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## Effects of West Nile Virus Mortality on Social Structure of an American Crow (Corvus brachyrhynchos) Population in Upstate New York

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## CHAPTER 4

# EFFECTS OF WEST NILE VIRUS MORTALITY ON SOCIAL STRUCTURE OF AN AMERICAN CROW (*CORVUS BRACHYRHYNCHOS*) POPULATION IN UPSTATE NEW YORK

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ABSTRACT.—In a marked population of cooperatively breeding American Crows (*Corvus brachyrhynchos*) studied for 17 years in Ithaca, New York, the effect of West Nile virus (WNV) was local but dramatic during 2002–2003. In two consecutive years, >35% of American Crows in well-known families died or disappeared between late July and early October, the primary WNV season in the state of New York. West Nile virus was confirmed as the cause of death in nearly all tested birds. Risk of mortality did not differ with age, sex, or breeding status of birds, but adult mortality increased 10-fold and juvenile mortality 3-fold above normal levels for this population as measured during 1990–1998. Four times as many breeders died during August–October as disappeared during an entire year between 1995 and 1998. Social effects were assessed by comparing changes from 2001, before WNV was present, through 2005, two years after the high mortality of 2003. Although no significant decreases in group size, frequency of helping, average age of breeders, or territory density were observed after two years of WNV presence, the direction of most changes suggested that repeated years of WNV presence would likely affect social structure. Unusual social events, including female territory-budding and adoption of and subsequent helping by unrelated juveniles, were documented in 2004–2005. American Crows filled territory vacancies very slowly. The presence of breeding-age auxiliaries on territories may counter rapid social change and breeding declines in cooperatively breeding crow populations, but repeated years of such high mortality are likely to cause both significant social disruption and severe population declines among American Crows. *Received 5 August 2005, accepted 30 November 2005.*

RESUMEN.—El efecto de el virus del Oeste del Nilo (VON) fue específico pero dramático durante el 2002-2003, en una población marcada de *Corvus brachyrhynchos* que presentaban reproducción cooperativa la cual fue estudiada durante 17 años en Ithaca, Nueva York. En dos años consecutivos mas del 35% de *Corvus brachyrhynchos* pertenecientes a familias conocidas murieron o desaparecieron entre finales de Julio y principios de Octubre, coincidiendo con la primera temporada del VON en el estado de Nueva York. Se confirmo que el virus del Oeste del Nilo fue la causa de mortalidad e casi todas las aves examinadas. El riego de mortalidad no fue diferente con la edad, sexo o estado de apareamiento de las aves, pero la mortalidad de adultos y juveniles se incremento diez y tres veces, respectivamente, arriba de los niveles normales para esta población de acuerdo a los datos obtenidos durante 1990-1998. La mortalidad de individuos en reproducción durante los meses de Agosto–Octubre fue cuatro veces mayor que los individuos que desaparecieron durante un ano completo entre 1995 y 1998. La evaluación de los efectos sociales se realizo mediante la comparación de cambios desde el 2001, antes de que el VON estuviera presente, hasta el 2005, dos anos después de la alta mortalidad del 2003. Aunque no se detectaron, después de dos anos de la presencia de el VON, reducciones significativas en el tamaño de los grupos, la frecuencia de ayuda, la edad promedio de los individuos en reproducción o la densidad territorial, la dirección de la mayoría de los cambios sugirió que la presencia de el VON en anos subsecuentes tendría una alta probabilidad de afectar la estructura social. Los eventos sociales no muy comunes, incluyendo hembras compartiendo territorio y la adopción y subsiguiente ayuda de individuos

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juveniles no emparentados, fueron registrados en el 2004 al 2005. *Corvus brachyrhynchos* ocuparon territorios disponibles muy lentamente. La presencia en los territorios de individuos auxiliares en edad reproductiva puede mostrar cambios sociales rápidos y reducciones en reproducción en las poblaciones de *Corvus* con reproducción cooperativa, pero subsiguientes anos de alta mortalidad pueden probablemente causar alteraciones sociales significativas y drásticas reducciones poblaciones entre *Corvus brachyrhynchos*.

HIGH RATES OF mortality among American Crows (*Corvus brachyrhynchos*; hereafter "crows") have accompanied the spread of West Nile virus (WNV) from New York in 1999 across the United States to California by 2003 (McLean 2006). Laboratory studies report nearly 100% mortality of crows from experimental infections with the New York 1999 strain of virus (McLean et al. 2001, Komar et al. 2003, Brault et al. 2004). Despite the obvious extent of crow mortality in many areas (Caffrey et al. 2003, 2005; Yaremych et al. 2003; see review in McLean 2006) and fears for threatened species (e.g. Naugle et al. 2004), only a few reports have been directly concerned with the effect on crow population dynamics (Caffrey et al. 2003, 2005). Crows are common, urbanized, and successful across North America, with increasing populations over the past 50 years (Marzluff et al. 2001, Sauer et al. 2005). Thus, it is understandable that there should be little immediate concern for crow population health. There are, however, several reasons for careful study of crow populations experiencing the initial effects of this disease.

