



*The Auk* 122(1):205–221, 2005  
© The American Ornithologists' Union, 2005.  
Printed in USA.

## DISPERSAL BY JUVENILE AMERICAN CROWS (*CORVUS BRACHYRHYNCHOS*) INFLUENCES POPULATION DYNAMICS ACROSS A GRADIENT OF URBANIZATION

JOHN C. WITHEY<sup>1</sup> AND JOHN M. MARZLUFF

*College of Forest Resources, University of Washington, P.O. Box 352100, Seattle, Washington 98195, USA*

**ABSTRACT.**—American Crow (*Corvus brachyrhynchus*) populations are increasing across North America, often at high rates in urban areas. A monthly survey of American Crows in the Seattle Christmas Bird Count (CBC) circle suggested that winter counts reflected American Crow abundance at other times of the year, so we used CBC results for American Crows as a measure of population trend. In the Seattle area, local survival and fecundity appear unable to account for exponential population growth. We tested the hypothesis that juvenile dispersal from outlying suburban and exurban areas contributes to growth in the urban population by radiotagging 56 juveniles 5–46 km away from the central business district of Seattle and tracking their movements. Juvenile American Crows' centers of activity were 0.2–22.2 km away from their natal territory during the first 3–12 months after fledging. An estimated 45% survived one year. Movements of dispersing American Crows varied in their consistency with simulated random-walk paths; the data suggested that, at the population level, American Crows were not drawn into urban areas, though some individuals may have been. Movements of dispersers produced a net influx into the city, because of greater reproductive success outside the city than in it. Simulations of urban population growth that included immigrants and emigrants accounted for most of the observed growth, which indicates the importance of distant suburban and exurban breeding pairs to urban population dynamics. *Received 15 October 2003, accepted 8 September 2004.*

**Key words:** American Crow, *Corvus brachyrhynchus*, dispersal, juvenile survival, population dynamics, post-fledging behavior, urban ecology, urban sprawl.

### La Dispersión de Juveniles de *Corvus brachyrhynchus* Influencia la Dinámica Poblacional a lo Largo de un Gradiente de Urbanización

**RESUMEN.**—Las poblaciones de cuervos *Corvus brachyrhynchus* están aumentando a través de América del Norte, a menudo a tasas altas en áreas urbanas. Un muestreo mensual de *C. brachyrhynchus* en el circuito del Censo de Aves de Navidad (CAN) de Seattle sugirió que los censos invernales reflejan la abundancia de *C. brachyrhynchus* en otros momentos del año, por lo que usamos los resultados del CAN como una medida de la tendencia poblacional de esta especie. En el área de Seattle, la supervivencia y la fecundidad local parecen incapaces de explicar un crecimiento poblacional exponencial. Evaluamos la hipótesis de que la dispersión de juveniles desde áreas suburbanas y no-urbanas contribuye al crecimiento de la población urbana. Para ello, marcamos con radios y seguimos los movimientos de 56 juveniles localizados a una distancia de 5 a 46 km del centro comercial de Seattle. Los centros de actividad de los juveniles de *C. brachyrhynchus* se ubicaron entre 0.2 y 22.2 km de distancia de sus territorios natales

---

<sup>1</sup>E-mail: jwithey@u.washington.edu

durante los primeros 3 a 12 meses luego de abandonar el nido. Un porcentaje estimado del 45% de los individuos sobrevivió un año. Los movimientos de dispersión de los cuervos variaron en su consistencia con rutas simuladas de movimientos aleatorios. Los datos sugieren que, a nivel poblacional, *C. brachyrhynchos* no se desplazó hacia áreas urbanas, aunque algunos individuos podrían haberlo hecho. Los movimientos de dispersión produjeron un flujo neto hacia la ciudad, debido a un mayor éxito reproductivo afuera de la ciudad que dentro de ésta. Las simulaciones de crecimiento poblacional urbano que incluyeron inmigrantes y emigrantes explicaron la mayoría del crecimiento observado, lo cual indica la importancia de parejas reproductivas distantes suburbanas y no-urbanas en la dinámica poblacional urbana.

DISPERSAL IS A fundamental process of ecology; it has important effects on biology in both the short term (population trends, local colonizations or extinctions) and the long term (gene flow and evolutionary change). Our knowledge of avian dispersal behavior and its effects on population dynamics and structure remains limited (Walters 1998, 2000). Researchers have studied avian dispersal directly, via mass mark–recapture (Paradis et al. 1998), intensive observations of marked individuals (Marzluff and Balda 1989, Koenig et al. 2000, Pyle 2001), and radiotelemetry (Walls and Kenward 1998, Lang et al. 2002); and indirectly, via genetic markers (Horn et al. 1996, Wang and Trost 2001) and stable isotope analysis (Hobson et al. 2001). Those studies point to the importance of dispersal in equalizing population sex ratio (Marzluff and Balda 1989), reducing inbreeding (Daniels and Walters 2000), limiting populations (Silleet and Holmes 2002), and saving insular and small populations from extinction (known as the “rescue effect”; Brown and Kodric-Brown 1977, Stacey and Taper 1992, Martin et al. 2000). Measuring dispersal in spatially heterogeneous environments is essential for testing population-dynamics models (Kareiva 1990), but obtaining unbiased dispersal data is difficult, because long-distance dispersers often go undetected (Koenig et al. 1996, 2000).

Dispersal may play a key role in the dynamics of American Crow (*Corvus brachyrhynchos*; hereafter “crow”) populations. Marzluff et al. (2001b) found that, in the Seattle area, Christmas Bird Count (CBC) data show crow populations growing exponentially, despite poorer reproduction in cities as compared with less urbanized areas. They hypothesized that urban population growth may be explained in part by juvenile dispersal from breeding populations in suburban and exurban or rural

areas. Ongoing residential and commercial development, or “urban sprawl,” creates new breeding habitat for crows by opening forest and adding foraging sites (e.g. lawns, roads, and dumpsters). If young crows disperse from those areas into urban populations, they may fuel population growth. Urban populations are not functioning as a “sink” (*sensu* Pulliam 1988) in that case, because demographic rates are sufficient to maintain the urban population in the absence of immigration. Instead of a rescue effect, there could be a “sponge effect” as urban populations absorb excess individuals dispersing away from less developed areas.

We tested two predictions based on the hypothesis of Marzluff et al. (2001b) that crows dispersing from outside the urban area contribute to population growth in Seattle: (1) movement patterns of dispersing crows will show that young crows are found in urbanized areas more than expected; and (2) whether or not young crows are drawn into urbanized areas, accounting for immigration and emigration will explain observed population growth. We also tested the alternative hypothesis that growth in CBC numbers derives not from immigration, but rather from movement of crows into the count circle because of roosting or migratory behavior. To test whether a winter count reflected local crow populations during the breeding season, we conducted monthly crow surveys within the Seattle CBC area.

We studied patterns of dispersal by first-year crows from different points on a gradient of urbanization extending from the urban core of Seattle, to the suburbs, to less-developed exurban areas in the foothills of the Cascade Mountains. We described basic characteristics of juvenile dispersal and measured survivorship of first-year crows. We did not describe natal dispersal, because none of the crows we

radiotracked bred as second-year birds, which is normal (McGowan 2001, Verbeek and Caffrey 2002). Rather, we described ex-natal dispersal (*sensu* Kenward et al. 2001), defined as movement away from the natal territory to a new area of activity.

#### METHODS

**Study area.**—We studied crows throughout a ~2,400 km<sup>2</sup> area north, south, and east of Seattle, Washington (Fig. 1; details in Rohila 2002, Withey 2002, Donnelly and Marzluff 2004). The area is within the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyness 1988), which is dominated by coniferous forest.

