

DEMOGRAPHIC FACTORS CONTRIBUTING TO HIGH RACCOON DENSITIES IN URBAN LANDSCAPES

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Abstract: We simultaneously studied raccoon (*Procyon lotor*) populations inhabiting urban, suburban, and rural open areas in northeastern Illinois, USA, to examine the effects of urbanization on raccoon demographics. We predicted that raccoon density was higher in urbanized than rural landscapes because of increased survival and reproduction rates and greater site fidelity in urbanized areas. Density estimates for both the urban and suburban sites were greater ($P < 0.001$) than for the rural site during all seasons. Density estimates for the urban and suburban sites were similar ($0.177 \leq P \leq 0.603$) during 4 of 6 seasons. Percentages of parous females were similar among sites. However, higher proportions of juveniles to adult females captured at the urbanized sites may indicate larger litter sizes. Adult female survival was highest at the urban site during the first 2 years, but dropped due to an unknown disease during the final year. Urban raccoons experienced the fewest mortality sources, whereas rural raccoons experienced the most. Disease was the greatest mortality factor at the urban site, while vehicle-related mortalities dominated at the suburban and rural sites. The high ratio of marked to unmarked raccoons captured may indicate greater site fidelity at urbanized sites. Our data suggest that multiple factors, including increased survival, higher annual recruitment, and increased site fidelity, are jointly responsible for high-density raccoon populations in urbanized areas. Direct management of raccoon numbers in urbanized areas likely will require continuous control measures, because raccoons are capable of quickly repopulating an area after the resident population has been reduced. The most effective control measure may be the reduction of anthropogenic food sources that support raccoons at high densities.

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Raccoons adapt readily to urbanized environments, and urban/suburban raccoon populations are capable of reaching higher densities than their rural counterparts (Hoffmann and Gottschang 1977, Rosatte et al. 1991, Feigley 1992, Riley et al. 1998). While abundant supplemental food sources in the form of refuse (Schinner and Cauley 1974, Hoffmann and Gottschang 1977, Slate 1985) and supplemental den sites, such as sewers and other artificial structures (Schinner and Cauley 1974, Hoffmann and Gottschang 1977, Hadidian et al. 1991), may allow for high raccoon densities, the demographic mechanisms responsible for the elevated densities are unclear.

Anthropogenic food sources in urbanized areas may result in raccoons having better physical condition and higher reproduction rates (Rosatte et

al. 1991). Supplemental food and the absence of mortality factors common in rural areas also may serve to increase survival rates (Riley et al. 1998). Vehicle-related mortality and the threat of disease, however, may be higher in urbanized areas. In suburban London, United Kingdom, survival of red foxes (*Vulpes vulpes*) was lower than that of a non-exploited rural population, primarily due to vehicle-related deaths (Harris 1981). Nuisance-related mortality, mortality occurring as a consequence of an animal becoming a nuisance to humans (e.g., euthanasia after being trapped by animal-control personnel), also is likely to be higher in urbanized areas where wildlife and humans live in close proximity.

While dense raccoon populations may result from an increase in reproduction or survival rates, increased site fidelity also may be a contributing factor. Decreased emigration/immigration rates may result from the isolated nature of open spaces. In urbanized areas, raccoons commonly use wooded areas, forest parkland, and residential areas (Hoffmann and Gottschang 1977, Rosatte et al. 1991), while open fields, commercial and industrial areas, and areas character-

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ized by major thoroughways (streets, subway lines, railways) are used much less frequently or avoided (Rosatte et al. 1991). High-density housing, commercial and industrial areas, and major thoroughways often surround natural areas within the urban landscape and may represent barriers to interpopulation movements by raccoons.

Raccoon abundance in urbanized areas often leads to nuisance problems. Over 40% of North American animal-damage-control jurisdictions named the raccoon as the primary urban/suburban nuisance animal (Williams and McKegg 1987). Furthermore, dense raccoon populations, in close proximity to high-density human populations, may represent a public health threat as reservoirs of parasites (Kazacos 1982) and diseases (Bigler et al. 1975, Rosatte et al. 1991). For these reasons, management of urban/suburban raccoon populations often is warranted. Currently, raccoon management is reactive, occurring after a problem has arisen. Effective proactive management requires the identification of the demographic mechanism that allows raccoon populations to reach high densities.

