K. J. McGowan. 2001. Pp 365-381 *in* Avian ecology and conservation in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donelly, eds.). Kluwer Academic Press, Norwell, MA.

Chapter 17

Demographic and behavioral comparisons of suburban and rural American Crows

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- Key words: American Crow, *Corvus brachyrhynchos*, cooperative breeding, demography, urban adaptation
- Abstract: American Crows (Corvus brachyrhynchos) have become common suburban and urban birds in the last 50 years, using these environments for roosting and breeding. I studied crows in upstate New York from 1989 to 1999, and compared reproductive success, survival, and social behavior of crows in suburban and rural areas. Although both suburban and rural crows maintained permanent territories, suburban American Crows had smaller territories and nested at higher densities. Both suburban and rural crows periodically left their territories in fall and winter to join foraging aggregations and to roost at night. The proportion of nests attended by auxiliaries did not differ, but suburban nests were attended by larger families. Overall nest success was higher in suburban areas. Success rates during the egg stage of the nest cycle did not differ between habitat, but suburban nests had higher success during the nestling stage of the nest cycle. Survival of crows post fledging was better in suburban areas, but after one year annual survival rates did not differ between the habitats. Birds raised in one habitat tended to breed in the same habitat. Although clutch sizes and egg hatchability did not differ between the habitats, rural nests produced nearly one more young per successful nest and significantly larger young than suburban crows, suggesting that food resources were better in rural areas. Data from a drought year, a time of apparent food shortage, suggested that suburban food resources also were less dependable than those in rural areas. The increase in American Crows over the last 25 years in eastern North America may be due in part to the successful exploitation of suburban nesting habitats.

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1. INTRODUCTION

Since the mid-1950's, American Crows (*Corvus brachyrhynchos*) have become common urban and suburban birds in North America, roosting and breeding in cities and towns (Jollie 1976, Houston 1977, Knight et al. 1987). Earlier, crows were more wary and avoided urban areas. Changing use of a landscape can affect such things as nesting structures employed, food used, exposure to predators, use of space (e.g., territory size and permanence, density), social structure (interaction with conspecifics, aggregations, family structure and cooperative breeding), and basic demographic factors. Some habitats may be attractive to immigrant birds, but if birds cannot reproduce successfully in these habitats, they may be an ecological trap (Gates and Gysel 1978). In Switzerland, Richner (1989) suggested that cities may be attracted to breed in cities, but they cannot produce offspring that can effectively compete for breeding opportunities.

I examined whether American Crows nesting in a suburban environment differed in nest success, survival of the young, or in social behavior from crows in a rural environment.

2. METHODS

I studied American Crows in the city of Ithaca and the village of Cayuga Heights (Fig. 17.1a), and the surrounding rural areas of Tompkins County (Fig. 17.1b), New York from 1989 through 1999. Ithaca is a small city in the central Finger Lakes region of New York State, containing approximately 29,000 people in its 14.2 km² (2,062 people per km²). Contiguous with Ithaca, Cayuga Heights is a residential area with a lower human density of 728 people per km². These areas are best classified as "suburban" (Marzluff et al. 2001). Just under 100,000 people live in Tompkins County (1995 data; Tompkins County Chamber of Commerce), with a density of 52 human per km² outside of the cities and villages. Rural areas surrounding Ithaca consist of agricultural fields, woodlots, extensive forests, cemeteries, and scattered residences. Approximately 50% of the county is wooded or reverting to forest (Smith et al. 1993), and 35% is in agriculture (1995 data; Tompkins County Chamber of Commerce).

The suburban areas used by crows consisted of residential and commercial districts, university and related properties, parks, and cemeteries. Much of the residential area contained many large mature trees. Rural areas varied from low density residential areas adjacent to agricultural and wildlands, to mixed agricultural fields and woodlots, to forest. For comparisons in this study, "suburban" crows were those located within Ithaca or Cayuga Heights with territories containing greater than 75% residential or commercial use (Fig. 17.1a). "Rural" territories fell outside of Ithaca and Cayuga Heights and contained greater than 50% forest, secondary scrubby growth, or agricultural fields and pastures. Rural territories could include residential area and some commercial use, but only if they composed less than 50% of the territory. Rural housing typically consisted of one or several well spaced homes along road frontage, bounded by extensive agricultural or wild lands (Fig. 17.1b). Territories with between 50 and 75% residential or other development were not used in analyses.