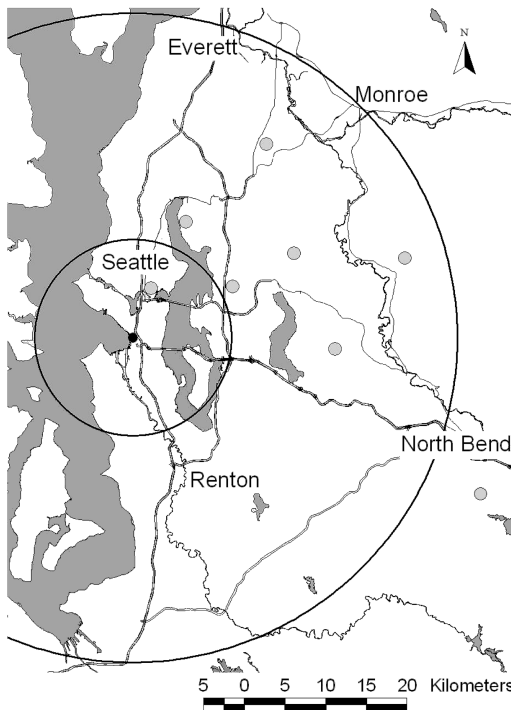


FIG. 1. Map of study area showing capture sites (dots), Seattle CBC area (inner circle, with center shown), and boundary used for calculating breeding area from which juvenile dispersers could immigrate into the urban population (outer arc). The area regularly scanned during radiotracking is approximately bounded by the towns of Everett, Monroe, North Bend, and Renton, and in the west by the edge of Puget Sound (dark shading represents water).

Landcover types were defined following Marzluff et al. (2001a), who described a gradient of urbanization from the most developed extreme of urban (>50% built area), to suburban (30–50% built), to rural and exurban (5–20% built; rural = agricultural matrix, exurban = native forest matrix), to the least-developed wildlands (<2% built).

**Crow survey.**—In October 2000, we initiated a monthly survey of crows in the Seattle CBC circle (centered at 47°36'N, 122°20'W; Fig. 1; National Audubon Society 1972). We divided the circle into eight sections, and for each section mapped a driving route with four to six planned stops. Volunteers surveyed each route at the end of every month through December 2001. Beginning ≥45 min after sunrise to avoid counting crows leaving their roosts, observers counted only crows seen or heard on the route and recorded the time spent counting (equivalent to the CBC's "party hours"). Observers also noted whether detections were made while driving or while walking (5–10 min) at planned stops.

To directly test the influence of observer effort on crow counts, we conducted an experimental survey from 10 to 14 March 2002. Three groups of observers counted crows in the same area within the Seattle CBC, but for different numbers of hours (3–8 h). The survey showed a close linear relationship between number of crows counted and time spent counting ( $r^2 = 0.99$ ,  $F = 197$ ,  $df = 1$  and  $1$ ,  $P < 0.05$ ), so we divided crow counts by party hours as a measure of relative abundance.

We calculated the proportion of active nests in the incubation stage on the University of Washington campus ( $n = 34$ ) and in downtown Seattle ( $n = 21$ ) on the date of each survey in 2001. We correlated that proportion with changes in monthly counts during the breeding season to determine if lower counts correlated with incubation.

**Capture sites.**—We captured 56 juvenile crows at eight sites from 8 July to 7 September in 2000 and 2001 (Fig. 1; mean capture date 7 August ± 2.6 days) for radiotagging. We identified juveniles before capture by behavior (begging for food from adults) and after capture by brownish feathers and bright-pink upper mandible lining (Emlen 1936, Pyle 1997). In trapping efforts separate from radiotagging, we captured 172 crows on 25 distinct trapping days between November and March, 1997 to 2001, at three sites: the

University of Washington campus in Seattle, a suburban neighborhood, and an exurban recreation area. To obtain an unbiased sample for age-ratio determination, we used captures for this sample only if specific crows were not targeted (e.g. breeding adults). We aged crows as young (as described above) or adult (black mouth and black to glossy black feathers). For all captures, we used a Netlauncher (Coda, Mesa, Arizona).

*Marking and radiotracking.*—In the group of 56 juvenile crows captured for radiotagging, we color-banded each crow and sent blood samples for DNA sexing to Zoogen (Davis, California). We used a backpack harness made of teflon (modified for crows following Buehler et al. 1995) to attach 11-g radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota). We attempted to relocate every radiotagged crow at least once a week during the entire 15-month expected life of the transmitter by scanning the area in which the individual was last found and moving outward. We also scanned for crows during the day from high points in the study area (signals could be heard from  $\leq 28$  km away), and at night by visiting five known communal roosts.

When we located a signal, we homed toward it until we located the crow or obtained a signal on the receiver without using an antenna (audible only within  $\sim 80$  m of the transmitter). We also used triangulation methods to obtain a relocation when access to the crow's location was impossible (4% of relocations), and used LOCATE II software (Nams 2000) to calculate coordinates. For each relocation, we recorded Universal Transverse Mercator (UTM) coordinates using a global positioning system (GPS) unit, and the date and type of relocation; for visual relocations, we recorded crow activity and number of other crows present when first observed. If the crow was observed foraging, we classified the food eaten into six categories: human refuse, food from bird-feeders, below-ground invertebrates, road kill, agricultural waste, and invertebrates on native vegetation.

*Landcover classification.*—The University of Washington's Urban Ecology Research Laboratory classified landcover data using a  $30 \times 30$  m 1999 Landsat image divided into eight classes:  $<35\%$  paved,  $35\text{--}75\%$  paved,  $>75\%$  paved, forest, grass-crops-shrubs, bare soil, clearcuts, and water (Alberti et al. 2002). We used ARCVIEW, version 3.2 (Environmental Systems Research

Institute, Redlands, California), FOCAL PATCH extension (Marzluff et al. 2004), to calculate number of pixels of each landcover class in a  $1\text{-km}^2$  circular area around each crow relocation point. We calculated the "percentage of urban landcover" for each crow relocation point using: (number of pixels  $35\text{--}75\%$  paved + number of pixels  $>75\%$  paved) / ([sum of all pixels] - number of water pixels).

To characterize landscape types in the study area, we first created a new sampling-point theme over the entire study area, using FOCAL PATCH in ARCVIEW. Points were separated from each other by 900 m in each cardinal direction. We then calculated percentage of urban landcover (using the calculation above) for each sampling point. We created a grid with  $900 \times 900$  m pixels, each of which took on the value of percentage of urban landcover for the sampling point at its center. We defined pixels of that grid as "urban" ( $>70\%$  urban landcover), "suburban" ( $15\text{--}70\%$  urban landcover), and "exurban" ( $<15\%$  urban landcover).

*Statistical analyses and definitions.*—We categorized juvenile crows' status as "local," "disperser," "transmitter failure," "unknown," or "early death" based on the following criteria. We designated crows' status as "transmitter failure" if we (1) resighted them with radiotransmitter intact, but could not detect a signal ( $n = 4$ ); or (2) could not relocate them after 31 August (the earliest date that we relocated crows  $>1$  km away from their capture site;  $n = 4$ ). We categorized crows' status as "unknown" if they were detected at least once after 31 August but not three or more times after 30 September and were not known to have died ( $n = 9$ ). We categorized their status as "early death" if they were not relocated alive after 30 September ( $n = 6$ ), because those crows never had the chance to exhibit ex-natal dispersal. We used 30 September as our cut-off date for expected independence, on the basis of fledgling behavior and the time of return to the large communal roosts at night (J. C. Withey and J. M. Marzluff pers. obs.).