To accurately assess the effects of urbanization on raccoon demographics, we simultaneously studied populations inhabiting urban, suburban, and rural open areas. We defined open areas as patches of at least seminatural habitat within an otherwise developed matrix. Thus, our study sites consisted of islands of seminatural habitat surrounded by urban, suburban, or rural development.

We addressed the general hypothesis that raccoon density is greater in urban and suburban areas than rural areas. The following predictions, based on this hypothesis, were tested to clarify the mechanism by which higher population densities are attained: (1) survival rates are higher in urbanized areas, (2) reproduction rates are higher in urbanized areas, and (3) urban and suburban raccoon populations exhibit greater site fidelity than those in rural areas.

STUDY SITES

We chose study sites in 3 protected open areas located in urban, suburban, and rural landscapes in northeastern Illinois. Relative urbanization was quantified by the mean daily traffic volume on roads adjacent to the sites, and surrounding land use and human population density within a 1-km radius of the sites (Table 1). We determined surrounding land use using the Illinois Land Cover Atlas (Illinois Department of Natural Resources 1996). We obtained additional land-use

information from recent aerial photos and ground truthing. We determined human population density within the 1-km buffer by U.S. census data (U.S. Bureau of the Census 1991). Total buffer area differed due to different study-site sizes. However, varying the spatial scale of the buffer did not result in significant changes in the relative urbanization parameters (S. D. Gehrt, unpublished data). Human density, calculated for the urban site, underrepresented the actual level of human presence in the surrounding area. Because the surrounding area was primarily commercial and industrial, substantially more people used the area than was indicated by the number of residents.

The rural site, Glacial Park (GP) in McHenry County, Illinois, was a public conservation area covering 1,052 ha. Habitats included wetlands (38%), old field (21%), grassland (19%), and oak woodlands and savannas (20%). Roads, parking lots, and buildings occupied 2% of the area. Only 2 picnic areas existed in GP, and little refuse was generated.

The suburban site, the Max McGraw Wildlife Foundation (MMWF), was a 495-ha managed natural area and private hunting preserve for upland game birds in Kane County, Illinois. The area was comprised of forests (46%), agricultural areas (22%), grasslands (15%), and wetlands (13%). Roads, parking lots, and buildings constituted 4% of the area. The MMWF was not open to the public, and little refuse was available on the property. Two amusement parks at the northeastern bound-

Table 1. Mean daily traffic volume on adjacent roads, and surrounding land use and human population density (persons/km²) within a 1-km radius for urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural study sites (Glacial Park, McHenry County) in northeastern Illinois, USA. Surrounding land use determined with the Illinois Land Cover Atlas (Illinois Department of Natural Resources 1996) and ground truthing. Human population density determined by U.S. census data (U.S. Bureau of the Census 1991). Com = Commercial, Ag. = Agricultural, Res. = Residential, Ind. = Industrial.

Site	Human density	Traffic volume	Surrounding land use (%)			
			Ag.	Res.	Com./ind.	Open space
Urban	3,420	302,550 ^a	0	35	43	22 ^b
Suburban	2,488	118,850 ^c	33	33	6	28
Rural	249	13,950 ^d	78	8	0	14

^a Source: 1994 Cook County Traffic Map, Illinois Department of Transportation, Office of Planning and Programming.

^b Includes school yards and cemeteries.

^c Source: 1997 Kane County Traffic Map, Illinois Department of Transportation, Office of Planning and Programming.

^d Source: 1997 McHenry County Traffic Map, Illinois Department of Transportation, Office of Planning and Programming.

ary, however, generated large amounts of refuse during the summer. Also, an adjacent restaurant, miniature golf area, and a small shopping plaza provided supplemental food for raccoons.

The urban site, the Ned Brown Forest Preserve (NBFP) in Cook County, Illinois, was 1,499 ha. The area consisted of mature second-growth forests (66%); wetlands and open water (15%); old field (10%); and paved roads, parking lots, and picnic shelters (9%). An estimated 1.5 million people visited NBFP annually (Dwyer et al. 1985), and picnicking constituted a major use of the area. Seventeen picnic areas were within the effective trapping area, as well as numerous additional garbage cans. The NBFP was open to the public from April to November.