I measured territory size in the spring of 1994 and 1995 by mapping observations of tagged individuals engaging in territory defense. Exact territory size was determined for only a small percentage of families. For families where spot maps did not provide a complete territory map, I used the length of the longest axis across the territory to determine a maximum territory diameter as a measure of territory size. Because most territories

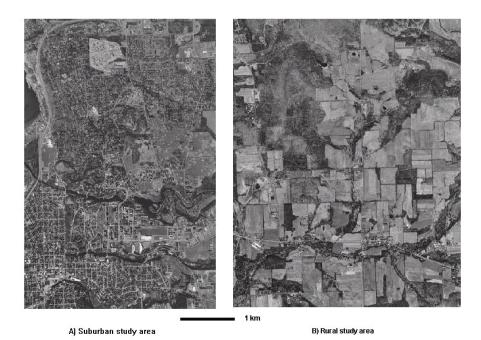


Figure 17.1. Aerial images of a) suburban study area in the city of Ithaca and the village of Cayuga Heights and b) rural study area, in the unicorporated areas of Tompkins County, east of Ithaca, NY. Photographs taken 27 March 1995.

that I accurately mapped were roughly circular, I estimated the area of all territories by assuming the longest axis represented the diameter of a circle and calculated the area of that circle. Each family of crows was used only once in the calculations; yearly fluctuations in territory size were not included. Instead, a best estimate from one year only was used for each family.

I located and monitored nests in each habitat in all years. I monitored nests from the ground for activity, and periodically climbed to the nests to examine nest contents. I marked nestlings at approximately one week before fledging (between day 24 and day 30 after hatch) with individually unique colored leg bands and patagial tags with unique combinations of letters or letters and numbers. All young were weighed and measured at that time.

Because nests were discovered at different stages in the nesting cycle, I calculated Mayfield daily survival probabilities (Mayfield 1961, 1975) to compare nest success at the various stages. Differences in nest success between the two habitats were tested using the *Z*-test developed by Hensler and Nichols (1981). A total of 215 suburban nests and 47 rural nests were used in the analyses. Incubation period was assumed to be 19 days, and nestling period 35 days.

No organized census of all marked individuals was conducted; sightings of individuals were recorded as they occurred throughout the seasons. I looked for crows at their home territories at irregular intervals throughout the year, and also searched foraging aggregations, and, less frequently, roosts for tagged individuals. An attempt was made to locate all banded individuals at the beginning of each breeding season. In addition, crows throughout the area were constantly checked for bands and tags. An extensive system of volunteer observers, recruited through public announcements and a high degree of bird awareness in the local area, contributed many important sightings of dispersing crows.

I used resightings of tagged individuals as capture/recapture data to estimate annual survival and recapture probabilities using the program MARK (White and Burnham 1999). All sightings and reports of individuals were tallied into 3 month blocks, roughly covering nestling and fledgling phases (May, June, and July); late summer and fall (Aug, September, and October); early winter (November, December, and January); and late winter and early spring, the pre- and early-nesting season (February, March, and April). All individuals entered the analyses at fledging (in the May-July block of their natal year). A total of 591 suburban crows and 162 rural ones were used in the analyses. I estimated survival assuming a constant yearly survival, but with age effects for the first and second years. Using MARK, I constructed a model to fit the data using age and environment as parameters for both survival and recaptures, then constructed another model combining environments in the survival component. I tested for a significant effect of environment by comparing the models using the Likelihood Ratio Test (Cooch and White 2000).

American Crows are known to be cooperative breeders, with extra individuals (auxiliaries) at nests in many parts of their range (Kilham 1984, 1989; Chamberlain-Auger et al. 1990; Caffrey 1992, 1999), including New York (McGowan 1995, 1996). Presence of auxiliaries and breeding group sizes were determined through nest watches and observations made during the fledgling feeding period. In suburban areas (but not rural areas; see Knight et al. 1987), crows typically mobbed me when I climbed to their nests. Although up to 75 crows from a neighborhood might join in a mobbing event, the core group of most persistent mobbers was a fairly accurate measurement of family size. In most families, not all members were individually marked; thus, I could not always determine the exact family size of groups with auxiliaries.

Values reported below are means \pm SD, unless otherwise noted. Probabilities given are for two-tailed tests (P < 0.05), using Student's *t* tests, ANOVA, and log likelihood *G*-tests.

3. **RESULTS**

3.1 Territory Size and Nest Placement

Crows defended territories in both suburban and rural habitats. Crows in both habitats were present on the breeding territories throughout the year, and active territorial defence was observed in every month. However, outside of the breeding season, individuals did not restrict their activities solely to these territories, but left them periodically to forage during the day and to roost at night (see Stouffer and Caccamise 1991, and Caccamise et al. 1997 for a description of this behavior). Territory size (diameter) differed significantly between the two habitats (suburban = 0.31 km \pm 0.12, n = 59; rural = 0.672 km \pm 0.17, n = 18; $t_{75} = 9.956$, P < 0.001). Assuming territories were circular, on average, crows defended 8.7 ha in suburban areas (range 0.8 to 28.3) and 37.7 ha in rural (range 12.6 to 95.0). Within both study areas, all space was occupied, but the density of nesting crows was higher in suburban (11.5 territories per km²) than in rural areas (2.6 territories per km²).