The remaining 33 crows were relocated at least three times after 30 September, including 15 crows that were found dead before April of the following year (in addition to the early deaths). We categorized those as "local" or "disperser" using two criteria. First, we used the site fidelity test in the ARCVIEW extension ANIMAL MOVEMENT, version 2.0 (Hooge and Eichenlaub 1997). The test compared

actual movement paths with 100 simulated random-walk paths and designated actual paths as random, more constrained than expected, or more dispersed than expected ( $P < 0.05$ ). If the path was more dispersed than expected, the crow was designated as a disperser ( $n = 2$ ). Movement paths could be more constrained than expected in two cases: if the crow generally moved around near its natal territory (we would designate that crow as a local), or if the crow first dispersed away from its natal territory and then moved around in a new center of activity (we would designate it as a disperser). To distinguish between the two possibilities, we measured the distance between the capture location and the mean north and east coordinates calculated from relocation points after 30 September of the capture year (to exclude relocations from the fledgling dependence period before 30 September). The mean coordinates, which we called the "post-September center of activity," were not intended to provide a precise settlement location, but gave a general indication of whether a crow had moved away from its natal territory. If the calculated dispersal distance was  $>2.0$  km, the crow was considered a disperser. If the distance was  $<1.5$  km, the crow was considered a local (no dispersal distances were between 1.5 and 2.0 km). On the basis of those criteria, 16 of the crows with more constrained movement paths were locals and 3 were dispersers. Likewise, 2 of the crows with random movement paths remained within 1.5 km of their natal territory and were designated as locals, and 10 moved  $>2.0$  km and were designated as dispersers (Table 1).

To test whether deaths of known-fate birds were more likely in any capture location type, we used Pearson's chi-square test. To compare dispersal distances among types of natal territories, we used a one-way ANOVA with distance as the dependent variable and location type (urban to exurban) as the only factor. We tested differences in young:adult ratios between urban and suburban-exurban locations using a chi-square test with Cochran's correction for continuity (Haber 1980). We used Fisher's exact test to test for (1) sex bias in the numbers of locals and dispersers surviving until at least April of the following year and (2) whether the proportion of crows found in habitat more urban than expected differed with regard to natal territory habitat (urban versus non-urban). We used SPSS for WINDOWS, version 11.0 (SPSS, Chicago, Illinois) to calculate  $P$  values for Fisher's exact test, Pearson's chi-square values, and  $F$  and  $P$  values for the ANOVA.

We calculated Kaplan-Meier survival estimates for crows on the basis of staggered entry and censored observation design (Kaplan and Meier 1958, Winterstein et al. 2001). We confirmed death by retrieving remains ( $n = 13$ ) or localizing a stationary signal  $>2$  times without observing crows ( $n = 7$ ). If we did not confirm death, we used the last date we heard the signal as the date to "censor" that individual. We removed from analysis crows that were never found after capture ( $n = 4$ ). We used EGRET for WINDOWS (Cytel, Cambridge, Massachusetts) for Kaplan-Meier survival estimates. To compare survivorship of males with that of females,

TABLE 1. Dispersal status (see text) of crows in different natal territory types for two groups: all crows ( $n = 56$ ) and crows confirmed alive past April of their second year ( $n = 18$ ). Dispersal status of surviving crows is also presented by sex, not including one crow of unknown sex (a local).

Natal territory type ( $n$ )	Local	Disperser	Early death	Transmitter failed	Unknown
<b>All crows</b>					
Non-urban (43)	12	12	5	7	7
Urban (13)	6	3	1	1	2
Total (56)	18	15	6	8	9
<b>Crows surviving past April</b>					
Non-urban (12)	9	3			
Urban (6)	3	3			
Female	0	5			
Male	11	1			



we used a log rank test in SPSS. Values reported are means  $\pm$  SE.

*Calculating the effect of dispersal.*—We used two approaches to model the effect of immigration and emigration on urban population growth. In both, we used demographic rates estimated by Marzluff et al. (2001b) using mostly Washington data (Appendix), changed survivorship of juveniles to that estimated here, and calculated standard deviations for fecundity based on the original nesting results (J. C. Withey and J. M. Marzluff unpubl. data). We calculated the probability of dispersal of crows from suburban and exurban areas into the urban population by using the number of crows captured in natal territories outside the Seattle CBC circle that were relocated inside the circle after December of their hatch year ( $n = 4$ ). To be conservative, we divided that number by the total number of crows captured in those areas ( $n = 43$ ). For the urban area, we used the number of crows relocated outside the Seattle CBC circle after December ( $n = 2$ ), divided by the number of urban captures ( $n = 13$ ; Table 1).

To simulate population growth, we used RAMAS GIS (Applied Biomathematics, Setauket, New York; Akcakaya 1999). We first modeled the growth of an urban population, given local birth and death rates, in the absence of dispersal. To account for immigration and emigration, we initially modeled growth of a single urban population and increased the fecundity of adult crows as if the net influx of crows (calculated in Appendix) were added to the reproductive output of the breeding population. In our second approach, we modeled the growth of two local populations, "urban" and "non-urban," in the metapopulation mode of RAMAS GIS. We used two methods for estimating initial population sizes. The first was based on the estimated number of breeding pairs in urban habitat inside the CBC circle (for the "urban" population) and the number of pairs in suburban habitat outside the CBC circle (for the "non-urban" population). The second method combined urban and suburban breeding pairs inside the CBC circle for "urban," and combined suburban and exurban breeding pairs outside the CBC circle for "non-urban" (see Table A1). We used dispersal rates between the two populations estimated (in the present study) for the first-year age class, and modeled population growth by allowing dispersal in (1) the first-year age class only, (2) first- and second-year age classes, and (3) first- through

third-year age classes. All models included demographic stochasticity. The metapopulation model included within-population correlation of fecundity and survival, and we varied between-population correlation of vital rates from 0 to 0.9. We ran one series of simulations as described, which assumed that immigrants stayed in their new local population to breed. To simulate the return of urban immigrants to the non-urban population to breed, we used the "translocate" management action to remove the proportion of the urban population that immigrated the previous year, based on our calculations of urban immigrants shown in the Appendix.

*Random-walk simulations.*—For each dispersing crow, we simulated 100 correlated random walks in ARCVIEW using ANIMAL MOVEMENT, version 2.0 (Hooge and Eichenlaub 1997), in which actual movement lengths from one relocation to the next were duplicated, but at random turning angles. The random-walk paths were constrained only by the Puget Sound to the west (Fig. 1), because we had no evidence of crows moving across that water body. We calculated the percentage of urban landcover for an area of 1 km<sup>2</sup> (see above) around each endpoint of the 100 random-walk paths for each disperser, creating a distribution of randomized endpoints and their associated percentage of urban landcover. Each disperser had a unique distribution. We calculated the mean percentage of urban landcover of the last three relocations for each crow (rather than just the last one, to avoid bias from a single atypical relocation area in which the crow happened to be last relocated). Then, we ranked the actual percentage of urban landcover of each crow's endpoint within its distribution of 100 random-walk endpoints (where a rank of 1 would be less urban than any randomized endpoint, a rank of 50 would be the median of the randomized endpoints, and a rank of 100 would be more urban than any randomized endpoint). We used a binomial test in SPSS (SPSS, Chicago, Illinois) to test whether more crows than expected by chance were found in more urbanized habitat.