Being common has not historically protected organisms against severe reductions from disease or overhunting. Being common in urban areas with plenty of appropriate vectors (e.g. *Culex pipiens* mosquitoes in the northeastern United States) may, in fact, put crows and other urban birds at greater risk of WNV infection (Ringia et al. 2004). To evaluate this risk, we need a better understanding of WNV transmission among urban crows, as well as evidence of whether they are developing resistance.

A second reason for study is the unpredictable effect of sudden high mortality on the demography of a typically long-lived organism. Crows are socially complex birds, relatively slow to mature and reproduce (Verbeek and Caffrey 2002), with low mortality rates (McGowan and Caffrey 1995, Marzluff et al. 2001, McGowan 2001). They are cooperative breeders across much of their range, with the basic social unit composed of a single breeding pair, dependent

offspring, and "auxiliaries" (i.e. independent offspring or other older crows, presumed nonbreeders, many of which provide care to dependent young as "helpers") (Kilham 1984, 1989; Chamberlain-Auger et al. 1990; Caffrey 1992, 1999, 2000; McGowan 2001; Verbeek and Caffrey 2002). In a normally long-lived, cooperative breeder, mortality from WNV could do far more than simply reduce population growth. High mortality among the most productive age-classes with normally high survival, or reduced numbers of helpers following increased juvenile mortality, could have unexpectedly large, lasting effects on the social system, as well as on population sizes. Heavy mortality could also disrupt continuity of space use or social traditions across generations. With reduced longevity, selection might shift to favor earlier, more intensive breeding effort. A large number of helpers of breeding age—on territories and able to begin reproducing—could cushion a population against the initial effects of unusually heavy breeder mortality, but for how long and with what effects on breeding biology are important questions.

How cooperative breeding systems respond to changes in mortality patterns is interesting also from a broader scientific perspective. Cooperative breeding and the associated "slow" life-history traits are hypothesized to evolve in the context of limited breeding resources, such as mates (Walters et al. 1992), space (Woolfenden and Fitzpatrick 1984), and high-quality territories (Koenig and Pitelka 1981, Stacey and Ligon 1991, Komdeur and Edelaar 2001). A sudden increase in mortality from WNV offers a natural, albeit uncontrolled, experiment on the factors influencing breeding, floating, and helping decisions in this cooperatively breeding species. The nature of the experiment depends on the pattern of mortality felt by the population and individual families within it. If breeders as well as younger birds are affected, several predictions can be made: (1) As breeding positions become available, breeding-age auxiliaries should disperse

to breed independently. (2) Family size should decrease as a result of family deaths and dispersals. (3) Average age of breeders should decrease as previous auxiliaries become independent breeders. (4) A greater proportion of families should be composed of pairs without helpers, a result of increased juvenile mortality and the establishment of new breeding pairs without previous offspring available to assist them.

Here, we report sex- and age-specific mortality patterns during two years (2002–2003) of WNV activity in a well-studied crow population in upstate New York (McGowan 2001). We assess evidence that WNV mortality affected social structure, density, and breeding patterns as predicted above.

## METHODS

*Study population.*—Crows in Ithaca and Cayuga Heights, Tompkins County, New York, have been marked, and their demographics and social behavior followed, since 1989 (for methods and description of this suburban study area, see McGowan 2001). Each year since 1989, ~100 nests have been located during nest building in March–May, and ~100 nestlings banded for individual recognition with leg bands and patagial tags at 24–30 days following hatching in successful nests. Approximately 1,450 crows have been banded since 1989; banded crows still represent a small proportion of the whole Ithaca population. Beginning in 2001, 10–20 of the year's nestlings have been radiotagged with ~10-g radiotransmitters attached with backpack harnesses (Karl and Clout 1987) for the purpose of studying fledgling social development (D. Robinson, Jr., unpubl. data) as well as determining roosting locations in relation to WNV risks (A. Clark et al. unpubl. data). We captured and marked additional birds on their territories or at communal foraging areas. Birds not tagged as nestlings were aged as juveniles (≤1 year old or 11 months postfledging; see Emlen 1936) or adults. Since 1998, the sex of banded birds has been determined molecularly (Fridolfsson and Ellegren 1999).