METHODS

We trapped raccoons in Tomahawk box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with commercial cat food. Trapping was conducted during spring (Mar–May) and autumn (Sep–Nov), 1995–1997. During each trapping session, 30 traps were placed in a standardized pattern within a 2.4-km² grid and maintained for 10–13 nights (Gehrt 2002). We immobilized captured raccoons with an injection of ketamine hydrochloride and acepromazine or Telazol® (Gehrt et al. 2001). Anesthetized raccoons were weighed and sexed, and adults were placed in 1 of 5 age classes (class I: 0–14 months, class II: 15–38 months, class III: 39–57 months, class IV: 58–86 months, class V: >86 months) by tooth wear (Grau et al. 1970). We noted reproductive condition by the length and pigmentation of the teats in females and size of testes in males (Sanderson and Nalbandov 1973). All raccoons were marked with individually numbered ear tags (Monel #3 or #4, National Band and Tag Company, Newport, Kentucky, USA). Approximately 20 adult female raccoons were fitted with radiocollars (Advanced Telemetry Systems, Isanti, Minnesota, USA) at each site.

Diurnal rest sites of radiomarked raccoons were located twice weekly from June 1995 to May 1998 by homing in on foot with a portable receiver and hand-held antenna. Nocturnal locations were taken from March 1996 to November 1997 and were established through triangulation using a truck-mounted 4-element Yagi antenna. We took ≥ 2 bearings for each radiomarked animal at 2-hr intervals, beginning 1–2 hr past sunset until 1 hr before sunrise. Typically, we surveyed each site 1 night/week, with the exception of trapping peri-

ods when nocturnal locations were not collected. All locations were recorded in Universal Transverse Mercator (UTM) coordinates; bearings were converted to UTMs using Locate II (Nams 1990).

We determined population size using model M_h (capture heterogeneity) generated by the program CAPTURE (Otis et al. 1978, Moore and Kennedy 1985a) and assessed differences among sites with z -statistics (White et al. 1982). Raccoon captures have been shown to vary by sex (Gehrt and Fritzell 1996), and model M_h is appropriate when capture probabilities vary by animal. Because urbanization may affect raccoon movements (Hoffmann and Gottschang 1977, Slate 1985, Feigley 1992, Hatten 2000), we based density estimates on the minimum effective trapping area, as defined by the total area traversed by radiomarked raccoons during each trapping season. Due to a lack of movement data in 1995, minimum effective trapping areas were extrapolated from 1996 and 1997 data.

We calculated a body condition index (CI) for adult female raccoons as follows: $CI = (\text{body mass [kg]} / \text{body length [cm]}) \times 100$. Differences in CIs among sites for each season were assessed with a 1-way analysis of variance and Newman-Keuls mean separation test. We determined departures from a 1:1 sex ratio for adult raccoons with a 1-sample, chi-square goodness-of-fit test. Adult age structures and sex ratios were compared among sites for each trapping season and within sites among seasons with chi-square tests of contingency tables.

We surveyed roads adjacent to study areas for raccoon carcasses once or twice/week from June 1995 to February 1998 to provide additional demographic information. Carcasses were sexed and examined for ear tags, teeth were extracted for aging (Grau et al. 1970), and uteri were examined for placental scars. Differences among sites in the sex ratio and age distribution of collected raccoons were determined with chi-square tests of contingency tables. Due to small sample sizes, particularly at the rural site, we pooled road-survey data across years for analyses.

We estimated annual survival rates of radiomarked females using the staggered-entry design modification to the Kaplan-Meier survival estimator (Pollock et al. 1989) and determined differences among sites with z -statistics. We examined differences in cause-specific mortality among sites with MICROMORT (Heisey and Fuller 1985). Intervals used in the analysis of cause-specific mortality were spring (Mar–May), summer (Jun–Aug), autumn (Sep–Nov), and winter

(Dec–Feb). Seasons were based on climatological changes, as well as raccoon biology. Pregnancy and parturition occur predominantly during the spring (Sanderson and Nalbandov 1973), juveniles begin to move with their mother during the summer, young are weaned and begin to move independently in autumn (Schneider et al. 1971), and winter represents a period of greatly reduced activity.

To test for differences in reproduction rates among sites, we compared the percentages of females captured each autumn and females collected via road surveys that exhibited evidence of recent reproduction. We also compared the ratios of juveniles/adult female (≥ 2 yr) captured each autumn among sites. Differences among sites in the percentages of parous females and proportions of juveniles to adult females were determined with chi-square tests of contingency tables.

In populations exhibiting high site fidelity, a larger proportion of marked individuals should remain within the population through time than in a population exhibiting lower site fidelity. Therefore, we used the ratio of marked to unmarked adults captured each autumn as a relative measure of site fidelity. Differences among sites in the ratio of marked to unmarked individuals were assessed with chi-square tests of contingency tables.