## RESULTS

*Crow survey.*—Monthly counts of crows in the Seattle CBC circle were similar, though variable, from October 2000 to March 2001, and then markedly lower in April (Fig. 2A). The low count

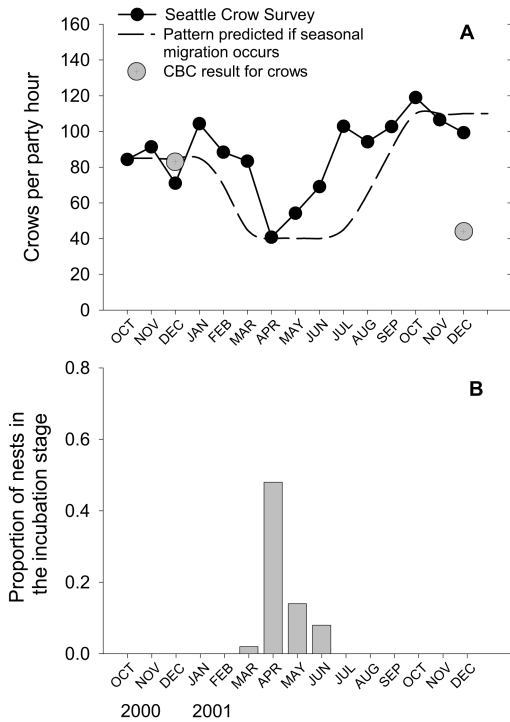


FIG. 2. (A) Monthly crow survey in Seattle CBC circle, with shape of predicted results if crows migrate seasonally into the CBC area. The predicted curve is based on movement of crows back to breeding territories outside the CBC area by late March, with crows returning to the Seattle area between August and October. Results for crows from the 2000 and 2001 Seattle CBCs are also shown. (B) Proportion of known nests in the incubation stage for each survey date.

in April was followed by an increase from May to July and then similarly high counts through December, again with some variation. The observed counts were different from the pattern predicted by seasonal migration, especially in March, when crows begin nest-building in our study area, and June to August, when crows were still on territories feeding fledglings.

The decrease in number of crows per party hour during April of the monthly survey occurred while 48% of known crow nests were in the incubation stage (Fig. 2B). Overall, numbers of crows per party hour in the monthly survey were related negatively to the proportion of nests in incubation ( $r^2 = 0.56$ ,  $F = 18.7$ ,  $df = 1$  and  $13$ ,  $P = 0.001$ ). Otherwise, counts in the winter months

in our monthly survey (December to February) were similar to nonwinter counts outside the nesting season (July to November; Fig. 2A).

In December 2000, the Seattle CBC result for crows was similar (83 crows per party hour) to the monthly survey result; but in December 2001, it was much lower (44 crows per party hour; Fig. 2A). The monthly survey indicated a ~25% per-year increase (28% increase,  $r^2 = 0.10$  if all months were used; 25% increase,  $r^2 = 0.46$  if April to June were excluded), higher than the long-term average of 7% per year in the Seattle CBC since 1938 ( $r^2 = 0.76$ ,  $F = 176$ ,  $df = 1$  and  $54$ ,  $P < 0.001$ ; year coefficient =  $0.030 \pm 0.002$ ,  $P < 0.001$ ).

*Juvenile dispersal.*—Of all 56 radiotagged crows, 27% ( $n = 15$ ) dispersed  $\geq 2$  km from their natal territory, and 32% ( $n = 18$ ) were locals (Table 1). The center of activity of crows after 30 September ( $n = 31$  with sufficient relocations) was a median 1.5 km ( $\bar{x} = 4.7 \pm 1.1$  km, range = 0.2–22.2 km) from their capture location. The distance moved to their ex-natal center of activity was similar for crows from different capture location types ( $F = 1.0$ ,  $df = 3$  and  $11$ ,  $P = 0.41$ ). Dispersing crows moved a median distance of 10.4 km ( $\bar{x} = 9.1 \pm 1.7$  km, range 2.1–22.2 km); locals moved 0.6 km ( $\bar{x} = 0.7 \pm 0.1$  km, range = 0.2–1.5 km). Twenty-eight percent ( $n = 12$ ) of those captured outside the urban locations dispersed, and 23% ( $n = 3$ ) of crows captured in urban locations dispersed (Table 1). Four of 43 crows (9%) radiotagged outside the Seattle CBC circle were relocated inside the circle, whereas 2 of 13 crows (15%) radiotagged inside were found outside the circle.

Probability of survival at one year after capture was 0.45 (95% C.I. = 0.27 to 0.61); males and females did not differ (log rank test,  $P = 0.95$ ). Eighteen crows (32% of all radiotagged) were known to have survived until at least the following April; of those survivors, six were dispersers (Table 1). Of that smaller group of survivors, females were more likely to be dispersers than males (Fisher's exact test,  $P < 0.01$ ). In addition, we observed all the males ( $n = 11$ ) that stayed on their natal territory "helping" their parents with at least one of the following behaviors: (1) defending the territory from other crows, (2) locating and mobbing predators, or (3) bringing food to the nest. Similar proportions of crows radiotagged in urban (23%,  $n = 3$  locals) and suburban to exurban habitat (21%,  $n = 9$  locals; Table 1) helped their parents.

*Random-walk simulations.*—We found 10 of the 15 dispersers in habitat with higher urban land-cover than expected by simulation, including 7 of the 12 dispersers from non-urban natal territories and all 3 crows dispersing from the urban site (Table 2). However, for our sample of the population, the tendency to move toward urban areas was not significantly greater than expected by chance (binomial test,  $P \geq 10$ ) = 0.15). The proportion of crows found in more-urban habitat than expected was similar for crows dispersing from non-urban versus urban sites (Fisher's exact test,  $P = 0.26$ ). Combined probability of a non-urban disperser ending a random walk inside the Seattle CBC circle was 0.08, which is similar to the observed frequency of 1 in 12 (8.3%) that actually ended their movements inside the circle (Table 2). Four of the non-urban dispersers (33%) were found inside the Seattle CBC circle after December of their hatch year.

*Foraging and flocking by juvenile crows.*—We observed 73 foraging events, and most were of crows eating refuse (40%) or below-ground invertebrates (37%, on lawns and sports fields; Fig. 3). The former category included crows eating from dumpsters and garbage cans, in parking lots, and on roads. We rarely observed crows foraging on native vegetation (10%), and crows on all points of the urbanization gradient used anthropogenic sources of food (Fig. 3).

Flocks of crows in urban locations caught between November and March included more young birds than those in suburban or exurban areas. The young:adult ratio was higher in crows captured at urban locations (97 young: 23 adults) than in crows captured at suburban and exurban locations (30 young: 22 adults,  $\chi^2_c = 9.1$ ,  $P = 0.003$ ). We observed dispersers in the company of more crows (median = 8 others,  $\bar{x} = 20.1 \pm 3.5$ ) than locals (median = 4 others,  $\bar{x} = 11.4 \pm 2.0$ , Mann-Whitney  $U$ -test,  $n = 374$  relocations,  $Z = 15.9$ ,  $P < 0.001$ ).

*Contribution of dispersers to population growth.*—Greater immigration than emigration produced a net gain to the urban crow population (as indexed by the Seattle CBC area) of 22% (Appendix). That occurred despite a low probability of any individual crow dispersing into the Seattle CBC area (0.09) and a greater probability of emigration (0.15), because of the large estimated number of breeders outside the Seattle CBC and the greater productivity of suburban–exurban than of urban breeders (Appendix).

Simulations of urban population growth, based on the best-known estimates of demographic rates, show a very mild increase (0.6% per year) in the absence of immigration (Fig. 4A). However, modeling dispersal into and out of the urban population produced growth in the urban population close to that observed over the past 50 years in the Seattle CBC (Fig. 4B, C). That occurred whether effects of dispersal were modeled as an increase in the juvenile cohort of a single population (Fig. 4B) or as movements between two local populations in a metapopulation model (Fig. 4C). Simulating the return of urban immigrants to the non-urban population to breed reduced average growth rates, but not dramatically (Table 3). Assuming that immigrants stayed in the urban population to breed and that dispersal was by first- and second-year age classes produced growth rates most similar to those observed (Table 3 and Fig. 4C).

