Marzluff, J. M., et al. 2001. Pp 332-363 *in* Avian ecology and conservation in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donelly, eds.).   Kluwer Academic Press, Norwell, MA.

Chapter 16

Causes and consequences of expanding American Crow populations

John M. Marzluff[1], Kevin J. McGowan[2], Roarke Donnelly[1], and Richard L. Knight[3]

[1]*College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195 USA, email: corvid@u.washington.edu*

[2]*Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14853 USA*

[3]*Department of Fishery and Wildlife Biology, Colorado State University, Fort* Collins, CO 80523 *USA*

Key words: American crow, diet, dispersal, metapopulation, nest predation, population growth, source-sponge, population dynamics, urban footprint, urban sprawl, urbanization

Abstract: Corvid populations are increasing worldwide in response to urbanization. We investigated the response of American Crows (*Corvus brachyrhynchos*) to urbanization by (1) comparing rates of winter population change between urban and nonurban locations (using standard Christmas Bird Counts); (2) quantifying population size along a gradient of urbanization in western Washington; and (3) pooling studies from eastern (New York), midwestern (Wisconsin), and western North America (Washington and California) relating survivorship, reproduction, and space use to urbanization. American Crow populations tend to be densest and increasing most rapidly in urban areas of North America. This appears to be facilitated by small space needs of crows in urban relative to suburban, rural, and exurban areas. Crow survivorship is high across the urban gradient, but reproduction and hence population growth, peaks in suburban and rural settings. Local demographic considerations appear unable to account for changing winter crow populations. Rather, we hypothesize that urban crow populations may be increasing primarily as surplus crows from suburban and rural areas disperse into the city where anthropogenic food sources are easily located, rich, and concentrated. This hypothesis likely is affected by local crow sociality. In the western United States, where pre-breeders often form flocks able to exploit urban riches, our dispersal hypothesis may be accurate. But, in midwestern and eastern areas, where crows migrate south for winter or remain on territories to help rather than float as pre-breeders, dispersal may not be adequate to fuel urban population growth. Refuse, invertebrates, and small vertebrates appeared to be more common food items than the nest contents of other birds. This, and the typically diverse suite of nest predators in any area, may explain why the rate of predation on artificial nests we placed throughout the urban gradient was not highly correlated with the abundance of crows. We encourage researchers to study how urbanization affects important mechanisms (like nest predators and predation) so environmental policy will benefit from a detailed, scientific understanding of how avian communities are structured.

1. INTRODUCTION

As a rule, bird community diversity in urban landscapes is markedly lower than in comparable rural/exurban communities (Marzluff 2001). Diversity is reduced because (1) some species' habitat requirements are no longer met and (2) other species able to exploit humans ('human commensals') increase in abundance and dominate resources such as food and nesting space, or reduce the productivity of other species by preying on their nest contents. Many magpies, jays, and crows are human commensals that have increased in urban areas worldwide (Konstantinov et al. 1982, Eden 1985, Fraissinet 1989, Konstantinov 1996, Hogrefe et al. 1998; Jerzak 2001). Their abilities to exploit anthropogenic food resources and their habit of preying on other species' eggs and young suggest that their success may be partly responsible for many other species' failure to thrive in urban areas.

American Crows (*Corvus brachyrhynchos*) are human commensals throughout the coterminous United States. Standardized surveys and historical records suggest that American Crows increased in response to European colonization of North America by spreading from east to west as the American frontier was opened and developed (Marzluff et al. 1994). Crows were uncommon throughout the Great Basin and Pacific Coast through the early 1900s, except along riparian areas (Monson 1946, Richards 1971). Populations increased substantially in Oregon, Washington, and the central valleys and northern portions of California from the late 1800s to mid 1900s (Brooks 1925, Robertson 1931, Emlen 1940). As agriculture and urbanization continued to spread, so did crows (Pitelka 1942, Richards 1971). Accounts from localities such as Las Vegas Hot Springs, New Mexico (where crows were rare in 1882, but one of the commonest species in 1959; Rickard 1959) are typical of the crow population explosion. The explosion has continued throughout the latter half of the 20th century, especially in areas of urban growth and sprawl (Marzluff et al. 1994, Hogrefe et al. 1998).

Although many researchers have documented the increase in crow population size and speculated on its effects, there are no published data on the attributes of crow populations that may explain the increase. Therefore, we pooled data from eastern, mid-western, and western crow populations to determine: (1) the relationship between the degree of urbanization and crow abundance, area use, and foraging behavior; (2) if crow demography varied with degree of urbanization; and (3) if a positive relationship existed between the rate of predation on other songbird nests and abundance of crows. We use this information to develop a general model of crow population dynamics that is amenable to empirical testing.

2. METHODS

2.1 Study Areas and Research Approaches

We studied crows in six locations (Table 16.1) along a gradient (defined by Marzluff et al. 2001) from urban (Seattle, WA; Los Angeles, CA; portions of Madison, WI) through suburban (Madison; Ithaca, NY; outlying areas near Seattle), exurban (Cascade and Olympic Mountains, WA), and rural (Tompkins County, NY) areas to wildland (Olympic Peninsula, WA). We monitored nests and individually marked birds in neighborhoods, campgrounds, golf courses, parks, cemeteries, campuses, and wildland reserves (Caffrey 1992, 1999, 2000; McGowan 2001).

2.1.1 Western Washington

The western Washington study areas span the entire gradient of urbanization from downtown Seattle to the heart of Olympic National Park (47°,40' N; 122°,20' W; Fig. 16.1). Our sites were predominantly coniferous forests (Douglas-fir [*Pseudotsuga menziesii*], western hemlock *[Tsuga heterophylla*], and western redcedar [*Thuja plicata*]) with 5 – 50% deciduous overstory (big leaf maple [*Acer macrophyllum*], and red alder [*Alnus rubra*]). Overstory trees ranged from 50 to >200 years old. Canopy cover was 50 – 90%. Understories were well developed and ranged from native shrubs (mainly *Gaultheria shallon, Vaccinium parvifolium, Sambucus racemosa, Oemleria cerasiformis, Rubus spectabilis, Acer circinatum, Mahonia nervosa, Rubus parviflorus, and Symphoricarpos albus*) in exurban and wildland sites, to complex mixes of native and exotic shrubs in urban and suburban sites. Timber harvest and recreation were the dominant land-uses in the wildland and exurban sites. There, landscapes ranged from contiguous mature forest to highly fragmented, managed timberlands (Fig. 16.1). Suburban sites usually contained >50% greenspace in the form of scattered parks and riparian corridors. Urban sites had <20% greenspace, predominantly in the form of parks that ranged in size from 1 – 600 ha.

The focus of our study in western Washington was to understand the population structure and dynamics of crows in relation to urbanization and to relate crow populations to the avian community structure and the productivity of other sympatric songbirds. To accomplish this we captured and tagged adult crows, located and monitored nests, banded and observed

Table 16.1. Attributes of study areas and aspects of crow biology recorded.

Location	Years studied	1990 human population	Points studied on gradient	Aspects of biology studied
Madison WI	1982 – 1985	191, 000	Urban neighborhoods, Suburban neighborhoods, woodlots, golf courses, parks, university campus, cemetery	Fecundity
Ithaca NY	1989 – 1999	29, 000	Suburban neighborhoods, woodlots, golf courses, parks, university campus, cemetery	Fecundity, survivorship, space use, social behavior
Tompkins County NY	1989 – 1999	67,000	rural deciduous woodlots, agriculture	Fecundity, survivorship, space use, social behavior
Los Angeles CA	1985 – 1990	11 million	Urban golf course	Fecundity, survivorship, space use, social behavior
Seattle and Cascade Mountains, WA	1998 - 2000	3 million	Urban and suburban neighborhoods, parks and university campus, exurban woodlands	Fecundity, survivorship, space use, foraging, nest predation
Olympic Peninsula, WA	1995 – 2000	0 – 2,500	Suburban and exurban neighborhoods, wildland campgrounds and reserves	Fecundity, survivorship, space use, foraging, nest predation

young, and radio-tagged a sample of birds each year to determine survivorship, foraging behavior, and patterns of space use (Table 16.1). We typically banded 100 adults, monitored 30 nests, banded 90 nestlings, and radio-tagged 30 crows each year. In addition, we monitored the reproductive success and abundance of other songbirds in our crow study areas.

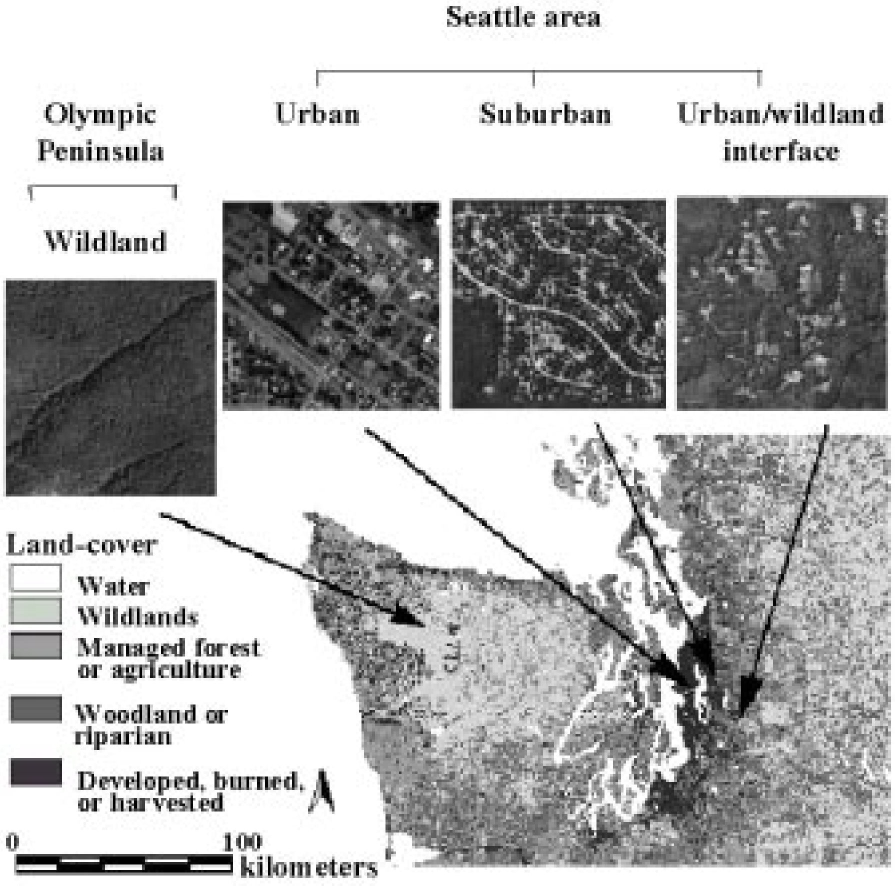

Figure 16.1. Land-cover on western Washington study areas with inset orthophotos. The Olympic Peninsula forms the left side of the figure and the Cascade Mountains form the right side. Seattle is the highly developed area in the center of the classified image.