For all tests, we deemed P -values ≤ 0.05 significant. However, we considered P -values > 0.05 but < 0.10 marginally significant, and present these for the reader's interpretation.

RESULTS

We captured 794 raccoons 1,563 times during 5,558 trapnights (Table 2). Density estimates for both the urban and suburban sites were consistently greater ($P < 0.001$ for all tests) than those of the rural site (Fig. 1). Suburban density was

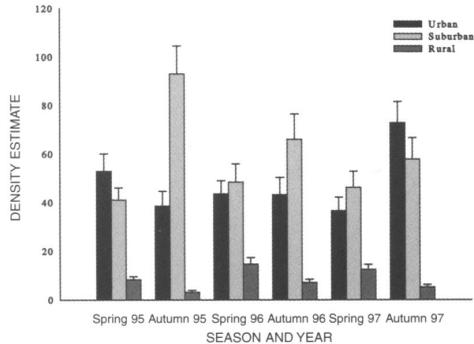


Fig. 1. Raccoon density estimates (raccoons/km²) and SE at an urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural open area (Glacial Park, McHenry County) in northeastern Illinois, USA, for spring and autumn, 1995–1997.

greater than urban density during autumn 1995 ($Z = 4.18$, $P < 0.001$) and marginally greater during autumn 1996 ($Z = 1.81$, $P = 0.070$). Otherwise, we detected no differences between the urban and suburban sites ($P \geq 0.177$ for all tests).

Urban females were in poorer condition during spring and exhibited the greatest percent change in CIs between seasons (Table 3). Condition indices were lower at the urban site than the suburban and rural sites in spring 1996 and 1997 (1996: $F_{2,71} = 54.01$, $P < 0.001$; 1997: $F_{2,53} = 6.35$, $P = 0.003$) and were lower at the urban and suburban sites than the rural site in autumn 1996 ($F_{2,65} = 12.2$, $P < 0.001$). We detected no differences in autumn 1995 ($F_{2,51} = 0.47$, $P = 0.626$) or 1997 ($F_{2,33} = 1.67$, $P = 0.203$).

We observed no consistent deviations from a 1:1 sex ratio at any site. More females than males were captured at the rural site in autumn 1996

Table 2. Raccoon trapping results at an urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural open area (Glacial Park, McHenry County) in northeastern Illinois, USA, spring 1995–autumn 1997.

Year	Season	Urban			Suburban			Rural		
		TN ^a	Total captures	Individual captures	TN	Total captures	Individual captures	TN	Total captures	Individual captures
1995	Spring	324	173	121	330	130	81	292	57	42
	Autumn	300	74	61	293	120	100	324	12	10
1996	Spring	293	155	80	281	93	69	366	50	40
	Autumn	320	91	70	307	102	77	329	54	46
1997	Spring	290	100	65	284	91	70	269	41	35
	Autumn	300	97	84	300	90	73	356	33	28
Totals		1,827	690	481	1,795	626	470	1,936	247	201

^a TN = Trapnights.

Table 3. Mean condition indices (CI), standard deviation (SD), and percent (%) change relative to previous trapping season for adult female raccoons at an urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural open area (Glacial Park, McHenry County) in northeastern Illinois, USA, autumn 1995–autumn 1997.

Season	Urban			Suburban			Rural		
	Mean CI	SD	% change	Mean CI	SD	% change	Mean CI	SD	% change
Autumn 1995	14.0 A ^a	2.6		13.5 A	1.9		13.1 A	0.9	
Spring 1996	7.3 A	0.8	-47.9	10.2 B	1.3	-24.4	9.9 B	1.5	-24.4
Autumn 1996	10.8 A	1.6	+47.9	11.3 A	2.0	+10.8	13.4 B	1.9	+35.3
Spring 1997	8.5 A	0.9	-21.3	9.6 B	1.7	-15.0	10.2 B	1.7	-23.9
Autumn 1997	12.4 A	1.7	+45.9	12.0 A	2.2	+25.0	10.9 A	1.3	+6.9

^a Mean CIs within rows with similar capital letters were not different ($P > 0.05$).