## DISCUSSION

*Reliability of a winter crow count.*—If seasonal movements of crows into the Seattle area boost winter counts, we should see counts drop before March, when crows in our study area start to build nests, and remain low until August or September, when crows start moving away from their breeding territories (Fig. 2A). The shape of the actual counts is similar to that prediction, but the counts are very different in two key months: March, when the actual count of 83 crows per party hour was similar to the counts in the previous five months; and July, when the actual count of 103 crows per party hour marked a return to high counts (Fig. 2A). Those results cannot be explained by crows that are moving seasonally, because they would have already moved out of the CBC area by late March and would not have returned as early as July. Rather, the decrease in actual counts from April to June correlates with the proportion of nests in the incubation stage in our study area (Fig. 2B). Our inability to see females that are incubating eggs or brooding young nestlings explains most of the ~50% decrease in the actual April count (to 41 crows per party hour). Therefore, in our study area, a long-term winter count of crows appears to accurately reflect populations during other times of the year. Our results resemble comparisons of CBCs and Breeding Bird Surveys, which show good



TABLE 2. Characteristics of juvenile dispersers ( $n = 15$ ) from different natal-territory types. Superscript after "date of last relocation" reflects whether bird was alive (a), dead (d), or unknown fate (u) after one year. "Urban landcover at end" is the mean percentage of urban landcover of the last three relocations of each disperser. We also present the median percentage of urban landcover of each disperser's 100 random-walk endpoints, and the rank of the actual urban landcover of each disperser among its 100 randomized endpoints (rank is from smaller percentage of urban to greater percentage of urban). Ranks higher than expected (>50) are shown in bold format. "Probability of endpoint inside CBC circle" is based on the number of random-walk endpoints (of 100) that were inside the Seattle CBC circle.

Natal territory type	Date of capture	Date of last relocation	Inside CBC circle after December?	Inside CBC circle at end?	Urban landcover		Median urban landcover of random-walk end		Rank of observed endpoint among random-walk endpoints		Probability of random-walk endpoint inside CBC circle
					at capture	at end (mean of last three)	end	end	random-walk endpoints	random-walk endpoints	
Exurban	8/10/00	1/11/01 <sup>u</sup>	✓		6%	30%	4%	90	90	0.00	
	8/10/00	5/18/01 <sup>a</sup>			6%	6%	2%	66	66	0.01	
	8/15/00	11/2/00 <sup>d</sup>			14%	9%	1%	94	94	0.00	
	8/11/00	11/17/00 <sup>u</sup>			8%	9%	12%	33	33	0.00	
Suburban	8/18/00	10/31/00 <sup>u</sup>			22%	10%	12%	41	41	0.00	
	8/18/00	9/4/01 <sup>a</sup>	✓		22%	50%	11%	83	83	0.07	
	7/26/01	1/21/02 <sup>d</sup>	✓	✓	19%	100%	3%	100	100	0.09	
	7/26/01	1/30/02 <sup>u</sup>			22%	9%	13%	37	37	0.00	
	8/10/01	1/1/02 <sup>u</sup>			23%	8%	13%	39	39	0.05	
	8/21/01	2/15/02 <sup>d</sup>	✓		9%	39%	5%	88	88	0.05	
Urban	7/17/00	9/4/01 <sup>a</sup>			20%	76%	52%	82	82	0.40	
	8/1/01	12/6/01 <sup>d</sup>			33%	6%	42%	14	14	0.26	
	8/19/00	8/31/01 <sup>a</sup>	✓		77%	57%	25%	80	80	0.12	
	8/25/00	5/2/01 <sup>a</sup>	✓		82%	61%	47%	63	63	0.31	
	7/28/01	4/1/02 <sup>a</sup>	✓	✓	78%	85%	61%	80	80	0.53	

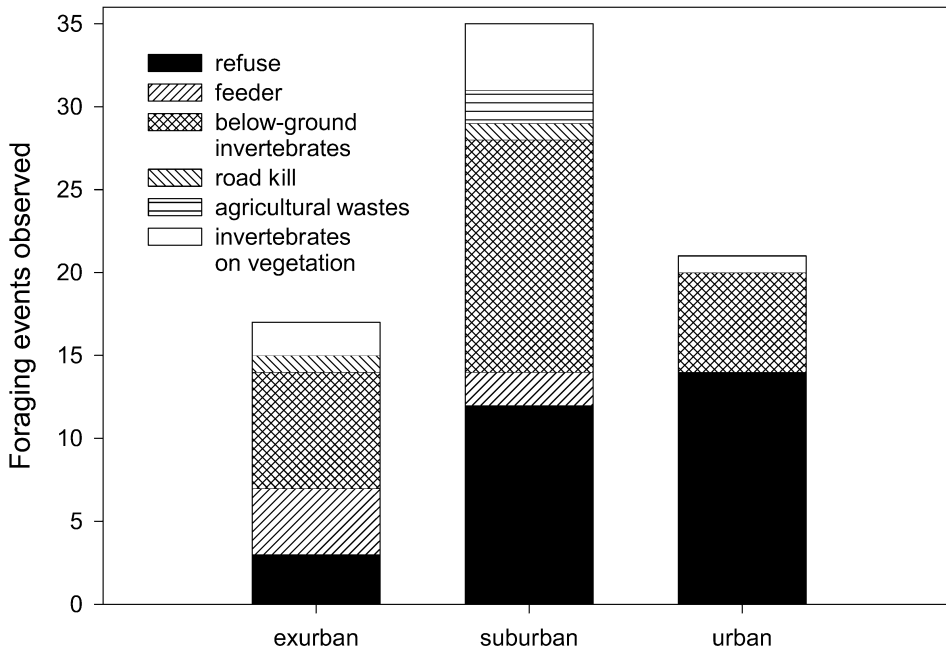


FIG. 3. Numbers of foraging events observed in different habitats (exurban = <15% urban landcover, suburban = 15–70% urban landcover, urban = >70% urban landcover) by crows with at least three relocations after September 30th. Type of foraging event classified by the food item (feeder = food from bird feeder).

concordance for a variety of species (Butcher et al. 1990, Sauer et al. 1994, Wells et al. 1996, Greenberg and Droege 1999).

Although we are confident in using CBC results as a long-term indicator of population trend for crows in Seattle, the single-year drop in the Seattle CBC crow total (Fig. 2A) highlights a potential problem with CBC results for a communally roosting species. Observers in 2001 counted crows leaving a major roost in a different way than was done the year before, which accounted for 84% of the decrease from 2000 to 2001 (H. Opperman pers. comm.). We advise keeping records of roost and nonroost counts distinct if the intention is to use CBC results for local population studies. For that reason, we started our monthly counts well after sunrise, after crows had left the roost.

*Patterns of juvenile dispersal.*—The process of avian dispersal begins when an individual fledges from its nest, and is then guided by a series of decisions: where to move, what to eat, with whom to associate, and ultimately where to attempt breeding. In our study area, juvenile

crows moved  $\leq 28$  km away from their natal territory during their first year of life. Mortality was >50%. Some individuals that lived until the following breeding season stayed on their natal territory; those were all males that helped their parents defend territories, locate and scold predators, or feed young. Others dispersed from their natal territory; most of those were female. Of the 12 dispersers hatched in suburban or exurban habitat, 4 were found inside the Seattle CBC circle after December as they dispersed (Table 2).