2.1.2 Los Angeles

Crows were studied on two contiguous golf courses that were part of the Sepulveda Dam Recreation Area (34^{o},30' N; 118^{o},30' W; elevation = 2100 m; Fig. 16.2a). In this area, tree cover was approximately 15-20% and understory was lacking. The park itself had little development and a mostly continuous ground cover of exotic, mowed grasses. It included ball fields, picnic areas and the golf courses. It was surrounded by dense housing (1405 dwellings per $mile^2$), a large human population (3300 per $mile^2$), and associated services of Encino, California.

The primary goal of the Los Angeles study was to understand social organization and the correlates of breeding success in this cooperatively breeding population (Caffrey 1992, 1999, 2000).

2.1.3 Madison

Crows were studied in a variety of settings (neighborhoods of various age, parks, woodlots, cemeteries, and university campuses) in the town of Madison, Wisconsin. Madison (43^{o},05' N; 89^{o},22' W; elevation = 270 m; Fig. 16.2b) is built on an isthmus between two lakes, and includes 21 golf courses and the most restaurants per capita of any U.S. city. The population of Madison at the time of this study (1980) was 170,616 and housing and population densities around all study sites varied from urban to suburban. The study sites varied from largely concrete and exotic plant species (business district) to largely native vegetation and native species (woodlots). The sites were ranked in order of increasing domination by humans as woodlots, parks, cemeteries, university campus, neighborhoods, and business district. Impervious surfaces covered approximately 80% of the business district, but less than 1% of the woodlots. Understory vegetation was non-existent in the business district, but covered about 50% of the woodlots.

The goals of the Madison study were to understand crow demography and population dynamics in a variety of suburban settings.

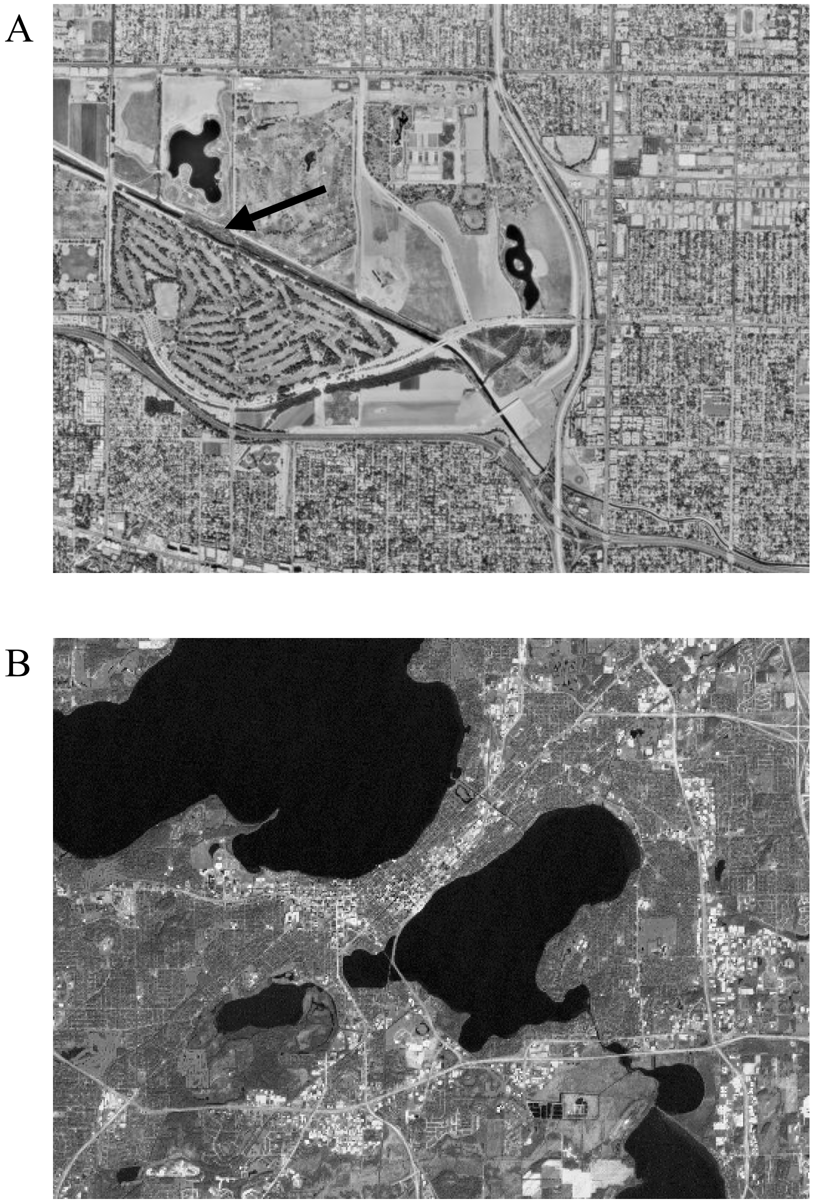

Figure 16.2. Study sites (A) in Encino, California near Los Angeles and (B) in Madison, Wisconsin. The focal golf course in Los Angeles is indicated by an arrow. The Los Angeles image is an orthophoto taken in 1998 covering ~16,000 ha. The Madison image is a Landsat image taken in 1999 covering ~7,000 ha.

2.1.4 Ithaca and Tompkins County

Crows throughout Ithaca, New York and surrounding Tompkins Country have been studied extensively by McGowan. The study areas, methods, and goals of this research are detailed in McGowan (2001, Fig. 17.1).

2.2 Abundance

2.2.1 Christmas Bird Counts

To determine if the recent growth of crow populations across the U.S. was related to the degree of urbanization, we selected 70 Christmas Bird Count (CBC; Audubon Society 2000) locations that could be classified as urban (>20% of the circle was developed in 1970) or exurban/rural (<5% of the circle was developed in 1970 and the 1996 human population size was <10,000). We used only sites that had at least 20 years of count data from 1960 – 1996 (Appendix 16.1). No single state was represented by more than two urban or two exurban/rural sites. We did not use Breeding Bird Surveys because few are conducted in urban areas (Droege 1990).

We related the number of crows (standardized per party hour) to year using standard linear regression. All crow species and subspecies were lumped (Fish Crows were rare in our sample; <0.07% of the total). We used the slope of the regression as an index of crow population growth in each circle. Slopes were compared between urban and exurban/rural sites with a Mann-Whitney *U*-test.

2.2.2 Surveys in Western Washington

We conducted fixed area (50m radius) point counts in all study sites in western Washington to determine if crow abundance (1995-2000) differed along the gradient of urbanization. We surveyed crows during the breeding season (April - August) using from 1 – 20 points spaced 250 m apart in each of our forested stands. At each point we recorded all crows heard and seen within 50 m during a 10-min count. At exurban and wildland sites we used crow calls at 2 points per stand to increase the chance that rare birds were detected. We censused each stand 2 – 5 times per season and used the maximum count (standardized as crows per point) per season to characterize abundance in the stand. Details of our survey procedure are in Luginbuhl et al. (in press).

2.3 Monitoring Crows in the Wild

We captured and marked crows in all our study sites as nestlings and adults using mist nets, noose carpets, walk-in traps, net guns, and leghold traps. We weighed each individual and measured its culmen length and wing chord. All individuals were uniquely banded with colored leg bands (Washington, Wisconsin) or patagial tags (California, New York). Field methods for New York and California are detailed elsewhere (Caffrey 1992, 1999, 2000; McGowan 2001).

A sample of individuals in the Washington study areas was instrumented with backpack-mounted radio transmitters. Transmitter harnesses were made from Teflon© ribbon following Buehler et al. (1995). We attempted to observe each radio-tagged bird at least once per week to confirm their survivorship. Tagging may influence demography, but without radio-tagging, survival could not be estimated across our large, remote study area. Any biases are likely to be slight (Vekasy et al. 1996, Withey et al. in press) and should be equal across treatments so that *relative* comparisons of demography between areas are unaffected.

In Washington, radio-tagged birds were the subjects of 1-2 hr focal observations approximately once each week throughout the spring, summer, and fall to quantify their foraging behavior and patterns of space use. We recorded the type of food, how it was obtained *(grab, pick, probe, hawk, kleptoparastize, glean*, etc.), and where it was obtained (*tree species, height and DBH*; *habitat* = cover classes defined on habitat map and structural complexity used to define our stands; *substrate* = branch, ground, various manmade structures, etc.; *microsite* = moss, lawn, asphalt, etc; distance to forest edge). We quantified the rate and success of foraging, when possible, by counting the total prey capture attempts and the percentage that were successful (indicated most reliably by swallowing) per unit time.