(M:F ratio = 0.5:1, $\chi^2 = 4.83$, $df = 1$, $P = 0.028$), and males outnumbered females at the suburban site in autumn 1997 (ratio = 1.9:1, $\chi^2 = 3.93$, $df = 1$, $P = 0.047$). A marginally greater number of males were also captured in autumn 1997 at the urban site (ratio = 1.8:1, $\chi^2 = 3.76$, $df = 1$, $P = 0.053$). Otherwise, sex ratios did not differ from 1:1 ($P \geq 0.116$ for all tests). Sex ratios of captured raccoons did not differ among sites ($P \geq 0.149$ for all tests) or within sites among seasons ($P \geq 0.155$ for all tests). Similarly, sex ratios of carcasses collected during road surveys did not differ from 1:1 at any site ($P \geq 0.292$ for all tests) and did not differ among sites ($P \geq 0.184$ for all tests).

Age structure did not differ among sites ($P \geq 0.144$ for all tests). The age distribution of raccoons collected via road surveys also was similar at all sites ($\chi^2 = 23.91$, $df = 20$, $P = 0.246$; Fig. 2). Age structure was marginally different among seasons at the rural site ($\chi^2 = 23.72$, $df = 15$, $P = 0.070$), with the difference primarily due to a lower proportion of age class II individuals in the spring 1995 sample. We detected no difference in

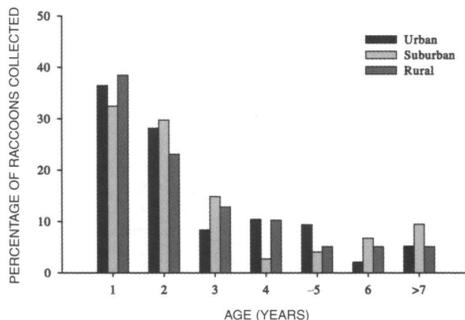


Fig. 2. Age distributions of raccoons (≥ 1 yr old) collected on road surveys at an urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural open area (Glacial Park, McHenry County) in northeastern Illinois, USA, Jun 1995–Dec 1997.

age structure among seasons for the urban ($\chi^2 = 25.12$, $df = 20$, $P = 0.197$) or suburban site ($\chi^2 = 27.98$, $df = 20$, $P = 0.110$).

Survival rates were higher at the urbanized sites during the first 2 years, but dropped during 1997–1998 due to an unknown disease at the urban site, and an increase in vehicle-related mortality at the suburban site (Fig. 3). Over half of all mortalities at the urban site occurred during 1997–1998. Conversely, annual survival at the rural site increased during the final study year.

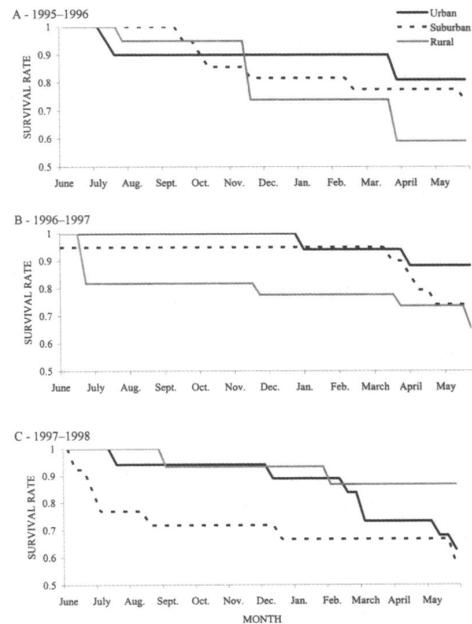


Fig. 3. Kaplan-Meier annual survival curves for adult female raccoons at an urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural open area (Glacial Park, McHenry County) in northeastern Illinois, USA.

Table 4. Annual survival estimates and standard deviation (SD) for adult female raccoons at an urban (Ned Brown Forest Preserve, Cook County), suburban (Max McGraw Wildlife Foundation, Kane County), and rural open area (Glacial Park, McHenry County) in northeastern Illinois, USA, Jun 1995–May 1998.

Year	Urban		Suburban		Rural	
	Survival	SD	Survival	SD	Survival	SD
1995–1996	0.81	0.09	0.74	0.08	0.59	0.11
1996–1997	0.88	0.07	0.74	0.10	0.65	0.09
1997–1998	0.63	0.11	0.57	0.10	0.87	0.10

Annual survival was marginally higher at the urban site than the rural site in 1996–1997 ($Z = 1.95$, $P = 0.051$; Table 4). In 1997–1998, annual survival at the rural site was higher than at the suburban site ($Z = 2.11$, $P = 0.035$) and marginally higher than at the urban site ($Z = 1.66$, $P = 0.097$).