The Ithaca population includes hundreds of crow families, only some with banded birds. From 2001 through 2005, we have been studying social behavior in a set of 20–30 crow families living primarily in Cayuga Heights, a residential neighborhood with several golf courses (Serrell 2003, MacKillop 2005, D. Robinson, Jr., unpubl. data). These studies provided regular monitoring of the behavioral events reported and the basis for classifying birds as breeders (central, territorial pair involved in nesting) versus auxiliaries. Here, "auxiliary" and "nonbreeder" are used interchangeably to mean that a bird was not a member of

the breeding pair. We do not know whether some of these had extrapair young in the nest.

*Direct and indirect measures of survival and loss.*—To estimate changes in mortality rates associated with WNV, we compared 2002 and 2003 mortality during August–October (the period of most WNV activity; see below) to juvenile and adult death rates during the decade 1990–1999. Before the arrival of WNV, we documented survivorship of each cohort through sightings during studies of nesting behavior, specific attempts to locate all known marked birds during the early breeding season, regular visits to winter communal foraging sites, and careful use of public reports. Normal juvenile mortality pre-WNV was based on resighting data for all 570 fledglings produced during 1990–1999 and calculated as the percentage of all fledglings known to be alive on 1 August that had died or permanently disappeared by 31 October. Normal postjuvenile survival was calculated on the basis of six cohorts of birds (those banded as nestlings from 1990 to 1995). Their resightings during each three-month block (February–April, May–July, August–October, November–January) from the year in which they were one year old through 1998 were used to calculate the mortality rate of a given age class as the percentage of those alive at the beginning of the block that were dead or permanently disappeared by the end of a block.

From 2001 to 2005, we tracked survivorship in focal families through regular location and counts of family members on territory and at communal foraging areas in addition to the incidental observations before 2001. In 2002, we established five census routes of 11–17 km each, covering most areas in which marked crows were known to live and extending beyond the central study area. Censuses one to three times each week in spring and summer, less frequently in fall and winter, gave us a quantitative estimate of local population size and an opportunity to detect missing, sick, or dead birds. Several radiotagged birds were found dead during tracking. Reports from the public and the Tompkins County Department of Health also alerted us to sick or dead crows.

Sick birds that permanently disappeared during this period were assumed to have died and were categorized as "known dead" in our analyses. In the laboratory, crows die within four to six days of infection with WNV (Komar et al. 2003). This time course agrees well with the rapid demise, within one to three days, of those birds found already clearly sick (lethargic, flying with poor coordination, or unable to fly). Birds noted as suddenly missing that did not reappear during August–October were counted as "disappeared, presumed dead" and are used in the mortality calculations. No bird seen sick or classified as "disappeared" in our data set ever subsequently reappeared.

In New York, WNV can appear in birds in May and is prevalent into October. The first frosts typically

reduce mosquito numbers, and cooler temperatures with shortening day lengths send mosquitoes into diapause (Spielman 2001). We used the second week in October as a reasonable, conservative cutoff for inferring that WNV caused disappearances. Note that normal mortality rates were calculated for a full three-month block ending 31 October; thus, calculated increases above the normal rate of mortality and disappearance are conservative.

*Testing and evidence of West Nile virus.*—Crow carcasses in presumed suitable condition were collected and submitted to Wadsworth Lab (Albany, New York) for virus isolation and reverse-transcription polymerase chain reaction assay with WNV-specific primers (Kauffman et al. 2003). Test results were taken from the New York State Health Information Network database.

*Choice of population samples.*—In 2002, we limited our analysis to 10 families with known membership, chosen because their territories included or abutted the two golf courses where most dead crows were found. The goal of this analysis was to use this "hot zone" to evaluate the pattern of mortality across age classes. In 2003, we included 30 families whose membership we knew well enough to track losses. This larger data set provided a second year of data on age-, sex-, and social-class-specific mortality and a better estimate of overall effects on the population.

The years 2001 (before any WNV was identified in our population) and 2004 through breeding season 2005 are considered to be periods functionally free of WNV, representing the situation before and after the effects of WNV.

*Crow density changes.*—Density of breeding families was calculated by determining the number of families defending territories within a 3.724-km$^2$ area in which we knew the resident families for the years 2001 to 2005. This analysis required a large continuous area in which the number of families was known for 2001–2005. The families included most but not all "core families" and several others whose presence was documented across years. Note that family density (number of families per unit area) is not the strict inverse of territory size, because some space was shared or vacant in some years.