Locations of radio-tagged crows were plotted on maps/photos of the Washington study sites (a global positioning system was used in remote areas) and used to calculate home range statistics with a computer program, Ranges V (Kenward and Hodder 1995). During each 1-2 hr focal observation period, we plotted the entire area used by a bird, then recorded 2 - 3 locations (extreme and mid points of area used) for subsequent definition of the home range. We occasionally recorded single locations of animals at their roosts and during our travels throughout the study area. We purposely recorded few locations per day on each animal to minimize dependence among relocations. We computed maximum use areas (100% convex polygons) and core areas within them (cluster techniques; Kenward 1987). We computed minimum convex polygon home ranges to facilitate comparison with other studies and to avoid assumptions about the statistical distribution of animal locations. We defined an animal as being 'adequately sampled' if >20 locations were obtained. Investigating the increase in range size with sampling effort (incremental analysis) suggests that an average of 60-75% of the entire range is defined by 20-25 locations; 95% confidence intervals around these means include 100% definition of the area used. Our definition of adequate sampling is supported by the lack of a strong positive correlation between the number of location estimates and the home range size of adequately sampled animals (the correlation was in fact *negative*; $r = -0.30$, $n = 37$, $P = 0.07$). In the Los Angeles and Ithaca study areas, core areas and defended territories were determined by spot mapping locations of color-marked individuals (e.g., McGowan 2001).

2.4 Calculation of λ

We pooled our demographic data across study areas to estimate age-specific fecundity and survivorship in urban, suburban, rural, and wildland settings. We assumed females in all areas first bred when four years old (modal age of reproduction in Ithaca; McGowan, unpublished data) and that productivity was constant until death. We calculated the annual production of fledglings separately for each area using data from (1) urban greenspaces in Wisconsin, Los Angeles, and Seattle, (2) suburban developments and parks in Wisconsin, Seattle, and Ithaca, (3) rural Tompkins County, New York, and (4) wildland forests on the Olympic Peninsula. We assumed all crows died by age 21 years. We assumed survivorship of 1-year old crows was equal across the urbanization gradient at 48% (McGowan 2001), while annual survivorship of 2- and 3-year-olds was 72% (all estimates based on results from Ithaca; McGowan, unpubl. Data and 2001). We calculated the annual survivorship of breeders separately for each area using data from (1) urban greenspaces in Los Angeles and Seattle, (2) suburban developments and parks in Seattle and Ithaca, (3) rural Tompkins County, New York, and (4) wildland forests on the Olympic Peninsula. Survivorship was calculated using color-marked birds in Los Angeles (Caffrey 1999), Ithaca, and Tompkins County (McGowan 2001) and radio-tagged birds in Washington. We used these data to create a transition matrix for each degree of urbanization and solved the matrix for λ by finding the largest positive eigenvalue using RAMAS (Akcakaya1999). Variation in λ resulting from demographic stochasticity also was estimated using RAMAS. To do this, we assumed the following standard deviations for demographic parameters for all populations (Fecundity: 1-year-old = 0.02, 2-year-old = 0.04, 3-year-old = 0.13, >3-year-old = 0.17; Survivorship: fledglings = 0.25, 1-year-old = 0.19, 2-year-old = 0.19, >2-year-old = 0.04).

2.5 Artificial Nest Experiments

We used a variety of artificial nests to quantify the risk of nest predation. In urban and suburban Seattle we placed handmade nests in (1) native ground cover (typically sword fern, *Polystichum munitum*) to simulate those of ground nesters such as Song Sparrows (*Melospiza melodia*), Spotted Towhees (*Pipilo maculatus*), and Wilson's Warblers (*Wilsonia pusilla*), and (2) in shrubs to simulate those of American Robins (*Turdus migratorius*) and Swainson's Thrushes (*Catharus guttatus*). Both types of nests were filled with two, small (12x18 mm), blue plastic, wax-coated eggs. The wax coating allowed us to infer the type of predator from the marks on the egg (identification was calibrated using cameras to record predators at an independent subset of nests). Details of these experiments can be found in Donnelly and Marzluff (in press). On the Olympic Peninsula, we simulated nest sites of Marbled Murrelets (*Brachyramphus marmota*) by placing an artificial egg or taxidermy-mounted chicken chick in a typical murrelet canopy nesting location. Details of these experiments can be found in Marzluff et al. (2000). Ground and shrub nests remained in place until preyed on or until 27 days had elapsed. Canopy nests remained in place until preyed on or for 30 days. We determined the rate of predation within a study plot by averaging the time until predation (all nests were checked every three days) for all nests within a given stratum.

3. RESULTS

3.1 Crow Abundance and Urbanization

In western Washington, the relative abundance of crows increased with increasing degree of urbanization. Crows were rarely found during surveys in wildlands far from campgrounds (Fig. 16.3). Exurban areas also had few crows in contrast to suburban and urban areas. Crow abundance in urban areas was approximately 30 times greater than in wildlands (Fig. 16.3).

Across the U.S., crow populations tended to increase in urban areas from 1960 – 1996, but they remained relatively constant in exurban and wild areas. The annual rate of increase in crow populations was marginally greater in urban areas (mean = 27.2%, SE = 13.5% , $n = 35$) than in exurban, rural, and wildland areas (mean = -5.1%, SE = 22.5%, $n = 35$). However, because locations varied tremendously in the rate at which crow populations changed (Appendix 16.1), this difference was only marginally significant ($U = 516$, $P_{(1\text{-tailed})} = 0.13$). Only one rural area had a substantial increase in the crow population (Rupert, ID; 372% annual increase). In contrast, five urban areas had substantial increases (Albuquerque, NM: 425%; Hartford, CN: 187%; Sacramento, CA: 122%; Seattle, WA: 57%; and Portland, OR: 51%).

3.2 Use of Space and Foraging Behavior

Breeding adult crows occupied areas during the spring and summer that varied from slightly over 1 ha to over 3500 ha. Across areas, this variation was positively correlated with the degree of urbanization (Fig. 16.4). In the extremely dense breeding population of Los Angeles, core area size was less than 2 ha, but where crows were rare (remote portions of the Olympic Peninsula) home range size averaged 2100 ha.

Certainly, part of this difference is due to our use of (1) a variety of measures of area use (defended territories in New York, core use areas in Los Angeles, and entire traveled areas in Washington) and (2) a variety of techniques (visual observations Los Angeles and New York, radio-telemetry in Washington). However, when we examine these patterns within two of

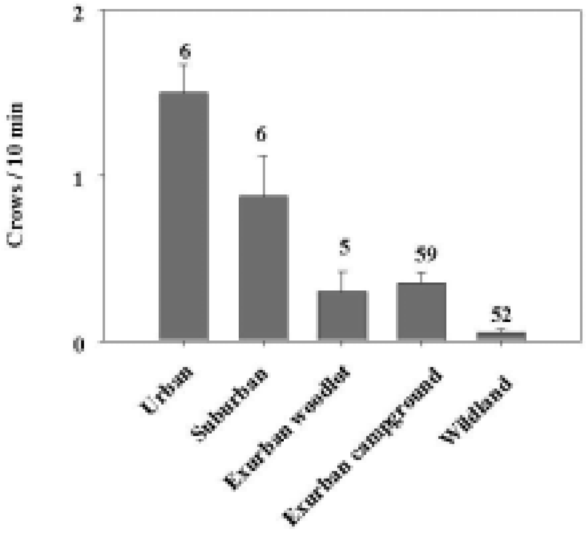

Figure 16.3. Variation in average (+SE) numbers of crows counted during the summer at various points along a gradient of urbanization in western Washington. Urban, suburban, and exurban woodlots are in the Seattle and Cascade Mountain study areas. Exurban campgrounds and wildland sites are on the Olympic Peninsula. Numbers above bars are sample sizes of independent study sites.

the study areas we still detect similar increases in area use as human settlement decreases. In upstate New York, breeding crows in the town of Ithaca used areas approximately four times smaller (mean = 8.7 ha, *n* = 18) than crows breeding in adjacent, rural Tompkins County (mean = 37.3 ha, *n* = 59; McGowan 2001; Fig. 16.4). In western Washington, crows breeding on the Olympic Peninsula had home ranges 7 times larger than those in nearby urban Seattle and suburban Snohomish (Fig. 16.4). Furthermore, on the Olympic Peninsula home range size was three times smaller for crows nesting in areas with human presence (rural and exurban developments and recreation areas; mean = 308 ha, *n* = 22, SE = 61.8) relative to crows nesting >5 km from such areas (mean = 2124 ha, *n* = 8, SE = 706; $F_{1,29} = 18.2$, $P < 0.001$). Variation in space use within areas of similar human settlement may be related to regional differences in social organization (crows in Los Angeles were colonial, but crows in our other urban study areas were territorial during the breeding season), breeding success (crows increased

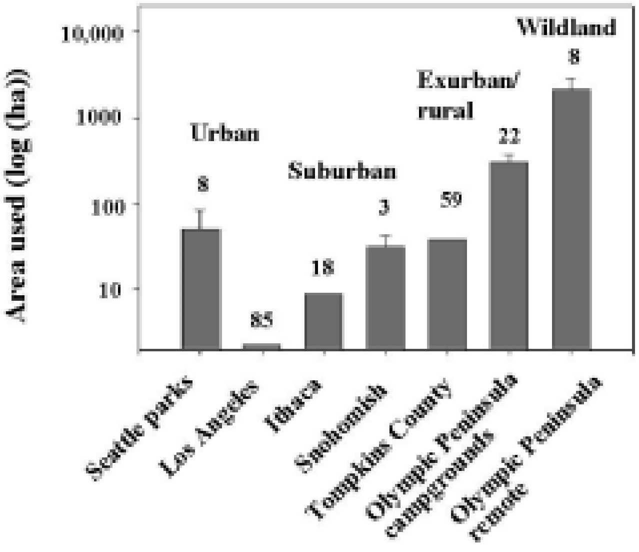

Figure 16.4. Average (+SE) space use by breeding crows in the United States. Crows in Seattle, Snohomish, and all sites on the Olympic Peninsula were monitored with telemetry using similar methodology. Likewise, crow in Ithaca and Tompkins County, New York were monitored as part of a single study with consistent methodology.

their range size in Seattle when their nests failed despite where they occurred on the urban gradient), and other aspects of locally important resources.