Nest placement varied between suburban and rural crows. Suburban nests were significantly higher than rural nests (suburban = 18.7 m \pm 5.92, *n* = 329, range = 4.75 to 34.2 m; rural = 14.9 m \pm 4.26, *n* = 85, range = 4.5 to 24.0 m; *t*₄₁₂ = 5.587, *P* <0.001), and were in taller trees (suburban = 21.2 \pm

6.18, n = 327; rural = 18.0 ± 4.82, n = 85, $t_{410} = 4.384$, P < 0.001). Suburban nests also were placed higher in the nest tree (suburban = 87.8% of nest tree height; rural = 82.5%; *t*-test on arcsine transformed data, $t_{410} = 5.14$, P < 0.001). Suburban nests were more frequently located in coniferous trees than rural nests (96.5% conifers suburban, n = 386; 83% conifers rural, n = 100; $G_1 = 19.338$, P < 0.001), and crows placed nests lower in deciduous trees than in conifers (deciduous mean = 69.8% of nest tree height, n = 38; conifer = 87.5%, n = 429; *t*-test on arcsine transformed data, $t_{465} = 11.087$, P < 0.001). Although nest position in a tree was affected significantly by both habitat ($F_{1,407} = 7.56$, P < 0.01) and tree type ($F_{1,407} = 53.30$, P < 0.001), nest height was affected significantly only by habitat ($F_{1,409} = 11.72$, P = 0.001) and not tree type ($F_{1,409} = 0.70$, P = >0.4). In neither analysis did an interaction between habitat and tree type exist.

3.2 Nest Success and Survival

Overall nest success was greater in suburban nests than in rural nests (Table 17.1). Survival of nests with eggs did not differ between habitats, but nests with nestlings had higher survival in the suburban habitat than in the rural habitat. Clutch size was identical in the two habitats (4.7; $n_{suburban} = 74$, $n_{rural} = 22$), and the number of eggs that hatched per nest did not differ (suburban = 3.9 ± 1.02 ; rural = 4.1 ± 1.50 ; $t_{47} = 0.43$; P > 0.5). A total of 830 nestlings was marked and measured in 271 nests. Number of fledglings produced per nest in the populations did not differ between the habitats, but suburban nests produced fewer fledglings in each successful nest than rural nests (Table 17.2). Suburban nests experienced greater rates of brood reduction, decreasing the number of fledglings produced per nest.

Predation was the primary source of nest failure, with only a few nests lost to weather (high winds, lightning) or abandonment. Perhaps the most important nest predator at all stages of the nest cycle was the raccoon (*Procyon lotor*). Evidence of raccoon predation were feces in the nest tree and in the nest, destruction of the nest, teeth marks on plastic leg bands, and raccoons sleeping in the depredated nest. Eastern gray squirrels (*Sciurus carolinensis*) also were potentially significant egg predators. Although no direct evidence of squirrel predation was obtained, squirrels were actively chased from the vicinity of the nest tree by crows. Raccoons and Great Horned Owls (*Bubo virginianus*) were known to kill nestlings. Evidence of owl predation included decapitated nestlings, and owl feathers in the nests. Incubating or brooding adult crows (female breeders) also were killed while on the nest on several occasions, presumably by Great Horned Owls. No evidence of crows depredating other crow nests was observed.

Known predators on crow fledglings included domestic cats (*Felis catus*), raccoons, Cooper's Hawks (*Accipiter cooperii*), Red-tailed Hawks (*Buteo jamaicensis*), and Great Horned Owls. Evidence included visual observations of cats with fledglings in their mouths, Red-tailed Hawks with banded crows in their talons, remains of banded crows below Cooper's Hawk nests, and bands found in Great Horned Owl pellets. Other observed sources of mortality for fledglings included collision with automobiles, becoming trapped in vegetation, electrocution on an electrical transformer, and being killed or removed by people.

Rural crow nestlings measured at banding were heavier and larger than suburban crows in all linear body measures, except feathers (Table 17.3). By banding age, tarsus length of nestlings had attained 100% of adult size.

Post-fledging survival was significantly higher for suburban-raised than rural-raised crows ($\chi^2_3 = 11.517$, P < 0.01), with the greatest difference in the first year of life (Table 17.4). Annual survival after the first year was high (>70%) in both areas (Table 17.4), but the recapture rate was significantly lower in rural areas ($\chi^2_3 = 29.038$, P < 0.01). Although the three-age-class model (first, second, and subsequent years) provided the best fit to the data (highest AICc weight, Cooch and White 2000), it did not differ

Table 17.1. Mayfield probability of American Crow nest survival in suburban Ithaca and the surrounding rural Tompkins County, New York.

	Pdaily (SD)	Ptotal (SD)	# nests	Ζ	Р
Eggs (19 days)					
Suburban	0.998 (0.002)	0.794 (0.008)	164		
Rural	0.989 (0.004)	0.815 (0.016)	39	1.2	n.s.
Nestlings (35 days)					
Suburban	0.991 (0.001)	0.721 (0.006)	155		
Rural	0.985 (0.004)	0.589 (0.015)	35	-8.2	< 0.001
Overall (54 days)					
Suburban		0.573 (0.008)	202		
Rural		0.480 (0.015)	45	-5.5	< 0.01

Table 17.2. Fledgling production by American Crows in suburban Ithaca and the surrounding Tompkins County. New York.