Urban raccoons experienced the fewest mortality sources, while rural raccoons experienced the most. Thirteen known deaths of radiomarked females occurred at the urban site, 18 at the suburban site, and 15 at the rural site. Disease ($n = 10$) and vehicle-related mortality ($n = 3$) were the only mortality factors observed at the urban site. At the suburban site, vehicle-related mortality was dominant ($n = 10$), followed by disease ($n = 7$), and nuisance-related mortality ($n = 1$). Rural mortality factors included vehicle-related mortality ($n = 6$), disease ($n = 4$), land-management practices ($n = 3$), and predation ($n = 2$). Deaths attributed to land management occurred when ground dens were destroyed during habitat-management activities.

A comparison of fit for cause-specific mortality models based on separate and pooled years did not reveal a difference ($\chi^2 = 71.7$, $df = 72$, $P = 0.488$); therefore, we pooled seasonal estimates across years (Table 5). Deaths due to mortality sources unique to the rural site (predation and land management) were greater during autumn ($Z = 2.26$, $P = 0.024$). Vehicle-related mortalities were marginally lower at the urban site than the suburban site during autumn ($Z = 1.88$, $P = 0.060$). We detected no other differences in cause-specific mortality ($P \geq 0.134$ for all tests).

The percentage of parous females did not differ among sites (Table 6). Captures of females sufficient to estimate reproduction at the rural site occurred only during 1996. The percentage of females showing evidence of reproduction was 84% ($n = 19$) for adults and 14% ($n = 7$) for yearlings. We detected no differences among sites for 1996 ($\chi^2 = 3.47$, $df = 2$, $P = 0.176$). Reproduction rates determined through the examination of carcasses collected during road surveys were 79% ($n = 14$) for the urban, 85% ($n = 20$) for the suburban, and 73% ($n = 11$) for the rural site. Reproduction rates did not differ among sites ($\chi^2 = 0.69$, $df = 2$, $P = 0.707$).

Although the percentage of parous females did not differ among sites, a greater number of juveniles relative to adult females occurred at the urbanized sites. The number of juveniles/adult female was 2.1 (1996) and 4.3 (1997) for the urban, 1.3 and 3.0 for the suburban, and 0.6 and 2.5 for the rural site. The proportion of juve-

Table 5. Estimated seasonal survival rates, total exposure days (Days), number of mortalities observed (m), and cause-specific mortality rates of adult female raccoons by study area (urban [Ned Brown Forest Preserve, Cook County], suburban [Max McGraw Wildlife Foundation, Kane County], and rural [Glacial Park, McHenry County]) and season in northeastern Illinois, USA, Jun 1995–May 1998. Seasons (summer 1995–spring 1998) pooled across years.

Site	Season	Total observed		Survival rate		Cause-specific mortality rates					
		Days	m	Mean	SE	Vehicle-related		Disease		Other	
						Mean	SE	Mean	SE	Mean	SE
Urban	Spring	4,282	7	0.637	0.109	0.052	0.050	0.311	0.105	0.000	0.000
	Summer	4,668	3	0.837	0.086	0.054	0.053	0.108	0.072	0.000	0.000
	Autumn	4,844	0	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Winter	4,719	3	0.842	0.083	0.053	0.051	0.105	0.070	0.000	0.000
Suburban	Spring	4,597	7	0.657	0.104	0.147	0.078	0.196	0.088	0.000	0.000
	Summer	5,266	5	0.769	0.090	0.184	0.083	0.000	0.000	0.046	0.045 ^a
	Autumn	4,864	5	0.755	0.095	0.147	0.078	0.098	0.066	0.000	0.000
	Winter	4,664	1	0.944	0.055	0.000	0.000	0.056	0.055	0.000	0.000
Rural	Spring	3,811	5	0.696	0.113	0.182	0.095	0.122	0.080	0.000	0.000
	Summer	4,009	3	0.813	0.097	0.124	0.082	0.000	0.000	0.062	0.060 ^b
	Autumn	4,320	6	0.684	0.111	0.053	0.051	0.053	0.051	0.210	0.093 ^c
	Winter	4,151	1	0.937	0.061	0.000	0.000	0.063	0.061	0.000	0.000

^a Includes a nuisance-related death.

^b Includes a death due to predation.

^c Includes predation and deaths due to land-management practices.

Table 6. Percentage (%) of parous adult and yearling raccoons and sample size (n) by year at an urban (Ned Brown Forest Preserve, Cook County) and suburban (Max McGraw Wildlife Foundation, Kane County) open area in northeastern Illinois, USA, 1995–1997.