Our observations in western Washington suggest that differences in space use by crows along the urban gradient may be due to differences in diet. Crow diets varied from urban to wildland settings in Washington (Fig. 16.5). Human refuse (prepared meats, bread products, and vegetables) was the dominant food item eaten by crows in Seattle (65% of observed food consumption; Fig. 16.5A). Road-killed mammals, live rodents and reptiles, and invertebrates composed <25% of Seattle crow diets. In contrast, crows on the Olympic Peninsula consumed roughly equal proportions of invertebrates (38%) and human refuse (35%) regardless of their proximity to small settlements and recreation areas (Fig. 16.4B). Wildland crows often flew tens of kilometers to utilize anthropogenic food sources (Marzluff and Neatherlin, unpubl. data).

We followed radio-tagged crows in Washington to obtain unbiased estimates of their reliance on nest contents for food. We rarely saw crows prey on other species of songbirds' nests (*n* = 2 times) during the five years of intensive observation (>1500 hrs yr^{-1}) of 54 radio-tagged birds on the Olympic Peninsula. Nest predation was not observed during two years of observation (>800 hrs yr^{-1}) of 14 radio-tagged crows in Seattle. However, we were occasionally (*n* = 8 times) attracted to songbirds mobbing marauding crows. The consciousness of this mobbing may lead to inflated estimates of nest predation by casual observers of crows.

3.3 Demography and Population Dynamics

Pairs breeding in urban areas produced fewer fledglings each year than pairs breeding in suburban, rural, or wildland areas (Table 16.2). Urban breeders averaged only 60% of the number of fledglings per pair (mean = 1.1, SE = 0.17, *n* = 3 studies) that were produced by suburban (mean = 1.90, SE = 0.15, 3 studies) breeders. Rural (1.6, *n* = 1 study), and wildland breeders (1.5, *n* = 1 study) produced intermediate numbers of fledglings. Lower productivity by urban crows resulted primarily from an overall decrease in nest success, rather than a decrease in the number of fledglings per successful nest (Table 16.2). However, in Ithaca suburban crows had significantly higher overall nest success but fledged significantly fewer nestlings per successful nest than did rural crows (McGowan 2001). Suburban crows consistently averaged around 60% nest success.

Annual survivorship of breeding crows was high in all study areas. It appeared to be lowest in our wildland and Seattle urban study areas (Table 16.3). There, nearly 20% of crows died each year, but sample sizes are small. All observed mortality in our wildland study areas occurred on crows

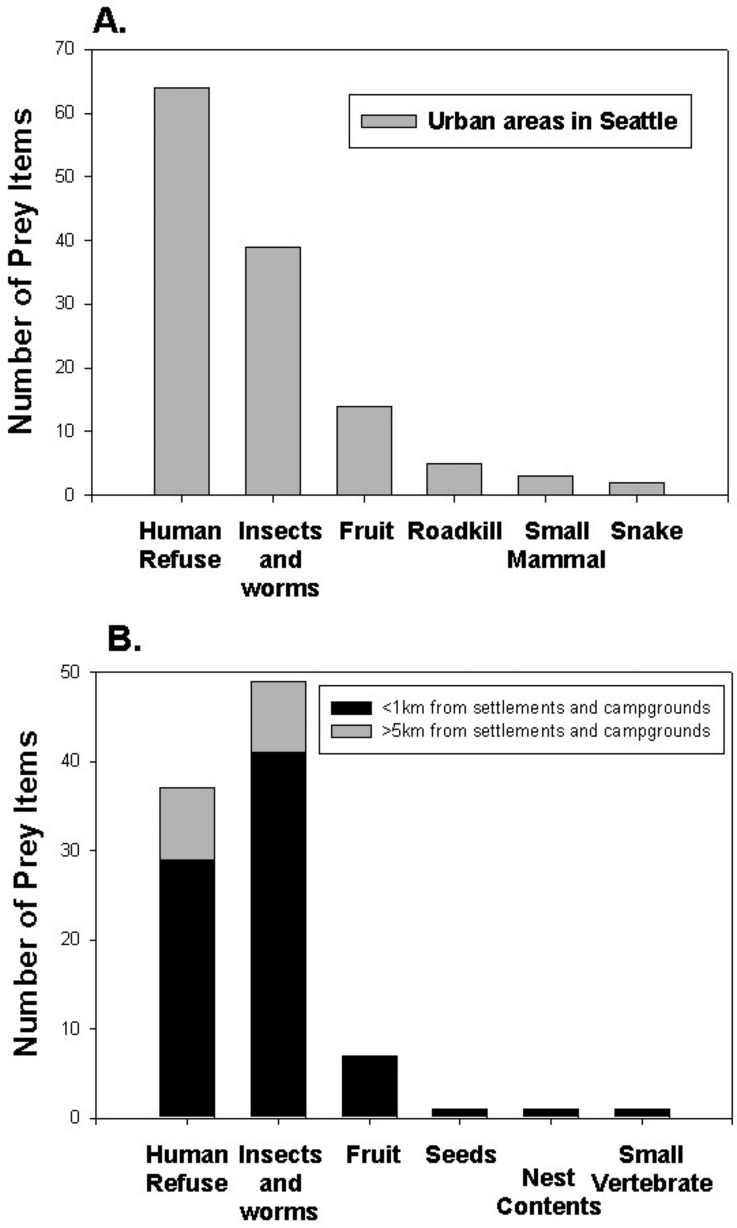

Figure 16.5. Diets of breeding crows during the spring and summer in western Washington. Numbers of each prey type that we observed crows eating are plotted separately for 12 crows in urban and suburban Seattle/Snohomish (A) and 37 exurban and wildland crows on the Olympic Peninsula (B).

nesting >5km from human settlement or recreation sites (3 of 9 such crows died). Wildland crows that bred adjacent to small settlements and recreation sites appeared long-lived (only 1 of 20 died during five years of observation).

Using the variation in annual breeder survivorship and reproduction in conjunction with our assumptions about age of first breeding, pre-breeder survival, and longevity (see Methods), we estimated λ (geometric rate of increase) for urban, suburban, rural, and wildland crow populations. This demographic analysis suggested that urban populations had the capacity for slight growth ($\lambda = 1.008$), suburban populations should grow 15.8% per year ($\lambda = 1.158$), rural populations should grow by 7.3% per year ($\lambda = 1.073$), and wildland populations should grow 3.9% per year ($\lambda = 1.039$). Incorporating observed annual variation in reproduction and survival into a model of population growth (as environmental variability) and incorporating demographic stochasticity (Akcakaya 1991) reveals that, *at best*, urban crow populations should only increase 6.3% per year. Growth of all crow populations was most sensitive to adult survivorship (elasticities: urban adult survival = 0.54; suburban = 0.36; rural = 0.47; wildland = 0.44). The predicted change in a crow population of 50 individuals living in each of these environments for 100 years is striking; suburban populations are

Table 16.2. Annual reproductive success of American Crows in areas of varying urbanization.

Site	No. breeding attempts	Years of study	% success	Mean no. fledged successful nest^{-1} yr^{-1}	Mean no. fledglings pair^{-1} yr^{-1}
Urban					
Seattle parks, campus, neighborhoods	80	1998 - 2000	53.3	2.0	1.1
Los Angeles golf course	147	1985-1990	43.0	1.93	0.83
Madison parks, campus, neighborhoods, golf course	123	1982 - 1985	44.7	3.1	1.4
Suburban					
Snohomish, WA	19	1998-2000	63.2	3.1	2.1
Madison, WI	56	1982-1985	68.1	2.9	2.0
Ithaca, NY	202	1989-1994	57.3	3.1	1.6
Rural					
Tompkins County, NY	45	1989-1994	48.0	3.6	1.6
Wildland					
Olympic Peninsula	54	1995-2000	78.0	2.0	1.5

predicted to be 4-6 orders of magnitude larger than urban, rural, or wildland populations (Fig. 16.6).

3.4 Effects on Other Birds

Although our data do not preclude the possibility that past contact with crows shaped nesting preferences of other songbirds or that crows may depredate the nests of susceptible species within a very narrow window following colonization, it seems that crows rarely prey on nests (Fig. 16.5). In Washington, we found nonsignificant, negative relationships between crow abundance and rate of predation in experiments using artificial ground nests, shrub nests, and canopy nests (Fig. 16.7). Crows have been photographed depredating artificial nests, but these events are rare (*n* = 2 of many hundred) and crows constitute only one of nearly 20 recorded nest predators (small and large mammals, several corvids, owls, and raptors; Luginbuhl et al., in press) in the Washington study area. Observations at over 900 artificial canopy nests designed to simulate Marbled Murrelet nests implicated crows or ravens as nest predators in only 6.2% of 451 eggs and 2.0% of 454 chicks (Luginbuhl et al., in press).

Table 16.3. Annual survivorship of breeding American Crows in areas of varying urbanization.

Area	No. crows	No. breeder years	% annual survivorship
Urban			
Seattle*	16	16	81.3
Los Angeles	23 (Female) 27 (Male)	67 (Female) 105 (Male)	94.3 (Female) 95.1 (Male)
Suburban			
Ithaca	35	87	92.0
Snohomish*	10	24	93.3
Rural			
Tompkins County	11	20	90.0
Wildland			
Olympic Peninsula*	29	29	86.0

*Survivorship determined using radio telemetry.