Tompking County, New Tork.					
	SUBURBAN	RURAL			
	Mean + SD(n)	Mean \pm SD (n)	<i>t</i> (df)	Р	
Fledglings per					
Nest	1.62 <u>+</u> 1.80 (287)	1.64 <u>+</u> 2.00 (72)	0.120 (357)	0.905	
Fledglings per					
Successful nest	3.06 <u>+</u> 1.30 (151)	3.58 <u>+</u> 1.46 (33)	3.339 (182)	0.044	

significantly from a two-age-class model ($\chi^2_4 = 8.814$, P = 0.07), which included only the first and subsequent years.

3.3 Dispersal

Fifty-seven individual crows marked as nestlings were later found breeding. Crows appeared to settle in areas similar to where they were raised. Of 49 crows raised in suburban territories, only two (one male and one female) bred on rural territories, and none of the eight rural-raised crows bred on suburban territories (Fisher exact test P < 0.001). Dispersal distance from natal site to first breeding ranged from 0 to 60 km and did not differ between the two habitats (suburban 3.2 km ± 8.80, n = 49; rural 3.3 ± 3.44, n = 8; $t_{25.7} = 0.06$, P > 0.5). Three suburban-raised females traveled to other cities to breed, and one rural female bred on a rural territory on the opposite side of Ithaca from where it was raised.

Table 17.3. Size of American Crow nestlings at day 28 in suburban Ithaca and the surrounding rural Tompkins County, New York (years 1989-1999).

	SUBURBAN, $n = 143$	RURAL, <i>n</i> = 38		
	Mean \pm SD	Mean \pm SD	t (179)	Р
Bill (nares-tip) (mm)	22.9 ± 1.57	24.0 ± 1.46	2.743	0.007
Tarsus (mm)	58.8 ± 3.24	60.6 ± 2.18	3.157	0.002
Tail (mm)	65.6 ± 14.98	71.6 ± 15.31	2.186	0.30
Weight (g)	367 ± 54.1	411 ± 39.5	4.647	< 0.001

Table 17.4. Survival and resighting (recapture) probabilities for American Crows in suburban Ithaca and the surrounding rural Tompkins County, New York.

	Age	Survival rate	Resighting rate		
	interval	± SE	95% CI	± SE	95% CI
Suburban					
	0-1	0.52 ± 0.02	0.48 - 0.56	0.90 ± 0.02	0.85 - 0.94
	1-2	0.81 ± 0.03	0.74 - 0.86	0.90 ± 0.03	0.82 - 0.94
	Adult	0.76 ± 0.02	0.71 - 0.80	0.81 ± 0.03	0.75 - 0.86
Rural					
	0-1	0.35 ± 0.05	0.26 - 0.44	0.80 ± 0.08	0.60 - 0.91
	1-2	0.73 ± 0.14	0.41 - 0.92	0.48 ± 0.11	0.28 - 0.69
	Adult	0.72 ± 0.07	0.56 - 0.84	0.49 ± 0.09	0.32 - 0.67

3.4 Social Behavior

The occurrence of auxiliaries did not differ between suburban and rural nests. Auxiliaries were present at 238 of 299 (79.6%) suburban nests and at 37 of 62 (77.4%) rural nests ($G_1 = 0.144$, P < 0.50). However, the mean number of crows in family groups was larger in suburban families (suburban 3.7 ± 1.56, n = 286; rural 3.2 ± 0.99, n = 50; $t_{334} = 2.001$; P < 0.05). Few rural crow families exceeded 5 members (Fig. 17.2).

Both suburban and rural crows left their territories to enter winter roosts. Suburban and rural crows were found together in roosts and could be present in roosts in either habitat. Both suburban and rural crows also were observed in the same foraging flocks. Tagged crows were observed in foraging flocks and at their territory during the same day.

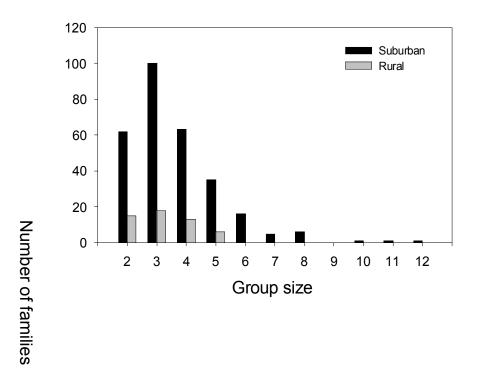


Figure 17.2. Distribution of American Crow family group sizes in suburban Ithaca (n = 286) and the surrounding rural Tompkins County, New York (n = 50), 1990-1998. Note that all groups larger than 5 were suburban groups.