Of the crows that survived until the start of the following breeding season, females were more likely to disperse and males were more likely to be helpers (Table 1), which supports the prevalence of female-biased dispersal in birds reported by Greenwood (1980) and supported by Clarke et al. (1997). Parr (1997) found similar numbers of both sexes as helpers in Michigan, but males were more likely to help for more seasons than females. McGowan (2001) also found males more likely to help and eventually to inherit their natal territories. Caffrey (1992), on

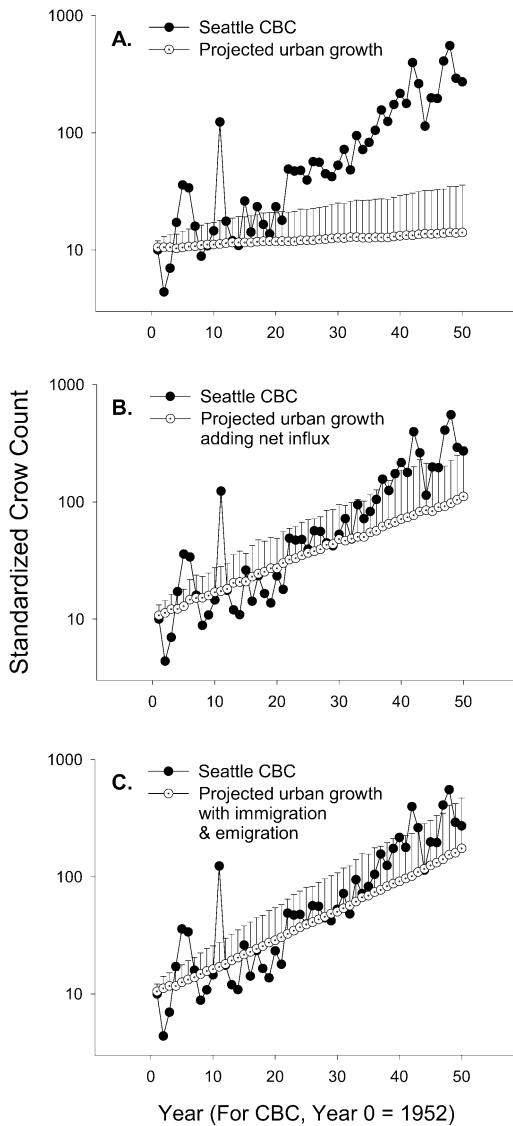


FIG. 4. Seattle CBC results and projections of urban population growth based on (A) local births and deaths alone, (B) modeling of net influx of dispersing crows as adding to urban reproductive output, and (C) modeling of immigration and emigration between two local populations, urban and non-urban. Seattle CBC results are crows per party hour from 1952 to 2001, standardized to start at 10 crows per party hour in year 0 (1952). The projected growth lines are average results ( $\pm 1$  SD) based on 1,000 simulations in RAMAS GIS, standardized to begin at 10 crows in year 0.

the other hand, found female crows in California more likely to stay and help than to disperse.

Two-thirds of the dispersing crows ended up in areas more urbanized than expected from random walk simulations, but that proportion was not different from the expected proportion of 50%, given our small sample size ( $n = 15$ ). It is possible that some crows are drawn into the urban areas, as one might expect from our population-growth simulations, but we were unable to detect a population-wide tendency to move into urban areas. We suspect that urban areas vary in their attractiveness to juveniles, perhaps because of individual differences in status, hunger, social partners, and resource quality or availability. Urban areas attract some juveniles: 8 of the 10 moving into areas more urbanized than expected (ranks 50 and above) were in the higher, more urban end of the distribution (ranks 80 and above; Table 2). In addition, all of the dispersers still alive after one year ( $n = 6$ , Table 2) were in areas more urbanized than expected. Although those results are suggestive, we do not currently have definitive evidence that crows are consistently being drawn into the city.

Our observations of dispersing crows indicate that crows are not moving randomly. They seem to “hopscotch” across the landscape. We often found individual crows in an area for a particular period, then in a different area, then perhaps in yet another area. Crows moving in such a manner may be attracted to more urban areas, given that the Seattle area is characterized by multiple centers of urbanization (Alberti 2001).

Juveniles routinely joined flocks of crows that included other nonbreeders. Such crows may be more likely to achieve dominant status there than with family groups and take advantage of breeding opportunities (Zack and Stutchbury 1992). Crows we followed tended to be in bigger groups if they were dispersers than if they were locals, which could also give them the opportunity to interact with more future mates that are unrelated. Caffrey (1992) described a resident nonbreeding flock in Los Angeles, but we rarely found dispersers with other marked crows, so we were not able to determine flock membership status. Dispersing crows were probably taking advantage of the increased opportunity to forage at a variety of anthropogenic food sources, whether landfills or refuse from urban

TABLE 3. Average population growth rates from simulations in RAMAS GIS that account for immigration and emigration. "Number of populations" indicates whether we modeled a single population by increasing fecundity of urban breeders (see Appendix for details) or modeled two local populations in the metapopulation mode. Initial population size was calculated from the estimated number of breeding pairs in urban and suburban habitat inside the Seattle CBC circle (Table A1; simulations with urban habitat only were similar). For the two-population model, results of simulations in which different age classes were allowed to disperse are presented, showing whether urban immigrants stayed in the urban population ("stay") or returned to the suburban population ("leave") to breed. We used a value of 0.9 for the correlation of variation in vital rates between local populations for the two-population results shown; average growth rates using correlation values of 0 and 0.5 were in the same range.

Number of populations	Occurrence of dispersal by age class					
	First year only		First and second year		First through third year	
	Stay	Leave	Stay	Leave	Stay	Leave
1	5.0% <sup>a</sup>	–	–	–	–	–
2	5.3%	4.7%	5.8% <sup>b</sup>	5.5%	5.7%	5.4%

<sup>a</sup>Result shown in Figure 4B.

<sup>b</sup>Result shown in Figure 4C.

and suburban businesses. Given that refuse was a common food item for crows in urban and suburban locations (Fig. 3), foraging opportunities may explain why some crows respond positively to urbanization as they disperse.

As with most studies of dispersal (Koenig et al. 1996), we have likely missed some long-distance dispersal events despite using radio-telemetry and covering a relatively large area (any of the nine crows of "unknown" status could have left the study area). We followed five juvenile crows that dispersed away from their natal territory and died before the next breeding season. Including those crows among dispersers may overestimate dispersal, because we do not know whether they would have returned to their natal territory if they had the chance; Caffrey (1991) found that half the crows that left her study area during the winter returned in the following breeding season. In the present study, one crow moved 10 km away from his natal territory between September and January, into more urbanized habitat, but returned to his natal territory. However, our observation of color-banded (but not radiotagged) juveniles

suggests that few dispersers ever return to natal territories. Even with our small sample size of juvenile crows known to have survived until the following breeding season, we observed dispersers from both non-urban (3 of 12) and urban (3 of 6) capture locations (Table 1); all were in habitat more urban than expected. We also relocated one non-urban disperser within 1 km of his ex-natal center of activity in July of his third year, which indicates that crows may continue to use the dispersed-to areas during their second and third years.

*Consequences of juvenile dispersal.*—Even though all juvenile crows do not appear to be drawn to urban areas, higher reproductive success outside the city and sufficient dispersal into it leads to urban population growth, which explains most of the observed rate of increase (Fig. 4). Our calculations depend on certain assumptions regarding demographic rates and the area available to breeding crows, but we were conservative in choosing figures and used estimates from local studies as much as possible. Our estimate of juvenile survival was very similar to that found by McGowan



(2001) in New York (0.45 compared with 0.48). The trend of higher breeding density but lower reproductive output as one moves into urban centers from exurban and suburban areas is supported by studies from Seattle, New York, and Madison, Wisconsin (Marzluff et al. 2001b, McGowan 2001). Modeling urban population growth under a variety of different scenarios resulted in average growth rates similar to that observed in the CBCs (Table 3 and Fig. 4). Despite the higher probability of emigration than immigration, the incoming tide of crows from suburban and exurban habitat more than makes up for the crows leaving the urban population. That we trap more young per adult from November to March at urban locations than at suburban and exurban locations further argues for a net influx of juveniles into the urban population. Without such an influx, we would expect to trap more young per adult outside of urban areas, because suburban and exurban pairs out-reproduce urban pairs. Our modeling results suggest that the scenario most consistent with observed growth is that dispersal occurs in the nonbreeding age classes, and that those urban immigrants stay to breed (Table 3). We consider that scenario a prediction we will have to test to understand crow population dynamics more completely.