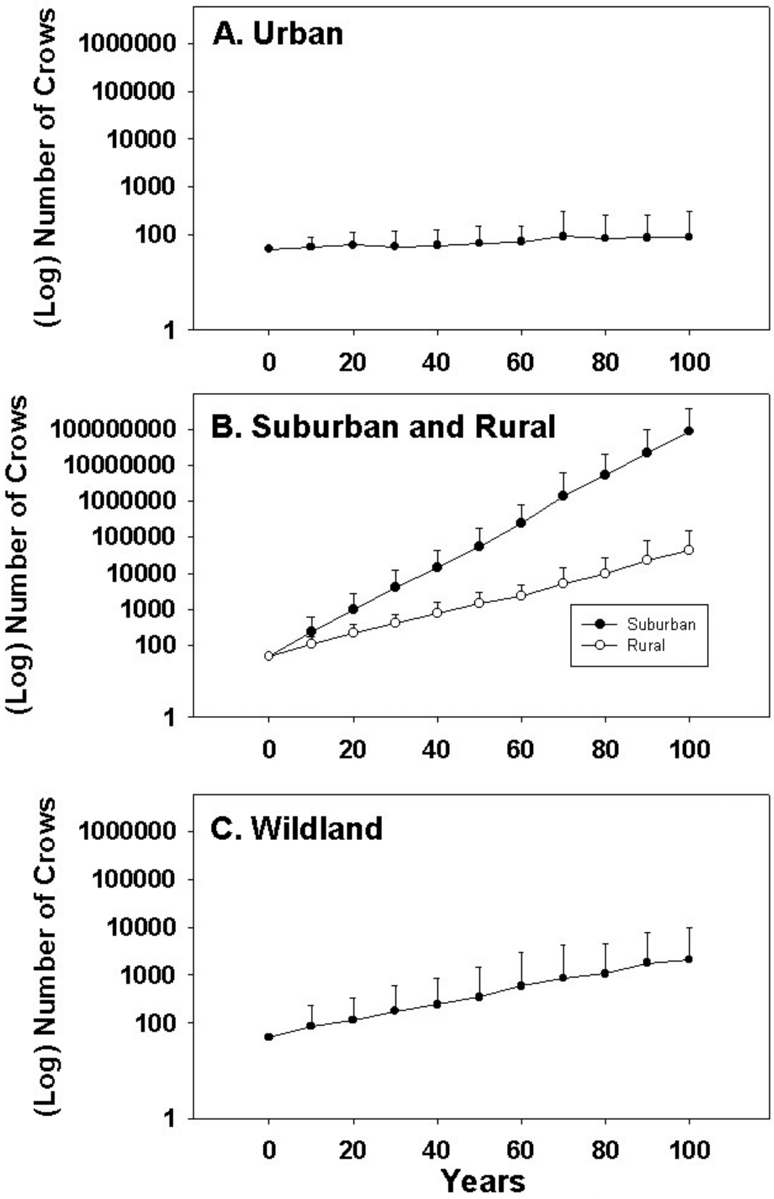

Figure 16.6. Projected change in simulated crow populations with demographic characteristics of crows in urban (A), suburban (B), rural (B), and wildland (C) areas. Average population size is plotted on a log scale (note range in B is greater than A and C). Error bars (1 SD) represent variation induced by demographic stochasticity. All populations were initiated at $n = 50$ birds.

4. DISCUSSION

4.1 Urban Life

American Crows have become human commensals or, as defined by Johnston (2001), they are synanthropic. They rarely are found breeding far (>5km) from human activity. Their abundance peaks and may be increasing most rapidly in urban and suburban areas (Fig. 16.3). Our results suggest that high abundance is possible because breeding pairs in urban areas use very little space (Fig. 16.4). This fact may be the result of food supplementation provided directly by human refuse, and indirectly by land-cover modification that replaces native forests and understories with forest-field ecotones and lawns rich in earthworms and other suitable invertebrates (Fig. 16.5; but see McGowan 2001). Without access to human settlement, crows require large areas for foraging (Fig. 16.4) which may limit population size in remote areas such as Washington's Olympic Peninsula.

There is a paradox in the commensalism between crows and humans. Despite being abundant and increasing in some urban areas (e.g., Albuquerque, Portland, and Seattle), the demographic patterns of urban crow populations are not sufficient to explain their explosive growth. Our estimates of population growth rates suggest that urban populations should grow relatively slowly, at rates less than 5% per year. (Tables 16.2, 16.3; Fig. 16.5). In contrast, the demographic patterns of suburban crow populations may allow rapid population increases. This pattern also is true of rural and wildland crow populations, albeit slower than suburban populations. Suburban and rural populations appear to be growing, as predicted by their demographic data, but exurban and wildland populations appear to be small and relatively stable, despite their capacity for growth. The difference between expected and observed population changes in urban areas is clearly seen in Seattle. There, winter counts suggest an exponentially increasing population, but demographic rates predict little population growth (Fig. 16.8).

Is this paradox real or is it simply a result of insufficient data and comparisons between breeding performance and winter populations? We think it is real. Breeder survivorship and reproduction are relatively constant between years and very similar across our different studies. Incorporating the observed variation in survivorship and fecundity into our demographic projections did not affect our conclusions (note error bars in Figs. 16.6 and 16.8). Thus it seems likely that they are accurate. A more likely source of inaccuracy involves the pre-breeding cohort. Our understanding of this age group is entirely dependent on McGowan's (2001) studies in New York.

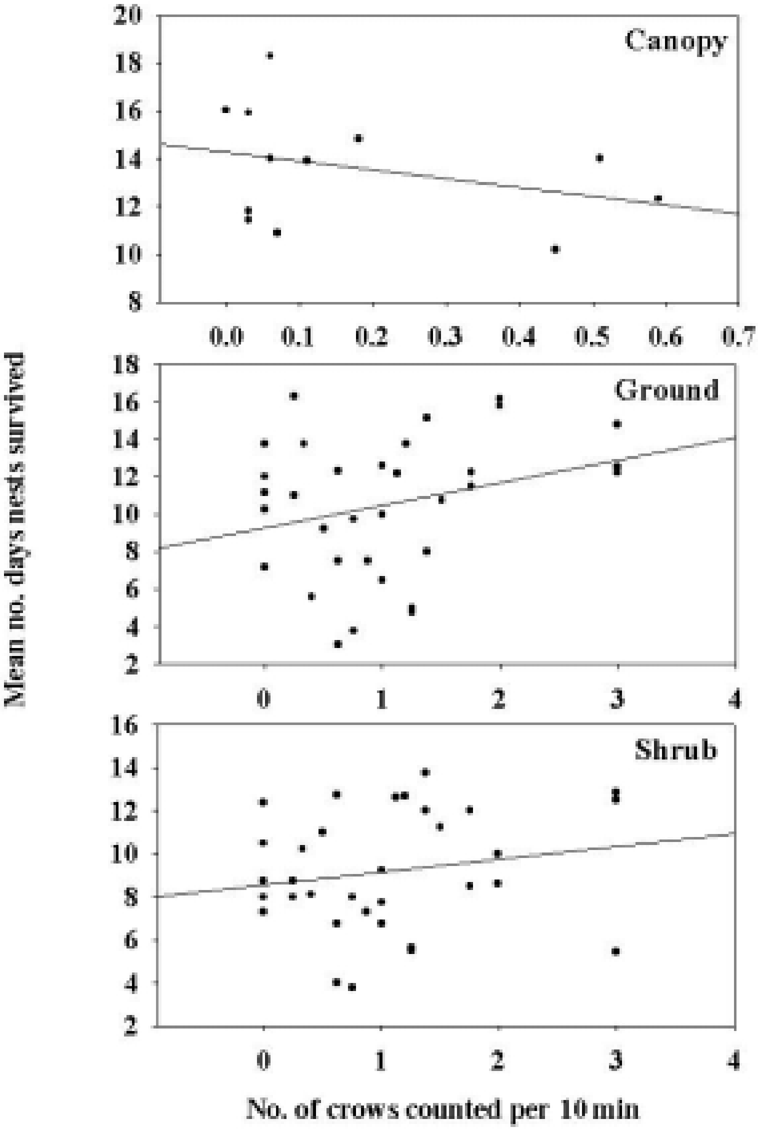

Figure 16.7. Relationships between rates of predation on artificial nests and relative abundance of crows in western Washington. Canopy nests simulated those of Marbled Murrelets on the Olympic Peninsula. Shrub and ground nests simulated thrushes and sparrows, respectively, in the Seattle and Cascade Mountain study areas. Average rates of predation within study landscapes (*n* = 3 - 5 study plots with 6 nests per plot in each landscape) are plotted for canopy nests. Average rates of predation in each study plot (*n* = 8 - 36 nests per plot) are illustrated for shrub and ground nests. Least-squares regression lines are provided for each nest type, although the relationships are not significant.

Perhaps urban crows breed at younger ages or have better survivorship in the pre-breeding period, than do other crows. However, this seems unlikely. In Seattle, breeding space appears to be saturated so early breeding would seem difficult. Young crows are also frequently killed by automobiles, suggesting low survival in urban areas, although McGowan (2001) found first year survival was higher in suburban than rural areas (Table 17.4). If the paradox is not real, our population estimates, which come from mid-winter counts (standardized CBC's; Butcher 1990), may not accurately reflect reproduction and recruitment from local surroundings. Rather they might simply indicate seasonal influxes (migration) of breeders into urban areas from the surrounding region, or that the CBC's rely heavily on counts at urban roosts, which are known to include rural crows (Caccamise et al. 1997; McGowan 2001).

Why is reproduction and survivorship lowest in urban areas? Productivity in urban areas may suffer because of a combination of (1) poor food quality (if it is abundant, it is likely of low quality relative to invertebrate rich suburban and wildland areas; McGowan 2001; Pierotti and Annett 2001), (2) high intraspecific interference during breeding, and (3) large populations of protected or subsidized nest predators (raccoons [*Procyon lotor*], eastern gray squirrels [*Sciurus carolinensis*], and Red-tailed Hawks [*Buteo jamaciensis*]). Survivorship in urban areas may be relatively low because (1) unnatural hazards are common (e.g., windows and golf balls), (2) automobiles collisions kill many fledglings, (3) predators of adults may thrive (Red-tailed Hawks and Great-horned Owls, *Bubo virginianus*, are important in this respect), and (4) toxins are common and may be concentrated in prey items. Urban environments are rapidly changing, challenging places for any animal to inhabit. The adaptability of crows is impressive, but appears to be just adequate to keep pace with the urban fast lane.