4. **DISCUSSION**

American Crows exploit urban and suburban habitats and crow populations have been expanding slightly but significantly across the continent (Robbins et al. 1986, Marzluff et al. 1994, Sauer et al. 1999, Marzluff et al. 2001). However, in many areas, recent changes reflect a shift in the distribution of resident crows rather than changes in population size. As crows move into urban areas, both to nest and to roost in the winter, humans perceive an increase in population size. However, in New York, only a slight increase in overall crow populations has occurred (1.5%/year; BBS data, Sauer et al. 1999), but more crows appear to be using urban and suburban habitats. Recently, between 25,000 and 75,000 crows roosted in downtown Auburn, Cayuga County, New York (personal observation). Emlen (1938) reported a roost of approximately 25,000 crows in a rural area three miles south of Auburn during the winter of 1932-33. The town of Auburn has not increased substantially during these years, suggesting that crows here have moved from rural to suburban roosts. Long-time residents of Ithaca have reported that crows were not present in the city prior to the 1950's, and that their presence during the breeding season has occurred only recently.

Why have American Crows moved into urban and suburban areas to breed and roost? Houston (1977) and Knight et al. (1987) suggested that urban crows were taking advantage of the prohibition of shooting in urban areas. In addition, the 1972 extension of the Federal Migratory Bird Treaty Act of 1918 included crows for the first time, regulating and presumably decreasing hunting pressure on crows. Reduced persecution may have decreased human avoidance by crows, which then would enable them to exploit the trees, food, and relative warmth of cities

Suburban crows nested in taller trees and more frequently in conifers than did rural crows. Conifers are more abundant in suburban areas, but suburban crows selected conifers preferentially relative to their availability in Ithaca (unpubl. data). Whether rural and suburban crows have real differences in nest site selection awaits further study. Tall trees may be one of the attractions for crows to nest in urban and suburban areas, especially where available nest sites outside of towns are scarce, such as the intensively farmed Midwest and the arid West.

With few exceptions, suburban-raised crows bred in suburban areas, and rural crows bred in rural areas. All crows had opportunities to visit both habitats, at least during the fall and winter when crows made extensive movements off their territories to forage and roost. The settlement pattern of crows likely was affected to some degree by strategies used to acquire territories. Many crows settled close to their natal territories. Males in particular frequently inherited their natal territories or budded a breeding territory from their natal territory (unpubl. data). However, some crows traveled long distances to find breeding opportunities, suggesting that crows have the opportunity to sample a large number of possible breeding sites.

At least in Ithaca, suburban areas appear to be productive breeding areas for American Crows, not ecological traps. Suburban crows had higher nest success and first-year survival than did rural crows. Higher survival of suburban nests and juveniles may be a result of fewer predators in these habitats. The primary predators of crows are Great Horned Owls (Caffrey 1999, pers. obs), and perhaps several large hawks (Accipiter gentilis, A. cooperii, Buteo jamaicensis, B. lineatus) (Bent 1946). Important nest predators are the same raptor species (Chamberlain-Auger et al. 1990, Caffrey 1999, this study), as well as raccoons (Kilham 1989, this study). Populations of these predators might be lower in cities than in rural areas. Nesting density of Red-tailed Hawks in urban/suburban Syracuse, New York, and perhaps Great Horned Owls as well, was approximately one third that of rural areas (Minor et al. 1993). Although no data exist for local predator populations, all of the predators mentioned above were present in the suburban study area, and raccoons, Great Horned Owls, Red-tailed Hawks and Cooper's Hawks all are becoming common urban residents throughout North America (Minor et al. 1993, Rosenfield et al. 1996, Boal and Mannan 1998, Riley et al. 1998). Cooper's Hawk densities in urban areas may reach the maximum known for the species (Rosenfield et al. 1996, Boal and Mannan 1998), and urban raccoon populations can reach very high levels (Riley et al. 1998). The survival data in this study suggest that egg predators (e.g., raccoon) might be present in equal densities in both habitats, but that predators of nestlings and/or fledglings (e.g. Great Horned Owl) may be present in lower densities in town.

Studies in Switzerland suggested that cities may be ecological traps for Carrion Crows (Richner 1989, 1990, 1992). Richner (1989) showed that Carrion Crows breeding in cities had slightly higher overall nest success than those breeding in agricultural areas, but that they produced fewer young per successful nest, and those fledglings were of inferior quality. The offspring produced were significantly smaller than rural young and size was related to eventual breeding success. Offspring with small tarsi rarely became breeders and more urban-raised crows than rural-raised crows (79% vs. 29%) had tarsi below a threshold that predicted future breeding. Richner (1990) also found auxiliaries at urban nests, something previously unknown for the species. Crows that could not successfully breed on their own stayed and helped their parents (Richner 1990). When the urban crows were provided with supplemental food, their nest success and the size of their young increased (Richner 1992).