Crows in the greater Seattle area appear to have surpassed population growth limits imposed by local fecundity and survival by taking advantage of their mobility. They are able to exploit productive breeding habitat in suburbs and exurbs, as well as anthropogenic food sources in urban areas. As human population growth and residential development continue, the area of breeding habitat will expand and breeding densities will increase as areas become more urbanized. In the Puget Sound region from 1991 to 1999, landcover change has created 11.5 km<sup>2</sup> of habitat per year supporting higher crow densities (forest conversion to a mixture of forest, grass, and urban landcover; Alberti et al. 2002).

If prebreeding populations of crows in the city are supplemented from the suburbs, an interesting question that remains is, "where do they go to breed?" McGowan (2001) found that crows almost always nested in the same habitat type in which they were hatched (suburban or rural). Because we have observed movements into and out of urban populations, a study of natal dispersal here might yield different results.

A crow hatched in suburban habitat that disperses into the city and survives to breeding age will have been exposed to different points on the urban gradient; will it use that knowledge in selecting breeding habitat? A number of bird species respond to reproductive success of conspecifics in selecting mates, breeding sites, or habitat (Marzluff and Balda 1988, Danchin et al. 1998, Doligez et al. 1999, Schjorring et al. 1999, Brown et al. 2000), and crows seem equipped both to gather such information and to use it. Our estimates of reproductive success suggest that a young crow would profit from returning to the suburbs to breed. Resolution of that point requires further study, but either sort of breeding-habitat selection will continue to fuel exponential growth of urban crow populations.

#### ACKNOWLEDGMENTS

We appreciate the effort of everyone who has participated in the irreplaceable Christmas Bird Counts and monthly crow surveys in Seattle. H. Opperman and the Seattle Audubon Society helped us obtain Seattle CBC data, start the monthly survey, and recruit volunteers. M. Moser, K. Smith, R. Vincent, C. Ianni, T. Piper, and R. Seguine helped collect field data on crows. P. Hurvitz provided invaluable GIS advice and the FOCAL PATCH extension. Comments by W. Koenig, C. Caffrey, and an anonymous reviewer improved the manuscript. W. Koenig's suggestion that we conduct random-walk analyses was especially valuable. A University of Washington Graduate School Fund for Excellence and Innovation stipend, Riffe Family Endowed Fellowship, NASA Space Grant Graduate Fellowship, University of Washington Sigma Xi grant, and National Science Foundation Graduate Research Fellowship supported J.C.W. while he conducted the study and wrote this manuscript.

#### LITERATURE CITED

- AKCAKAYA, H. R. 1999. RAMAS GIS. Linking Landscape Data with Population Viability Analysis. Applied Biomathematics, Setauket, New York.
- ALBERTI, M., E. BOTSFORD, AND A. COHEN. 2001. Quantifying the urban gradient: Linking urban planning and ecology. Pages 89–115 in *Avian Ecology and Conservation in an*

- Urbanizing World (J. M. Marzluff, R. Bowman, and R. Donnelly, Eds.). Kluwer Academic Publishers, Norwell, Massachusetts.
- ALBERTI, M., R. WEEKS, D. BOOTH, K. HILL, S. COE, AND E. STROMBERG. 2002. Landcover change analysis for the Central Puget Sound Region. Final report for the Puget Sound Water Quality Action Team, Seattle.
- NATIONAL AUDUBON SOCIETY. 1972. 72nd Annual Christmas Bird Count, Seattle, Washington. *American Birds* 26:489–490.
- BROWN, C. R., M. B. BROWN, AND E. DANCHIN. 2000. Breeding habitat selection in Cliff Swallows: The effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology* 69:133–142.
- BROWN, J. H., AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445–449.
- BUEHLER, D. A., 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. *Journal of Field Ornithology* 66:173–180.
- BUTCHER, G. S., M. R. FULLER, L. S. McALLISTER, AND P. H. GEISSLER. 1990. An evaluation of the Christmas Bird Count for monitoring population trends of selected species. *Wildlife Society Bulletin* 18:129–134.
- CAFFREY, C. 1991. Breeding group structure and the effects of helpers in cooperatively breeding western American Crows. Ph.D. dissertation, University of California, Los Angeles.
- CAFFREY, C. 1992. Female-biased delayed dispersal and helping in American Crows. *Auk* 109:609–619.
- CLARKE, A. L., B.-E. SÆTHER, AND E. RØSKAFT. 1997. Sex biases in avian dispersal: A reappraisal. *Oikos* 79:429–438.
- DANCHIN, E., T. BOULINIER, AND M. MASSOT. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology* 79:2415–2428.
- DANIELS, S. J., AND J. R. WALTERS. 2000. Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. *Condor* 102:482–491.
- DOLIGEZ, B., E. DANCHIN, J. CLOBERT, AND L. GUSTAFSSON. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the Collared Flycatcher. *Journal of Animal Ecology* 68:1193–1206.
- DONNELLY, R., AND J. M. MARZLUFF. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology* 18:733–745.
- EMLEN, J. T., JR. 1936. Age determination in the American Crow. *Condor* 38:99–102.
- FRANKLIN, J. F., AND C. T. DYRNNESS. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis.
- GREENBERG, R., AND S. DROEGE. 1999. On the decline of the Rusty Blackbird and the use of ornithological literature to document long-term population trends. *Conservation Biology* 13:553–559.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- HABER, M. 1980. A comparison of some continuity corrections for the chi-squared tests on 2×2 tables. *Journal of the American Statistical Association* 75:510–515.
- HOBSON, K. A., K. P. McFARLAND, L. I. WASSENAAR, C. C. RIMMER, AND J. E. GOETZ. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable isotope analyses of feathers. *Auk* 118:16–23.
- HOOG, P. N., AND B. EICHENLAUB. 1997. ANIMAL MOVEMENT extension to ARCVIEW, version 1.1. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage.
- HORN, P. L., J. A. RAFALSKI, AND P. J. WHITEHEAD. 1996. Molecular genetic (RAPD) analysis of breeding Magpie Geese. *Auk* 113:552–557.
- KAPLAN, E. L., AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistics Association* 53:456–481.
- KAREIVA, P. 1990. Population dynamics in spatially complex environments: Theory and data. *Philosophical Transactions of the Royal Society of London, Series B* 330:175–190.
- KENWARD, R. E., S. S. WALLS, AND K. H. HODDER. 2001. Life path analysis: Scaling indicates priming effects of social and habitat factors on dispersal distances. *Journal of Animal Ecology* 70:1–13.
- KOENIG, W. D., P. N. HOOG, M. T. STANBACK, AND J. HAYDOCK. 2000. Natal dispersal in the cooperatively breeding Acorn Woodpecker. *Condor* 102:492–502.