4.2 Causes of Population Growth

If the local demography of urban populations is stable, but not growing, then what is causing the urban crow population explosion? In mobile species such as crows, immigration and emigration can decouple local population trajectories from local demography. However, the usual process is for dispersal to "rescue" declining populations ($\lambda < 1$; Brown and Brown 1977, Stacey and Taper 1992). We are unaware of examples where dispersal from a productive region or population simultaneously limits growth at the source, while it fuels a population explosion at a distant site where the local breeding population appears to be at its carrying capacity (territory size is extremely small and obvious breeding habitat appears saturated). That is,

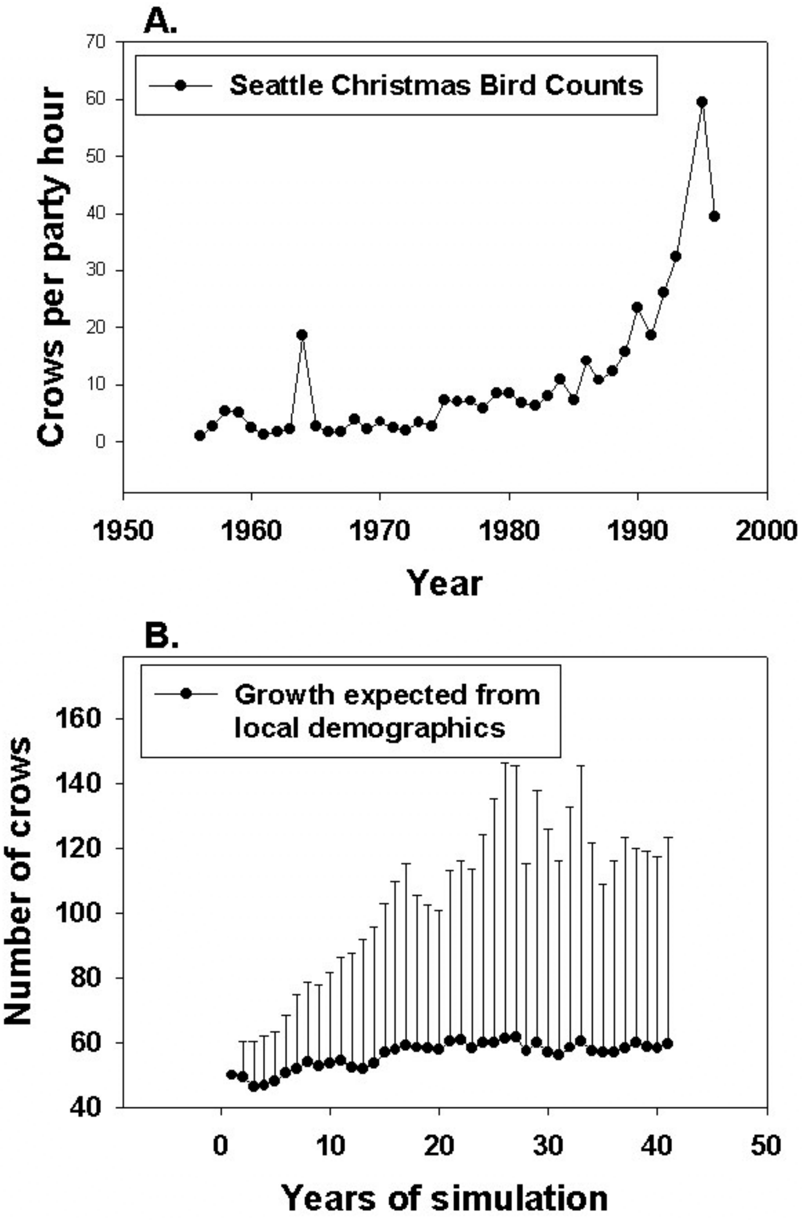

Figure 16.8. Growth in urban American Crow populations observed (A) and expected (+1 SD) from local demographic potential (B). In contrast to expectation, local demographics predict stasis, but observed growth is exponential.

nonetheless, what seems to be happening with urban crows. It is theoretically possible for dispersal from sources ($\lambda > 1$) to increase populations in sinks ($\lambda < 1$; Pulliam 1988), but in such settings sink populations typically barely persist rather than thrive (Robinson et al. 1995).

Although territoriality limits the urban breeding population of crows, crow populations may be able to grow even where natality and mortality are balanced. It is possible that unlimited urban food may enable exponential increase, fueled by immigration, in the urban non-breeding population. Additionally, suburban sprawl continually creates new breeding habitat that can be colonized by crows unable to obtain breeding space in the city core. Sprawl opens forests and juxtaposes newly created foraging habitat (lawns, roads, and dumpsters) with discrete, easily defended breeding sites (patches of trees). Refuse in the urban core is renewed daily and allows large aggregations of crows to gather at scattered, highly visible, reliable, and rich feeding areas where foraging occurs with minimal aggression because resources are not economically defensible (Brown 1969). This also occurs in many rural areas, so is not the only driver of population size.

We hypothesize that dispersal from breeding populations in suburbs and/or rural and wildlands cause urban populations to increase. Young crows produced by successful suburban, exurban, and rural breeders presumably should find it difficult to obtain breeding space in those habitats. Dispersal to the city, where food and social partners are abundant, and the shooting of crows is prohibited, would seem to be a successful strategy for a pre-breeding crow. The ability of crows to easily traverse large areas, share rich food resources, and quickly colonize rapidly expanding breeding opportunities made suitable by sprawling cities enables crow populations to increase rapidly and escape local demographic constraints on population growth.

If pre-breeding crows disperse from suburban, exurban, and rural areas into urban areas, then we should observe pre-breeding flocks in urban areas. We have observed them in Seattle and Los Angeles, but not in midwestern (Oklahoma; Caffrey, unpublished data) or eastern (New York) areas. Conspicuous differences in crow social systems may partly explain this. Crows from the northern Great Plains and in the most northern reaches of the range migrate south during winter rather than congregate in local urban areas (Aldous 1944, Ignatiuk and Clark 1991, Root 1988). Additionally, suburban and rural pre-breeding crows in New York typically remain on their territories as helpers rather than floaters (McGowan 2001). Helping occurs in western crows, but less frequently (Verbeek and Butler, 1981; Caffrey 1999). Clearly we need a better understanding of the options pursued by pre-breeding crows across the urban gradient in a variety of social systems. However, rapid crow population growth in some western cities indicated in our survey of CBC data confirms our suspicion that social systems of western crows may be especially conducive to fueling urban growth.

Suburban crow populations have the potential to bolster urban populations. For illustration, we started two hypothetical populations that were proportional in size to the populations we surveyed along the urban gradient in western Washington. This gave us initial populations of 82 suburban crows and 114 urban crows. We grew these populations for 50 years according to our calculated geometric rate of increase. This gave us nearly 145,000 suburban, but virtually unchanged numbers of urban crows. If we allow carrying capacity to be proportional to the space requirements of urban breeders (Seattle park data; Figure 16.4), then a 500 ha^2 area could support 2500 pairs in the suburbs and >5,000 pairs in the urban area. Our model suggests that the urban population would only attain its carrying capacity if crows from suburbs dispersed into the urban area at a rate proportional to the degree to which their populations were above their respective carrying capacities. During our simulated growth, suburban populations produced a sufficient number of dispersers to increase urban populations beyond their expected carrying capacity in only 35 years.

If our model of crow population dynamics is correct, then urban populations function more like a *sponge* than either a sink or a source. They soak up the surplus from nearby source populations and grow by augmenting their pre-breeding segment (Fig. 16.9). Breeder numbers likely remain constant once carrying capacity is reached because of extremely dense packing of small urban territories. Pre-breeders may wander within towns to track spatio-temporally variable food sources in the urban environment and eventually disperse back to suburbs or wildlands to breed, or quickly colonize new settlements on the urban fringe. Indeed, the sponge may function primarily in the winter, when subordinate and inferior juvenile foragers are most stressed for food resources.

The importance of urban sprawl is obvious in our model. As food resources grow in new settlements, new breeding space is created as the former wildlands or suburbs becomes new suburban or urban areas where, respectively, breeders need only 10% of their former space. The subsidized surplus of pre-breeders in nearby urban areas can quickly fill these openings. As new suburbs grow, an ever increasing number of young birds are produced to fuel growth in the original and expanding urban area. This is an interesting case of the urban ‘footprint’ (Wackernagel and Rees 1996) affecting the urban core. The far reaching effects of urban growth fuel changes in animal populations residing in the core. Put in an ecological context, it is an example of population regulation occurring at multiple scales as the features of the surrounding landscape (large scale) affect local populations (small scale).

4.3 Consequences of Population Growth

American Crows are nest predators that may be particularly adept at finding and destroying shrub and canopy nests (Marzluff and Balda 1992). As urbanization clearly increases crow populations, could this change result in low nesting success of other birds in urban areas? Our observations in western Washington suggest that this idea is too simplistic. Crow population increases do not necessarily correlate with increasing rates of nest predation (Fig. 16.6). Poor congruence between crow population size and nesting success of other birds is likely the result of a complex suite of nest predators whose sum, rather than individual, effect determines the rate of nest predation in any local area (Marzluff and Restani 1999, Luginbuhl et al., in press). Where crows are rare, mice, squirrels, or jays may be abundant and therefore nest predation may remain high. The singular importance of crows as limiting factors on other species also is cast into doubt by management actions that removed crows but did not document increases in nesting

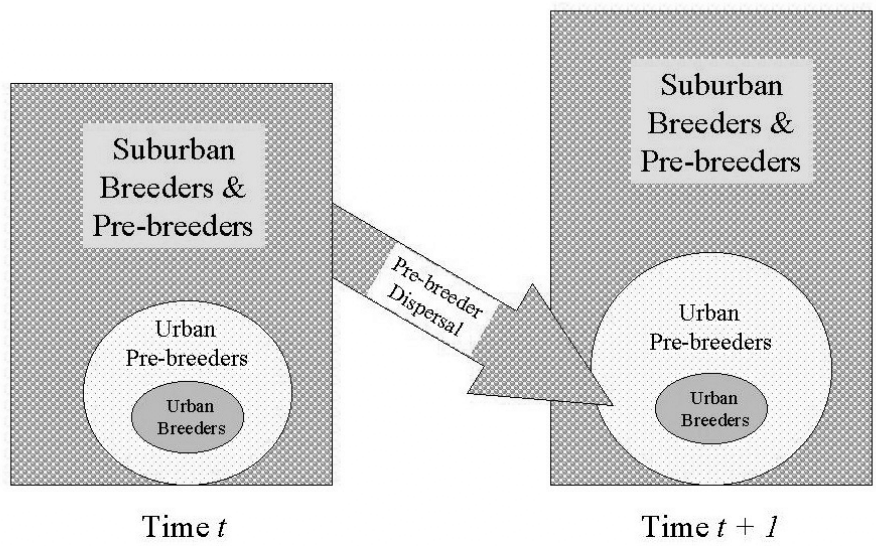

Figure 16.9. Source-sponge hypothesis of urban crow population growth. Growth is not expected in the saturated breeding segment of the urban population. Rather, the pre-breeder population swells as dispersers from surburban source populations disperse into the urban core to exploit abundant anthropogenic foods.

success of other species (Chesness et al. 1968, Parker 1984, Parr 1993, Broyer et al. 1995, Clark et al. 1995).