I observed a similar pattern of higher nest success, but fewer and smaller young in successful suburban nests. However, size at fledgling did not appear to affect the probability of attaining breeding status in American Crows. Because breeding is delayed in American Crows for up to six years (unpubl. data), relatively few data were available. Of 624 suburban crows banded, 49 (8%) are known to have become breeders, compared to only 8 of 171 (5%) rural crows ($G_1 = 2.20, P > 0.10$). However, suburban families had more auxiliaries than rural families (Fig. 17.2), a pattern which Richner (1990) suggested meant that urban Carrion Crows were less competitive and more likely to remain as auxiliaries. The apparent difference in group size could be the result of sampling bias. Rural crows tend to be less aggressive to people visiting their nests (Knight et al. 1987) and consequently provide fewer opportunities to accurately assess their group sizes.

The consistent pattern of fewer and smaller young from urban nests observed in two crow species (Richner 1992, this study), suggests that food may be limiting in urban populations. Although urban areas provide anthropogenic sources of food for crows, availability of natural food sources may be lower or the overall quality of food may be lower than in rural areas (Pierotti and Annett 2001).

During a severe drought in 1995, (unpubl. data, Northeast Regional Climate Center, Cornell University), I noticed several indications of hardship amongst the crows. Drought may affect crows by reducing their primary food source during nesting (earthworms and other terrestrial invertebrates; personal observation). During this year, nestlings appeared limp and flaccid instead of plump and turgid. During 1995, crows abandoned more nests in response to my visits than in any other year. During six previous years, I observed only one suspected abandonment as a result of my activities; in 1995 six abandonments occurred. One family abandoned a two-week-old nestling after I visited the nest.

Because suburban birds had access to food unlikely to have been affected by the drought, I predicted the impact of the drought would be smaller in the suburban area than in the rural area. In fact, I observed the opposite pattern. Crows in both habitats produced fewer fledglings in 1995 than in other years, although the difference was not significant (Table 17.5). Suburban crows produced fewer fledglings per nest and successful nest than rural crows, but again the differences were not significant. However, the relative differences between suburban and rural were greater in 1995 than in previous or subsequent years, suggesting the impact of the drought was greater on the suburban birds. As in previous years, suburban young were smaller, but the differences in 1995 were more pronounced (Table 17.6), and even tail differed significantly ($t_{38} = 2.470$, P < 0.02). The drought did not appear to affect the size of rural-raised young, but suburban young were smaller in 1995 than in other years. Whether the drought reduced the availability of natural foods for suburban crows or forced them to switch to anthropogenic sources of food of lower quality is unknown, but it suggests that food resources for suburban crows may be less predictable between years.

Why do suburban crows have smaller territories than rural crows if food is more limited? Most foraging to feed nestlings and fledglings is conducted on the territory, thus it seems logical that a larger territory would provide more food. It is possible that crowding may force smaller territory size in urban areas. Alternatively, the cues used by crows to determine the appropriate territory size may be inadequate or inappropriate in urban or suburban environments.

Table 17.5. Fledgling production by American Crows in 1995 in suburban Ithaca and the surrounding Tompkins County, New York.

	SUBURBAN	RURAL		
	Mean \pm SD (<i>n</i>)	Mean \pm SD (<i>n</i>)	<i>t</i> (df)	Р
Fledglings per				
Nest	1.59 ± 2.89 (32)	1.79 ± 3.86 (18)	0.242 (48)	0.810
Fledglings per				
Successful nest	2.68 ± 1.89 (19)	3.44 ± 1.53 (9)	1.408 (26)	0.17

Table 17.6. Size of American Crow nestlings at day 26 in suburban Ithaca and surrounding rural Tompkins County, New York, during a drought year (1995) and other years.

Measurement	1989-1994, 1996-1999	1995 only		
(mm)	Mean \pm SD (<i>n</i>)	Mean \pm SD (n)	<i>t</i> (df)	Р
Bill (nares-tip)				
Suburban	22.7 ± 1.46 (83)	20.8 ± 1.72 (11)	3.929 (92)	< 0.001
Rural	23.9 ± 1.60 (29)	22.8 ± 0.74 (11)	2.156 (38)	0.037
Tarsus				
Suburban	59.3 ± 3.71 (83)	56.0 ± 4.18 (11)	2.735 (92)	0.007
Rural	61.2 ± 1.82 (29)	62.0 ± 2.50 (11)	1.198 (38)	0.238
Tail				
Suburban	55.7 ± 11.81 (80)	48.4 ± 14.82 (11)	1.865 (89)	0.065
Rural	60.1 ± 12.79 (29)	55.5 ± 11.51 (11)	1.033 (38)	0.308
Weight (g)				
Suburban	378 ± 53.7 (82)	328 ± 57.0 (11)	2.884 (91)	0.005
Rural	398 ± 47.4 (29)	421 ± 25.3 (11)	1.488 (38)	0.145

In Ithaca and elsewhere (Stouffer and Caccamise 1991, Caccamise et al. 1997), crows defended territories, but left those areas for foraging and roosting, especially in winter. Kilham (1985) noted year-round territoriality in crows in New Hampshire, and Chamberlain-Auger et al. (1990) reported the same in Massachusetts. In Ithaca, territories appeared to be important in winter; the breeding pair and varying numbers of offspring were present every day and actively defended the territory by calls, displays, and fights. During the breeding season, crows foraged exclusively within their territory. Attendance at foraging flocks dropped off sharply when breeding began (unpubl. data).