Year	Urban				Suburban			
	Adults		Yearlings		Adults		Yearlings	
	%	n	%	n	%	n	%	n
1995	58	12	25	5	50	24	33	9
1996	69	13	0	9	57	21	22	9
1997	56	9	17	7	63	11	0	5

niles/adult female was higher at the urban site ($\chi^2 = 7.00$, $df = 1$, $P = 0.008$) and marginally higher at the suburban site ($\chi^2 = 3.12$, $df = 1$, $P = 0.077$) than the rural site in 1996. We detected no other differences ($P \geq 0.363$ for all tests).

We used the ratio of marked to unmarked individuals as a relative measure of site fidelity, with a higher ratio indicating greater site fidelity. A general trend existed for a higher proportion of marked adults at the urbanized sites than the rural site. Ratios of marked to unmarked adults were 0.4 (1995), 2.0 (1996), and 0.6 (1997) for the urban; 0.8, 0.8, and 1.3 for the suburban; and 0.3, 0.5, and 0.4 for the rural site. The proportion of marked individuals captured was higher at the urban site than the suburban ($\chi^2 = 4.02$, $df = 1$, $P = 0.045$) and rural sites ($\chi^2 = 8.23$, $df = 1$, $P = 0.004$) in 1996. The proportion at the suburban site was higher than the rural site ($\chi^2 = 5.04$, $df = 1$, $P = 0.025$) and marginally higher than the urban site ($\chi^2 = 3.18$, $df = 1$, $P = 0.075$) in 1997. We detected no other differences in ratios of marked individuals ($P \geq 0.133$ for all tests).

DISCUSSION

We hypothesized that raccoon densities are greater in urban and suburban areas than rural areas. Our findings support this hypothesis for our study sites and are consistent with studies that have documented high densities of raccoons in urban and suburban areas. Further, because our study directly compared urbanized and rural areas, our data provide additional evidence in support of this hypothesis.

Density estimates for the urban and suburban sites fell within the lower range of densities reported from other urban/suburban areas (41–333 raccoons/km²). Other researchers computed estimates using either the size of the trapping grid (Rosatte et al. 1991) or study area (Schinner and Cauley 1974, Hoffmann and Gottschang 1977, Feigley 1992, Riley et al. 1998),

which may have resulted in overestimates of actual density. Had we used the trapping grid area, our urban and suburban densities would have been 31–102% larger than those reported. Animals often range beyond artificial boundaries, and the use of static boundaries may confound comparisons among sites where home-range size and movement patterns differ. We believe that using the minimum effective trapping area to calculate density, particularly when comparing ≥ 2 populations whose movement patterns differ, is more appropriate and provides a better estimate of raccoon density.

We further hypothesized that the mechanism allowing densities to build in urbanized areas involved higher survival and reproduction rates and greater site fidelity. Overall, our results suggest that survival in urbanized areas relative to that in rural environments is high during most years and likely contributes to the observed differences in density. However, dense raccoon populations are at greater risk of disease outbreaks, which may periodically reduce survivorship. Such a reduction occurred during 1997–1998 at the urban site. In addition to relatively high density, other factors served to increase the urban population's susceptibility to disease, including a highly aggregated spatial distribution (Hatten 2000) and poor physiological condition of individuals during spring. An aggregated distribution may result in increased intraspecific contact in an already dense population, further facilitating disease transmission. Poor physical condition may increase an individual's probability of contracting a disease upon exposure, as well as decrease its chances of recovery. Most disease-related deaths in 1997–1998 occurred during late winter and early spring (Fig. 3) when urban females were in extremely poor condition.

While raccoons often lose 50% of their body mass over winter (Mech et al. 1968, Moore and Kennedy 1985b), previous urban and suburban studies have reported much lower overwinter losses. Suburban raccoons lost only 16% of their body mass over winter in Ohio (Hoffmann 1979) and only 10% in Washington, D.C. (Riley et al. 1998). Rosatte et al. (1991) reported average overwinter losses of 17% for males and 24% for females in metropolitan Toronto, Canada. Although results from our suburban site were similar to these studies, losses were much more pronounced for urban females. The urban preserve was closed during the winter months, and supplemental resources were not available. Although we

expected raccoons to utilize food sources outside of the preserve during winter, this did not occur, and natural resources within the preserve apparently were insufficient to adequately support the number of raccoons residing there (Hatten 2000).

