squirrels. Although gray squirrels do not defend a specified territory, they do protect areas that are important for food resources (Flyger 1974; Koprowski 1994; Steele and Koprowski 2001). Therefore, in response to higher densities, the need to protect areas that provide food resources may be increased.

Several studies on urban wildlife have provided insights into the adaptations made by wildlife that have undergone synurbization (Flyger 1955, 1970; Cooke 1980; Shargo 1988; Gliwicz et al. 1994; Burger 2001; Smith and Engeman 2002; Ditchkoff et al. 2006). These studies have described reduced wariness and increased intraspecific aggression in various urbanized species; however, a driver for these changes has not been described. While the mechanisms for synurbization may have several drivers associated with the attributes of urban landscapes, the results of this study suggest that density may be a driver for reduced wariness and increased intraspecific aggression exhibited by urbanized wildlife. However, it should be noted that animal behaviors are often correlated with numerous biotic and abiotic factors; therefore those factors which influence population densities of urban wildlife may also influence behavior.

The causes of population and behavioral changes displayed by urban wildlife may be complex and interrelated to a host of correlating factors. However, the results of this study demonstrate a strong association between squirrel abundance and reduced wariness and increased intraspecific aggression. Future research should incorporate factors that influence population density in urban landscapes. These studies should evaluate micro and landscape level factors that may be correlated with population dynamic characteristics. Although this study did not include other species, there have been numerous studies indicating similar adaptations in other urbanized species. In order to gain a better understanding of the drivers for the behavioral adaptations displayed by urban wildlife, the results of this study should be tested on other species that live in close association with humans.

Acknowledgments This project was conducted as part of the Baltimore Ecosystem Study (BES) and supported by the National Science Foundation Long-term Ecological Research program (grant number DEB 0423476). We thank the researchers associated with BES and the USDA Forest Service Northeastern Research Station for the technical support, research staff time, equipment, and in kind services. In addition, we thank the Parks and People Foundation of Baltimore City for their assistance with the geographical and land use data. We also thank the Wildlife Initiative Program at Lincoln University Missouri for providing students to aid in the collection of field data.

References

Bowers MA, Breland B (1996) Foraging of gray squirrels on an urban–rural gradient: use of the GUD to assess anthropogenic impact. Ecol Appl 6:1135–1142

Burger J (2001) The behavioral response of basking Northern water (*Nerodia sipedon*) and Eastern garter (*Thamnophis sirtalis*) snakes to pedestrians in a New Jersey park. Urban Ecosyst 5:119–129

Cooke AS (1980) Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biol Conserv 18:85–88

Ditchkoff S, Saalfeld S, Gibson C (2006) Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecoysyst 9:5–12

Flyger VF (1955) Implications of social behavior in gray squirrel management. Trans North Am Wildl Nat Resour Conf 20:381–389

Flyger VF (1959) A comparison of methods for estimating squirrel populations. J Wildl Manage 23:220–223
Flyger VF (1970) Urban gray squirrels—problems, management, and comparisons with forest populations. Trans Northeast Fish Wildl Conf 27:107–113
Flyger VF (1974) Tree squirrels in urbanizing environments. In: Noyes JH, Progulske DR (eds) Wildlife in an urbanizing environment. Univ. Mass. Coop. Ext. Serv., Amherst, MA, pp 235–248
Gliwicz J, Goszczynski J, Luniak M (1994) Characteristic features of animal populations under synurbization—the case of the Blackbird and of the Striped Field Mouse. Memorabilia Zool 49:237–244
Gustafson EJ, VanDruff LW (1990) Behavior of black and gray morphs of *Sciurus carolinensis* in an urban environment. Am Midl Nat 123:186–192
Hadidian J, Manski D, Flyger V, Cox C, Hodge G (1988) Urban gray squirrel damage and population management: a case history. Proceedings of the Third Eastern Wildlife Damage Control Conference, pp 219–227
Hein EW (1997) Demonstration of line transect methodologies to estimate urban gray squirrel density. Environ Manage 21:943–947
Kinzig AP, Warren P, Chris M, Hope D, Katti M (2005) The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. Ecology and Society 10(23). Available at http://www.ecologyandsociety.org/vol10/iss1/art23
Koprowski JL (1994) *Sciurus carolinensis*. Mamm Species 480:1–9
Manski DA, VanDruff LW, Flyger V (1980) Activities of gray squirrels and people in a downtown Washington, D.C. park: management implications. Trans North Am Wildl Nat Resour Conf 46:439–454
McPherson EG, Nilon C (1987) A habitat suitability index model for gray squirrel in an urban cemetery. Lands J 6:21–30
Merwe M, Brown J, Jackson M (2005) The coexistence of Fox (*Sciurus niger*) and gray (*S. carolinensis*) squirrels in the Chicago metropolitan area. Urban Ecosyst 8:335–347
Nilon CH, Berkowitz AR, Hollweg KS (1999) Understanding urban ecosystems: a new frontier for science and education. Urban Ecosyst 3:3–4
Olszweski GJ (1964) Lafayette Park. Nat. Cap. Reg. Hist. No. 1. USDI, Nat. Park Serv
SAS Institute (2005) SAS/STAT user's guide. SAS Institute, Cary, NC
Schwartz CW, Schwartz ER (1981) The wild mammals of Missouri. University of Missouri Press, Columbia
Shargo ES (1988) Home range, movements, and activity patterns of coyotes (*Canis latrans*) in Los Angeles suburbs. Ph.D. Dissertation, University of California, Los Angeles
Steele MA, Koprowski JL (2001) North American tree squirrels. Smithsonian Institution Press, Washington
Smith H, Engeman R (2002) An extraordinary raccoon, *Procyon lotor*, density at an urban park. Can Field Nat 116(4):636–639
Thompson DC, Thompson PS (1980) Food habits and caching behavior of urban grey squirrels. Can J Zool 58:701–710
Warren P, Tripler C, Bolger D, Faeth S, Huntly N, Lepczyk C, Meyer J, Parker T, Shochat E, Walker J (2006) Urban food webs: predators, prey, and the people who feed them. Bull Ecol Soc Am 87(4):387–393
Williamson RD (1983) Identification of urban habitat components which affect eastern gray squirrel abundance. Urban Ecol 7:345–356