Territory size and nesting densities found in this study are within the range reported in other studies, although these estimates vary widely. In Saskatchewan, Ignatiuk and Clark (1991) found a significant difference in the density of nesting crows between two different study sites; one in relatively open parkland, the other more highly developed for agriculture (0.59 - 0.80 vs. 0.36 - 0.40 nests/km², respectively). They suggested that these differences might be due to differences in production rates of young, nest site availability, or food between habitats. Sullivan and Dinsmore (1992) calculated average breeding season home ranges of crows in Manitoba of 2.6 km² (0.38 pairs/km²). Chamberlain-Auger et al. (1990) reported a mean territory size of 42 ha (2.4 pairs/km²) for crows in Massachusetts. They indicated that territory size differed significantly between an urban study area and a barrier beach, but presented no data nor indicated which was larger. Kilham (1989) reported an average territory size of 90 ha for two rural territories of resident Florida crows, although one territory eventually split into two of approximately 40 ha each. Caffrey (1992) found that crows on an urban golf course in California did not defend territories, but did maintain "core areas" on which they nested and spent most of their time. She reported a mean nesting density of 0.8 pairs/ha = 80 nests/km², far higher than the density found in suburban areas in this study. Emlen (1942), reported a "colony" of crows breeding in a rural walnut orchard in California, with approximately 60 pairs in the 108 acres (= 140pairs/km²). Still, it is not clear why territories tend to be small in urban areas. Food as well as social organization may play a role in the variability in home range size and density observed among studies and between rural and urban habitats.

Crows frequently depredate the nests of other birds (Sodersrom et al. 1998, Buler and Hamilton 2000). The movement of crows into urban and suburban areas potentially could affect songbird populations there. In Ithaca, two species frequently cited by the public as being negatively affected by crows are American Robin (*Turdus migratorius*) and Northern Cardinal (*Cardinalis cardinalis*), both common nesters in suburban Ithaca.

However, cardinals have not changed in abundance survey-wide from 1966 to 1996, and robins have increased at nearly the same rate as crows (BBS data; Sauer et al. 1999). In New York, cardinals have increased and robins have not changed in abundance (BBS data; Sauer et al. 1999), suggesting urban crow populations are not adversely affecting these two species. It is possible that urban crow populations could impact bird species with habitats that make them vulnerable to crow predation. Common Nighthawks (*Chordeiles minor*) have declined significantly over North America, and especially in New York (BBS data; Sauer et al. 1999). Urban nighthawks nest on gravel roofs of buildings. Although I have no evidence to suspect crows contributing to the decline of nighthawks, it is conceivable that urban crows could discover and then specialise on such nests. Any species with such a specialised nest site, such as a gravel or beach nest that is vulnerable once a search image has been formed, might well be adversely affected by increasing crow populations.

In conclusion, American Crows are now nesting in cities and towns in large numbers. Suburban crows have higher nest success, but produce fewer and smaller young. However, their subsequent survival is higher than that of rural crows and they appear to be equally able to recruit into the breeding population. Therefore I conclude that cities are breeding opportunities and not ecological traps for American Crows. This conclusion is supported by evidence from other regions in the U.S. (Marzluff et al. 2001). A small, steady and significant increase in American Crow populations, especially in the eastern USA (BBS data; Robbins et al. 1986, Sauer et al. 1999) is perhaps the result of exploitation of the "new" urban habitat.

ACKNOWLEDGMENTS

Financial support for part of the crow research was provided by U.S. Dept. Agriculture, Hatch Project Grant NYC-183429. I thank a large number of diligent field assistants, paid and volunteer, who have helped me find and monitor crow nests over the last decade, and, most importantly, held securely on to the other end of my rope. Thanks to Frank Joyce, David Winkler, and Mark Stanback, for advice early in the study on how to climb trees, and especially to Rob Roy Ramey II for one vital technique and the imperative to do it all safely. Thanks to Carolee Caffrey for boundless crow enthusiasm and for teaching me her tagging technique, and to Kimberly Kline for tireless construction of the tags. The manuscript was significantly improved by the comments of Jon Greenlaw, Reed Bowman, and an anonymous reviewer. Special thanks must be extended to the extensive bird-

aware community of people living in and around Ithaca, who provided me with numerous crow sighting reports.