The suite of nest predators along the urban gradient and their resulting effect on nests is determined by a complex interaction of landscape- and local-scale factors. Where the landscape is extremely urbanized, crows, introduced tree squirrels, and rats are likely to be the dominant nest predators. They may destroy many nests if local conditions are suitable. Important local conditions might include grass cover for crows, ground cover for rats, feeders for squirrels and crows, and nesting cover for songbirds. However, in extremely manicured or altered settings nest predation may be low despite abundant crows because rats and squirrels are rare. That is, increased crow abundance may not compensate for reduced mammalian predators, in terms of the rate of nest depredation. Indeed, predators that are adapted to fragmented and urban landscapes in the western U.S. may not compensate for the loss of native predators, in general (Tewksbury et al. 1998; Haskell et al. 2001).

In the suburban landscape jays, crows, native mice, chipmunks, and squirrels are abundant. Local conditions (such as landowner practices, recreation, forest composition, forest remnant size and shape) may determine the exact mix and abundance of nest predators and resulting nest predation in a study plot. In this setting, nest predator diversity may be dictated by a few keystone predators like Red-tailed Hawks, coyote (*Canis latrans*), and short-tailed weasels (*Mustella ermina*). Regardless of the cause, the diverse predator community in this setting will likely obscure a direct relationship between crow abundance and rate of nest predation. In the wildland landscape, a similarly diverse nest predator community is determined by forest cover and patch structure, topography, presence of water, degree of recreation, and landowner practices. Nest predator communities should be extremely diverse and result in moderately high rates of nest predation that are independent of crow abundance.

4.4 Remaining Questions

Our description of crow population structure along the urban gradient is based on circumstantial evidence that needs to be tested. The generality of suburban sources needs to be validated across years and in a variety of areas. The prediction that urban breeding populations are relatively stable through time, while their non-breeding populations increase, also needs testing. In particular, estimates of adult survivorship deserve more attention, due to their relatively large influence on landscape-specific population growth. Three predictions arise from our conceptual model of urban crow populations. First, urban populations will have a larger non-breeder to breeder ratio than will suburban or wildland crows. The critical hypothesis of dispersal from wildland and suburban areas to urban areas presently has only little data (McGowan 2001). However, this hypothesis is tractable in crows with radio telemetry or observations of color-marked birds. We expect young produced in wildland, rural, and suburban areas to wander widely and disperse to urban sponges. In contrast, young produced in urban areas should be incorporated into nearby urban pre-breeding groups (if they exist) or remain as helpers in their natal territories. The second prediction is that young produced in urban settings should help parents at the nest (i.e., not disperse) more than young born in source populations further out on the urban gradient, unless urban food resources are extremely patchy (Jerzak 2001). McGowan (2001) found that although the percentage of nests with helpers did not differ between suburban and rural areas, urban families were significantly larger. The third prediction is that in rapidly urbanizing areas, like the American west, newly settled areas should be colonized by pre-breeders residing in existing and nearby urban core locations.

Our suggestion that increasing crow populations do not necessarily mean increasing rates of nest predation also should serve as a hypothesis rather than as a statement of fact. It is an appropriate null hypothesis that should be tested at various points on the urban gradient. Important contributions can be made by observing the rate of predation on real nests in areas with vastly different abundances of crows. However, ornithologists need to monitor a sizeable fraction of the suite of nest predators across this gradient to fully understand the role of crows (Marzluff and Restani 1999; Haskell et al. 2001). We predict that the rate and magnitude of predation will vary directly with crow abundance only in landscapes depauperate of other nest predators.

Population ecologists also will find urban environments to be fertile research areas. Our work on crows suggests the structuring of populations in an area of limited spatial extent with vastly different local conditions is complex. It is likely that replicates of population sources, sinks, and sponges exist within a study area of only a few hundred square kilometers. This situation would provide a fertile laboratory to quantify, perturb, and understand the viability of the metapopulation paradigm.

5. MANAGEMENT AND POLICY IMPLICATIONS

The urban gradient is an excellent experimental stage where avian communities assembled through individual- and population-level processes, can be observed before, during, and after major habitat changes. Documenting local extinctions and colonizations in rapidly developing areas, as well as in urban reserves surrounded by human-dominated ‘seas’, will perhaps allow urban planning to proceed in a more ecologically sustainable way. By studying successful species such as crows, we may be able to determine how they come to survive in such a radically and rapidly changing environment. What novel adjustments do they make to city life?

Urban ornithologists can make an important contribution to conservation by better elucidating how landscape-level changes interact with local conditions to determine avian community structure. The urban environment provides varied local conditions in proximity to one another within similar landscapes. For example, within the urban landscape, areas exist varying in the pattern of development, the degree to which vegetation is native or exotic, the percentage of the land-cover that is impermeable, and the degree to which homeowners feed birds or allow their cats to roam. Do these local conditions determine bird communities, or is the general urban landscape more important? We hope future studies will address these and related questions. We suggest the answers will require community surveys and detailed studies of population ecology. Studies of potential keystone species, like predators, parasites, and exotic invaders, may be especially important.

Studies of how urbanization affects mechanisms (like nest predation) that may structure avian communities can inform policy makers with reliable science. Such studies are more likely to reveal causal relationships that policy makers can use to construct sound and legally defensible decisions. Our studies of crows suggest that uncontrolled sprawl will greatly accelerate crow populations. This may not be desired. However, our results and those of others suggest that increasing crow populations are not causally linked to reduced songbird productivity. Removing crows is not a reliable way to increase productivity of songbirds. Rather, controlling sprawl itself is more likely to keep crow populations in check and provide the suitable habitat required by many species of declining songbirds.

ACKNOWLEDGEMENTS

Research on crows in western Washington was supported by grants from the National Science Foundation (DEB-9875041), the Washington Department of Fish and Wildlife, the University of Washington's Royalty Research Foundation, the U.S. Forest Service, the U. S. Fish and Wildlife Service, Rayonier, and the Washington State Department of Natural Resources. We are especially indebted to Lenny Young, Dan Varland, Marty Raphael, Scott Horton, and John Pierce for their support. Roarke Donnelly, Karla Kaczoroski, John Luginbuhl, Kim McKillip, Erik Neatherlin, and John Withey provided unpublished results and field assistance. Research was done under the auspices of UW ACUC permit #3077-03. Financial support for the Ithaca crow research was provided by U.S. Dept. Agriculture, Hatch Project Grant NYC-183429. RLK appreciates the insights and mentoring from Stanley A. Temple of the University of Wisconsin's Department of Wildlife Ecology, who also provided financial assistance to support Knight's crow research in Madison.

REFERENCES

Akcakaya, H. R. 1999. RAMAS GIS. Linking landscape data with population viability analysis. Applied Biomathematics. Setauket, NY.

Audubon Society. 2000. Audubon Christmas Bird Counts. http://www.mp1-pwrc.usgs.gov/birds/cbc.html.

Brooks, A. 1925. Anent the crow. Condor 27: 83-84.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445-449.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293-329.

Broyer, J., Fournier, J. Y., and P. Varagnat. 1995. Effect of carrion crow (*Corvus corone*) reduction on predation on artificial anatid (Anatidae) nests. Gibier Faune Sauvage 12:95-107.

Buehler, D., J. D. Fraser, M. R. Fuller, L. S. McAllister, and J. K. D. Seegar. 1995. Captive and field-tested radio transmitter attachments for bald eagles. J. Field Ornith. 66:173-180.

Butcher, G. S. 1990. Audubon Christmas bird counts. USDI FWS Biological Report 90:5-13.

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 of cooperatively breeding western American crows. Auk 116:836-841.

Caffrey, C. 2000. Correlates of reproductive success in cooperatively breeding western American crows: If helpers help, it's not by much. Condor 102:333-341.

Chesness, R. A., Nelson, M. M., and W. H. Longley. 1968. The effect of predator removal on pheasant reproductive success. J. Wildl. Manage. 32:683-697.

Clark, R. G., Meger, D. E., and J. B. Ignatiuk. 1995. Removing American Crows and duck nesting success. Can. J. Zool. 73:518-522.

Donnelly, R. E., and J. M. Marzluff. In press. Designing research to advance the management of birds in urbanizing areas. *In* W. Shaw and L. Harris [EDS.], Proceedings of the 4th International Urban Wildlife Conservation Symposium. Arizona State University, Tempe.

Droege, S. 1990. The North American breeding bird survey, p 1-4. *In* J. R. Sauer and S. Droege [EDS.], Survey designs and statistical methods for the estimation of avian population trends. U.S. Dept. Inter., Washington, DC.

Eden, S. F. 1985. The comparative breeding biology of magpies Pica pica in an urban and a rural habitat. J. Zool., Lond. (A) 205:325-334.