- KOENIG, W. D., D. VUREN, AND P. N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 11:514–517.
- LANG, J. D., L. A. POWELL, D. G. KREMENTZ, AND M. J. CONROY. 2002. Wood Thrush movements and habitat use: Effects of forest management of Red-cockaded Woodpeckers. *Auk* 119:109–124.
- MARTIN, K., P. B. STACEY, AND C. E. BRAUN. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured White-tailed Ptarmigan populations. *Condor* 102:503–516.
- MARZLUFF, J. M., AND R. P. BALDA. 1988. The advantages of, and constraints forcing, mate fidelity in Pinyon Jays. *Auk* 105:286–295.
- MARZLUFF, J. M., AND R. P. BALDA. 1989. Causes and consequences of female-biased dispersal in a flock-living bird, the Pinyon Jay. *Ecology* 70:316–328.
- MARZLUFF, J. M., R. BOWMAN, AND R. DONNELLY. 2001a. A historical perspective on urban bird research: Trends, terms, and approaches. Pages 1–18 in *Avian Ecology and Conservation in an Urbanizing World* (J. M. Marzluff, R. Bowman, and R. Donnelly, Eds.). Kluwer Academic Publishers, Norwell, Massachusetts.
- MARZLUFF, J. M., K. J. MCGOWAN, R. DONNELLY, AND R. L. KNIGHT. 2001b. Causes and consequences of expanding American Crow populations. Pages 331–363 in *Avian Ecology and Conservation in an Urbanizing World* (J. M. Marzluff, R. Bowman, and R. Donnelly, Eds.). Kluwer Academic Publishers, Norwell, Massachusetts.
- MARZLUFF, J. M., J. J. MILLSPAUGH, P. HURVITZ, AND M. S. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- MCGOWAN, K. J. 2001. Demographic and behavioral comparisons of suburban and rural American Crows. Pages 365–381 in *Avian Ecology and Conservation in an Urbanizing World* (J. M. Marzluff, R. Bowman, and R. Donnelly, Eds.). Kluwer Academic Publishers, Norwell, Massachusetts.
- NAMS, V. 2000. LOCATE II User's Guide. Pacer, Truro, Nova Scotia.
- PARADIS, E., S. R. BAILLIE, W. J. SUTHERLAND, AND R. D. GREGORY. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- PARR, C. S. 1997. Social behavior and long-distance vocal communication in eastern American Crows. Ph.D. dissertation, University of Michigan, Ann Arbor.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132: 652–661.
- PYLE, P. 1997. Identification Guide to North American Passerines, part 1. Slate Creek Press, Bolinas, California.
- PYLE, P. 2001. Age at first breeding and natal dispersal in a declining population of Cassin's Auklet. *Auk* 118:996–1007.
- ROHILA, C. M. 2002. Urbanization in the greater Seattle, Washington area: Impacts on vegetation, snags, and cavity-nesting birds. M.S. thesis, University of Washington, Seattle.
- SAUER, J. R., S. ORSILLO, AND B. G. PETERJOHN. 1994. Population status and trends of grouse and prairie-chickens from the North American Breeding Bird Survey and Christmas Bird Count. *Transactions of the 59th North American Wildlife and Natural Resources Conference* 59:439–448.
- SCHJORRING, S., J. GREGERSEN, AND T. BREGNBALLE. 1999. Prospecting enhances breeding success of first-time breeders in the Great Cormorant, *Phalacrocorax carbo sinensis*. *Animal Behaviour* 57:647–654.
- SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- STACEY, P. B., AND M. TAPER. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18–29.
- VERBEEK, N. A. M., AND C. CAFFREY. 2002. American Crow (*Corvus brachyrhynchos*). In *The Birds of North America*, no. 647 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- WALLS, S. S., AND R. E. KENWARD. 1998. Movements of radio-tagged Buzzards *Buteo buteo* in early life. *Ibis* 140:561–568.
- WALTERS, J. R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. Pages 181–192 in *Avian Conservation: Research and Management* (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, D.C.
- WALTERS, J. R. 2000. Dispersal behavior: An ornithological frontier. *Condor* 102:479–481.
- WANG, X.-H., AND C. H. TROST. 2001. Dispersal

pattern of Black-billed Magpies (*Pica hudsonia*) measured by molecular genetic (RAPD) analysis. *Auk* 118:137–146.

WELLS, J. V., K. V. ROSENBERG, D. L. TESSAGLIA, AND A. A. DHONDT. 1996. Population cycles in the Varied Thrush (*Ixoreus naevius*). *Canadian Journal of Zoology*:2062–2069.

WINTERSTEIN, S. R., K. H. POLLOCK, AND C. M. BUNCK. 2001. Analysis of survival data from radiotelemetry studies. Pages 352–380 in *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, Eds.). Academic Press, San Diego, California.

WITHEY, J. C. 2002. Dispersal behavior of juvenile American Crows and the relationship of crow populations to human population density. M.S. thesis, University of Washington, Seattle.

ZACK, S., AND B. J. STUTCHBURY. 1992. Delayed breeding in avian social systems: The role of territory quality and ‘floater’ tactics. *Behaviour* 123:194–218.

Associate Editor: M. Brittingham

APPENDIX

We used the following estimates for calculating the net influx of dispersing crows into the urban population and modeling population growth in RAMAS GIS. We estimated breeding density on the basis of home-range size for urban ( $17.6 \pm 6.5$  ha, or 5.7 pairs per kilometer squared), suburban ( $31.3 \pm 7.8$  ha, or 3.2 pairs per kilometer squared), and exurban ( $308 \pm 61.8$  ha, or 0.32 pairs per kilometer squared) crows studied in Washington (Marzluff et al. 2001b). We used the Seattle CBC circle (radius = 12.1 km) to delineate our “urban” population, because of the documented increase there. Excluding that area, we extended the radius another 27.7 km to delineate the suburban–exurban area, because that was the maximum

distance we relocated a dispersing crow from its natal territory (Fig. 1). However, to calculate breeding area, we excluded water bodies and the islands across the Puget Sound to the west. For both the suburban–exurban area and the CBC circle, we calculated land area classified as “exurban,” “suburban,” and “urban” (see text). Outside the CBC area, we did not include potential breeding areas classified as urban, because none of our radiotagged crows was trapped in such areas.

We estimated the number of young produced per pair in urban, suburban, and exurban habitat using Marzluff et al. (2001b). Urban (1.1 young per pair per year,  $n = 80$ ) and exurban (1.6 young per pair per year,  $n = 54$ ) rates were based on nesting attempts in Washington only, but the suburban rate was based on nesting attempts

TABLE A1. Calculations used to estimate the net influx of dispersing crows into the urban population. Actual calculations used more significant digits than shown.

	Outside Seattle CBC area		Within Seattle CBC area	
	Suburban	Exurban	Urban	Suburban
Breeding density (number per kilometer squared)	3.2	0.32	5.7	3.2
× available area (km <sup>2</sup> )	981	1,132	153	110
= number of breeding pairs	3,137	367	872	352
× number of young produced per pair	1.8	1.6	1.1	1.8
= number of young produced	5,737	573	930	644
Sum for area		6,310		1,574
× probability of immigration–emigration		0.09		0.15
= number of juvenile dispersers		587 (immigrants)		242 (emigrants)
Net dispersal into urban area (immigrants – emigrants)		345		



in Washington ( $n = 19$ ), Wisconsin ( $n = 56$ ), and New York ( $n = 202$ ). We included sites outside of Washington for the suburban rate because of the low sample size in Snohomish County; the result was slightly lower (and therefore conservative for our purposes) than when using nesting attempts in Washington alone (1.8 vs. 2.0 young per pair per year).

As one approach to modeling urban population growth in RAMAS GIS (see text), we summed the young produced in each habitat type outside and within the Seattle CBC circle.

Probability of immigration and emigration from our study area was used to calculate the numbers of juvenile dispersers (1) immigrating into the urban population from outside the Seattle CBC and (2) emigrating away from the urban population. Net dispersal was the difference between the two figures, which represents 22% (345 of 1,574) additional young in the urban population over those produced by local breeders (see Table A1). That net influx was added to the reproductive output of the urban population to simulate growth (Fig. 4B).