REFERENCES

- Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. U. S. Nat. Mus. Bull. 191:1-495.
- Boal, C. W., and R. W. Mannan. 1998. Nest-site selection by Cooper's Hawks in an urban environment. J. Wildl. Manage. 62: 864-871.
- Buler, J. J., and R. B. Hamilton. 2000. Predation of natural and artificial nests in a southern pine forest. Auk 117:738-747.
- Caccamise, D. F., L. M. Reed, J. Romanowski, and P. C. Stouffer. 1997. Roosting behavior and group territoriality in American Crows. Auk 114:628-637.
- Caffrey, C. 1992. Female-biased delayed dispersal and helping in American Crows. Auk 109:609-619.
- Caffrey, C. 1999. Feeding rates and individual contributions to feeding at nests in cooperatively breeding Western American Crows. Auk 116: 836-841.
- Chamberlain-Auger, J. A., P. J. Auger, and E. G. Strauss. 1990. Breeding biology of American Crows. Wilson Bull. 102:615-622.
- Cooch, E., and G. White. 2000. Program Mark: a gentle introduction. http://canuck.dnr.cornell.edu/misc/cmr/mark/docs/.
- Emlen, J. T., Jr. 1938. Midwinter distribution of the American Crow in New York state. Ecology 19:264-275.
- Emlen, J. T., Jr. 1942. Notes on a nesting colony of Western Crows. Bird-Banding 13:143-154.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in fieldforest ecotones. Ecology 59: 871-883.
- Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nest success: a model, estimators, and simulation results. Wilson Bull. 93:42-53.
- Houston, C. S. 1977. Changing patterns of Corvidae on the prairies. Blue Jay 35:149-155.
- Ignatiuk, J. B., and R. G. Clark. 1991. Breeding biology of American Crows in a Saskatchewan parkland habitat . Can. J. Zool. 69:168-175.
- Jollie, M. 1976. Species interrelationships of three corvids. The Biologist 58: 89-111.
- Kilham, L. 1984. Cooperative breeding of American Crows. J. Field Ornithol. 55:349-356.
- Kilham, L. 1985. Territorial behavior of American Crows. Wilson Bull. 97:389-390.
- Kilham, L. 1989. The American Crow and the Common Raven. Texas A & M University Press, College Station, Texas.
- Knight, R. L., D. J. Grout, and S. A. Temple. 1987. Nest-defence behavior of the American Crow in urban and rural areas. Condor 89: 175-177.
- Marzluff, J. M., R. B. Boone, and G. W. Cox. 1994. Historical changes in populations and perceptions of native pest bird species in the West. Stud. Avian Biol. 15:202-220.
- Marzluff, J. M., K. J. McGowan, R. Donnelly, and R. L. Knight. 2001. Causes and consequences of expanding American Crow populations, p. 333-365. *In J. M. Marzluff*, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456-466.

- McGowan, K. J. 1995. A test of whether economy or nutrition determines fecal sac ingestion in nesting corvids. Condor 97:50-56.
- McGowan, K. J. 1996. Family lives of the uncommon American Crow. Cornell Plantations 51:1-4.
- Minor, W. F., M. Minor, and M. F. Ingraldi. 1993. Nesting of Red-tailed Hawks and Great Horned Owls in a central New York urban/suburban area. J. Field Ornithol. 64:433-439.
- Pierotti, R., and C. Annett. 2001. The ecology of Western Gulls in habitats varying in degree of urban influence, p. 309-331. *In J. M. Marzluff, R. Bowman, and R. Donnelly* [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.
- Richner, H. 1989. Habitat-specific growth and fitness in Carrion Crows (*Corvus corone corone*). J. Anim. Ecol. 58:427-440.
- Richner, H. 1990. Helpers-at-the-nest in Carrion Crows Corvus corone corone. Ibis 132:105-108.
- Richner, H. 1992. The effect of extra food on fitness in breeding carrion crows. Ecology. 73:330-335.
- Riley, S. P. D., J. Hadidian, and D. A. Manski. 1998. Population density, survival, and rabies in raccoons in an urban national park. Can. J. Zool. 76:1153-1164.
- Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965-1978. U. S. D. I., F. W. S., Res. Publ. 157.
- Rosenfield, R. N., J. Bielefeldt, J. L. Affeldt, and D. J. Beckmann. 1996. Urban nesting biology of Cooper's Hawks in Wisconsin, p. 41-44. *In* D. Bird, D. Varland, J. Negro [EDS.], Raptors in human landscapes. Academic Press, New York.
- Sauer, J. R., J. E. Hines, I. Thomas, J. Fallon, and G. Gough. 1999. The North American Breeding Bird Survey, Results and Analysis 1966 - 1998. Version 98.1, USGS Patuxent Wildl. Res. Center, Laurel, MD.
- Smith, B. E., P. L. Marks, and S. Gardescu. 1993. Two hundred years of forest cover in Tompkins County, New York. Bull. Torrey Botanical Club 120:229-247.
- Sodersrom, B., T. Part, and J. Ryden. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: An experiment and a review. Oecologia 117:108-118.
- Stouffer, P. C., and D. F. Caccamise. 1991. Roosting and diurnal movements of radio-tagged American Crows. Wilson Bull. 103:387-400.
- Sullivan, B. D., and J. J. Dinsmore. 1992. Home range and foraging habitat of American crows *Corvus brachyrhynchos* in a waterfowl breeding area in Manitoba. Can. Field-Nat. 106:181-184.
- White, G.C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Suppl. 120-138.