Emlen, J. T., Jr. 1940. The midwinter distribution of the crow in California. Condor 42:287-294.

Fraissinet, M. 1989. Espansione della taccola, Corvus monedula, nei capoluoghi italiani. Riv. Ital. Orn. 59: 33-42.

Haskell, D., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization, p. 245-260. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Hogrefe, T. C., and R. H. Yahner. 1998. Depredation of artificial ground nests in a suburban versus a rural landscape. J. Penn. Acad. of Science 72:3-6.

Ignatiuk, J. B. and R. G. Clark. 1991. Breeding biology of American crows in Saskatchewan parkland habitat. Canadian J. Zool. 69:168-175.

Jerzak, L. 2001. Synurbanization of the Magpie in the Palearctic, p. 405-427. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Johnston, R. F. 2001. The synanthropic birds of North America, p. 49-67. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Kenward, R. E. 1987. Wildlife radio tagging. Academic Press, Sand Diego, CA. 222p.

Kenward, R. E. and K. H. Hodder. 1995. Ranges V: software for analysing animal location data. Institute of Terrestrial Ecology, Wareham, UK.

Konstantinov 1996. Antropogenic transformations of bird communities in the forest zone of the Russian Plain. Acta Ornithologica 31: 53-65.

Konstantinov, V. M., and V. G. Babenko. 1982. Numbers and some ecological features of synanthropic populations of the corvidae under the conditions of intensive urbanization. 12:1837-1845.

Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland. In press. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. J. Field Ornithol.

Marzluff, J. M. 2001. Worldwide increase in urbanization and its effects on birds, p. 19-47. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Marzluff, J. M., and R. P. Balda. 1992. The Pinyon Jay. T & A D Poyser, London.

Marzluff, J. M., R. B. Boone, and G. W. Cox. 1994. Native pest bird species in the West: why have they succeeded where so many have failed? Studies Avian Biol. 15:202-220.

Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms and approaches, p. 1-17. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Marzluff, J. M., Raphael, M. G., and R. Sallabanks. 2000. Understanding why forest management may affect avian species: mechanisms, experimental approaches, prioritization, and funding strategies. Wildl. Soc. Bull. 28:1132-1143.

Marzluff, J. M., and M. Restani. 1999. The effects of forest fragmentation on avian nest predation. Pp: 155-169. In: Forest Fragmentation: Wildlife and Management Implications (J. A. Rochelle, L. A. Lehmann, and J. Wisniewski eds.). Brill Academic Publishing, Leiden, The Neatherlands.

McGowan, K. 2001. Demographic and behavioral comparisons of suburban and rural American Crows, p. 367-383. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Monson, G. 1946. Notes on the avifauna of the Rio Grande Valley, New Mexico. Condor 48:238-241.

Parker, H. 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. J. Wildl. Manage. 48:1197-1205.

Parr, R. 1993. Nest predation and numbers of Golden Plovers *Pluvialis apricari*a and other moorland waders. Bird Study 40: 223-231.

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.

Pitelka, F. A. 1942. High population of breeding birds within an artificial habitat. Condor 44: 172-174.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652-661.

Richards, G. L. (1971). The Common Crow, *Corvus brachyrhynchos*, in the Great Basin. Condor 73:116-118.

Rickard, W. H. 1959. Changes in winter bird species of two habitats in San Miguel County, New Mexico, after three-fourths of a century. Condor 61:438.

Robertson, J. M. 1931. Some changes in the bird life of western Orange County, California. Condor 33:204-205.

Robinson, S. K., Thompson, F. R. III, Donovan, T. M., Whitehead, D. R., and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Stacey, P. B. and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecol. App. 2:18-29.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.

Verbeek, N. A. M., and R. W. Butler. 1981. Cooperatively breeding of the Northwestern Crow Corvus caurinus in British Columbia. Ibis 123:183-188.

Vekasy, M. S., J. M. Marzluff, M. N. Kochert, R. N. Lehman, and K. Steenhof. 1996. Influence of radio transmitters on Prairie Falcons. J. Field. Ornithol. 67:680-690.

Wackernagel, M., and W. E. Rees. 1996. Our ecological footprint : reducing human impact on the earth.**:** New Society Publishers, Philadelphia, PA.

Withey, J. C., Bloxton, T. D., and J. M. Marzluff. In press. Effects of tagging animals and estimating locations on inferences derived from wildlife radiotelemetry studies, p. 43-75. *In* J. J. Millspaugh and J. M. Marzluff [EDS.], Radiotelemetry and animal populations. Academic Press, San Diego, CA.

Appendix 16.1. Christmas Bird Count description and data summary.

CBC circle	Circle class[a]	Count years included	Average no. crows per party hr	% Fish Crows	Regression coefficient
Afton, MN	R	1960-1989	10.7	0.00	0.215
Aiken, SC	R	1961-1989	2.0	0.00	0.023
Albuquerque, NM	U	1962-1989	115.5	0.00	4.246
Arnett, OK	R	1967-1989	3.5	0.00	-0.064
Baker,OR	R	1960-1989	0.7	0.00	0.09
Baldwin, KS	R	1960-1989	4.6	0.00	0.089
Bismark, ND	U	1960-1989	0.0	0.00	0.001
Black Forest, CO	R	1960-1985	0.2	0.00	0.009
Boise, ID	U	1967-1989	0.3	0.00	0.055

CBC circle	Circle class[a]	Count years included	Average no. crows per party hr	% Fish Crows	Regression coefficient
Cedar, MN	R	1960-1989	5.5	0.00	0.323
Central Berkshire, MA	U	1968-1989	3.5	2.43	0.256
Chapel Hill, NC	U	1960-1989	2.7	0.00	0.016
Chicago, IL	U	1967-1989	5.5	0.00	0.296
Cincinnati, OH	U	1960-1989	8.2	0.00	-0.164
Colorado Springs, CO	U	1960-1989	4.3	0.00	0.19
Columbia, MO	R	1961-1989	2.4	0.00	0.037
Concord, NH	U	1965-1989	2.8	0.00	0.04
Dallas, TX	U	1960-1989	3.5	0.00	-0.062
Decorah, IA	R	1960-1989	5.7	0.00	0.296
Denver. CO	U	1960-1989	2.0	0.00	-0.068
Des Lacs, ND	R	1960-1989	0.0	0.00	0.001
Dubois, WY	R	1966-1989	0.0	0.00	0
Elverson, PA	R	1960-1989	10.9	0.19	-0.156
Espanola, NM	R	1960-1989	5.1	0.00	-0.064
Eugene, OR	U	1960-1989	9.1	0.00	0.018
Fargo, ND	U	1960-1989	1.2	0.00	0.109
Ferris, VT	R	1962-1989	42.2	0.00	0.084
Green Bay, WI	U	1964-1989	2.6	0.00	0.137
Gunnison, CO	R	1960-1989	1.0	0.00	0.019
Hackensack-Ridgewood, NJ	U	1960-1989	6.0	1.34	0.425
Hartford, CT	U	1960-1989	25.6	0.02	1.872
Houston, TX	U	1960-1989	0.9	0.00	0.015
Huntington, WV	U	1961-1987	4.7	0.00	-0.37
Indian, OH	R	1960-1988	0.4	0.00	0.03
Indianapolis, IN	U	1960-1989	8.9	0.00	0.121
Los Angeles, CA	U	1960-1989	0.5	0.00	0.034
Madison, SD	R	1961-1989	1.8	0.00	0.031
Maryville, MO	R	1966-1989	1.3	0.00	-0.053
Memphis, TN	U	1960-1989	0.8	0.00	0.024
Moscow, ID	R	1960-1989	0.2	0.00	0.014
Niles, MI	R	1962-1989	0.9	0.00	-0.053
Oklahoma City, OK	U	1960-1989	1.4	0.00	0.012
Omaha, NE	R	1962-1989	1.8	0.00	0.026
Orange Co (NE), CA	R	1960-1989	2.7	0.00	-0.152
Peshtigo, WI	R	1965-1989	5.3	0.00	0.441
Portland, OR	U	1960-1989	11.0	0.00	0.514
Point Reyes, CA	R	1971-1988	2.7	0.00	0.072

CBC circle	Circle class[a]	Count years included	Average no. crows per party hr	% Fish Crows	Regression coefficient
Putnam Co., NY	U	1960-1989	2.4	0.02	0.034
Rapid City, SD	U	1960-1989	0.8	0.00	0.052
Rock Run, MD	R	1964-1989	7.0	2.43	-0.216
Rupert, ID	R	1968-1989	4.8	0.00	3.722
Sacramento, CA	U	1960-1989	17.8	0.00	1.219
Scranton, PA	U	1960-1989	1.9	0.00	-0.035
Seattle, WA	U	1956-1997	10.2	0.00	0.573
Sioux Falls, SD	U	1960-1989	5.6	0.00	-0.026
Salt Lake City, UT	U	1960-1989	0.0	0.00	0
Spokane, WA	U	1960-1989	0.1	0.00	0.003
St. Paul, MN	U	1960-1989	3.2	0.00	0.215
Terre Haute, IN	R	1961-1989	2.7	0.00	-0.061
Topeka, KS	U	1960-1989	1.8	0.00	0.04
Traverse City, MI	U	1960-1989	1.1	0.00	-0.065
Trinidad, TX	R	1963-1989	4.8	0.00	0.025
Truckee, NM	U	1960-1989	0.0	0.00	-0.172
Tyler, TX	R	1960-1989	5.1	0.00	0.16
Walnut Valley, NJ	R	1968-1989	7.2	0.10	-0.302
Washita NWR, OK	R	1964-1989	1.8	0.00	-0.003
Watertown, NY	R	1960-1989	2.6	0.00	0.325
Waukegan, IL	R	1960-1989	44.6	0.00	-6.738
Wenatchee, WA	R	1961-1989	0.0	0.00	0.002
Wilmot, SD	R	1967-1987	0.5	0.00	0.04

[a] U=urban, R=rural or exurban.