Despite better physical condition, survival may play less of a role in the population-building mechanism at the suburban site due to the greater incidence of vehicle-related mortality. While refuse was easily obtainable inside the urban site during most of the year, supplemental food at the suburban site was confined to adjacent businesses and residences. Consequently, use of surrounding areas was greater and roads were crossed more frequently than at the urban site. Movements to and from cornfields further contributed to the incidence of vehicle-related deaths (Hatten 2000). This cornfield use was contradictory to the results of a New Jersey study, which indicated that suburban raccoons made little use of cornfields in the area and rarely went out of their way to visit them, preferring to remain within the suburbs (Slate 1985). Greater use of developed areas at the suburban site also was reflected in the occurrence of nuisance-related mortality, a mortality factor not observed at the urban site.

Although we failed to detect differences in age structure among sites, captures of age class V individuals (>86 months) only occurred at the urban ($n = 6$) and suburban sites ($n = 13$). However, detecting differences among sites in the number of individuals in age class V is difficult due to the small proportion of the population in this age class. Therefore, despite the lack of significance among sites in respect to age structure, the capture of older individuals exclusively at the urbanized sites supports our findings of higher survival at the urbanized sites during most years.

Our analyses of differences in the proportion of parous females did not support the hypothesis of higher reproduction rates in urbanized areas. However, higher proportions of juveniles captured at the urbanized sites may indicate larger litters. Unfortunately, we did not collect sufficient data to adequately address this aspect of reproductive output. Alternatively, increased juvenile survival may account for the greater proportion of juveniles observed at these sites. Rosatte et al. (1991) reported that the proportion of juveniles to adults captured each month did not vary from July to November in metropolitan Toronto and concluded that juvenile survival rates during this period may be high. Additional research is needed to identify the responsible factor and to deter-

mine whether a larger number of individuals are annually recruited into these populations.

In general, larger proportions of marked individuals were captured at the urbanized sites. Therefore, the urban and suburban populations appeared to be more stable, exhibiting greater site fidelity than the rural population. Both sites consisted of high-quality raccoon habitat that was further enhanced by the presence of anthropogenic food sources. A number of studies on mammalian species have shown an inverse relationship between habitat quality and emigration rates (Lurz et al. 1997, Virgl and Messier 2000, Lin and Batzli 2001). Harris and Trehwella (1988) concluded that dispersal distances for urban foxes were shorter in high-quality than low-quality fox habitat. Our findings also agree with previous studies, which have suggested that raccoon populations migrate less in urbanized than rural environments (Hoffmann and Gottschang 1977, Slate 1985, Feigley 1992).

Urbanized habitats generally are of relatively high quality due to the presence of supplemental food. However, a habitat-quality gradient undoubtedly exists in urbanized areas as in rural environments, which affects the direction of interpopulation movements. If emigration of raccoons is reduced in high-quality urban habitats, the resultant density of the resident population may limit the opportunity for dispersers from lower-quality areas to settle there. An increase in the proportion of unmarked individuals occurred at the urban site during autumn 1997, and was preceded by the lowest density estimate for this site in spring 1997. Most unmarked individuals were yearling males. The previous reduction in density and the preponderance of yearlings in the unmarked sample suggest that these individuals were immigrants. Therefore, while the urban matrix may be a deterrent to interpopulation movement, it is not an impassable barrier for raccoons.

MANAGEMENT IMPLICATIONS

Dense raccoon populations in close proximity to human developments often result in nuisance-related problems and raise concerns regarding the transmission of diseases and parasites from raccoons to humans and domestic animals. Proactive management aimed at the reduction of urban raccoon numbers requires knowledge of the demographic factors governing population size. Our data suggest that multiple factors, including increased survival, higher annual recruitment, and increased site fidelity, are jointly responsible

for the density of raccoon populations in urbanized areas. However, site-specific differences in the relative contribution of these factors may exist. We found that differences in movement patterns affected the relative importance of mortality sources and annual survival rates for 2 urbanized populations with similar densities.

High annual recruitment will require that direct control measures, such as a trapping and removal program, be continuous. Furthermore, since the urban matrix does not appear to restrict raccoon movement, high-quality habitat may be quickly repopulated if a trapping/removal program reduces the resident population. Therefore, the most effective control measure likely will be the reduction or elimination of anthropogenic food sources (e.g., covering refuse containers, removing refuse before dusk), which support raccoons at these densities.

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