*Statistical analyses.*—Logistic analysis was used to compare the occurrence of death versus survival as a categorical response variable among subsets of the overall population (male vs. female, among status classes, among age classes and, where possible, interactions). For comparisons with normal, pre-WNV mortality for this population, we used 2xK contingency tests or chi-square tests. To address immediate population-level changes as a result of deaths and disappearances, we analyzed family size, change in family size, and age of breeders and nonbreeders from 2001 to 2005 for differences among years, using analysis of variance (ANOVA) where

sample size and normality requirements were met and contingency tests where they were not. Data for these analyses were based on family composition during the breeding season (April–June) of each year. Analyses were calculated with SPSS, version 11.5 (SPSS, Chicago, Illinois), or DATADESK, version 6.2 (Data Description, Ithaca, New York).

## RESULTS

*West Nile virus in Tompkins County, New York.*—The incidence of WNV in crows in Tompkins County, New York, has varied markedly between 2000, when the first positive birds were identified, and 2004 (Table 1; also see the West Nile Virus Maps and links at the U.S. Geological Survey website—see Acknowledgments for address). As described below, the annual variation for the county has been reflected in the annual mortality and incidence of WNV in our study population.

*Patterns of mortality in West Nile virus season in 2002.*—A recent fledgling in June 2002 was the first known WNV death in the study area. During the period of late June through early October 2002, ≥33 crows were reported sick or dead in the Ithaca–Cayuga Heights area, of which 10 tested positive for WNV, 3 were negative, and the rest were too decomposed to be tested. Nineteen of these carcasses were found during late July to October in an area of ~84 ha, on the territories of 10 families consisting of 65 birds (20 breeders, 24 helpers, and 21 successfully fledged juveniles). Thus, in this "hot zone," 29.2% of the birds present in early July were found dead by October. Of the nine families with banded juveniles, only 63.7% of all family members ($n = 58$) were still present in early October. Juvenile and adult survival rates were 50.0% and 70.7%, respectively, but did not differ statistically ($\chi^2 = 0.64$, df = 1, nonsignificant). Both rates are markedly and significantly lower than normal survivorship (Table 2; juveniles: $\chi^2 = 18.1$, df = 1, $P < 0.001$; adults: $\chi^2 = 113.8$, df = 1, $P < 0.001$).

TABLE 1. New York State Department of Health test results for crows dying between 1 August and 10 October in Tompkins County, New York. (Crows reported dead but not tested are not included.)

| WNV test result | 2000 | 2001 | 2002 | 2003 | 2004 |
|---|---|---|---|---|---|
| Positive | 5 | 0 | 11 | 33 | 1 |
| Negative | 3 | 5 | 6 | 1 | 16 |
| Total tested | 8 | 5 | 17 | 34 | 17 |

TABLE 2. Survivorship of juvenile and adult American Crows in Ithaca, New York, during WNV season (August–October) for pre-WNV years 1990–1999[a] and the two years with significant WNV (2002 and 2003).

| Age class | Year | Number alive | | Percentage surviving | Percentage mortality |
|---|---|---|---|---|---|
| | | Pre-WNV season | Post-WNV season | | |
| Juvenile | 1990–1999 | 485 | 415 | 85.6 | 14.4 |
| | 2002 | 16 | 8 | 50.0 | 50.0 |
| | 2003 | 60 | 31 | 51.7 | 48.3 |
| Adult | 1991–1998 | 546 | 528 | 96.7 | 3.3 |
| | 2002 | 41 | 29 | 70.7 | 29.3 |
| | 2003 | 103 | 67 | 65.0 | 35.0 |

[a]Adult survival data for 1991–1998; see methods.

*Patterns of mortality in 2003.*—Sixty-three dead crows, banded and unbanded, were recovered from the study area or nearby communal foraging areas used by study birds during summer 2003. All those found in a condition potentially suitable for testing were submitted to the New York State Wildlife Pathology Lab. Of these, 29 birds from families described here ($n$ = 21) or nearby families ($n$ = 8) were tested. The one bird found before 1 August, a banded juvenile, was negative for WNV. The rest ($n$ = 28) all died between 1 August and 8 October, and all but one tested positive (Wadsworth Laboratory; reported in the New York State Health Information Network database). The one negative bird was diagnosed with aspergillosus.

For 2003, we extended our analysis to include 30 families of known membership (193 birds, including surviving fledglings; 140 birds were banded) with particular emphasis on 23 core families (163 birds, of which 117 were banded). No significant differences in results were found between the 23- and 30-family data sets, but we considered the core-family data set to be more accurate and have used it unless otherwise stated.

The proportion of all birds dead and missing by the end of the 2003 WNV season was remarkably similar to that in 2002 (36.3%), whether based on the core families (39.9%) or all 30 families for which we knew membership (37.6%).

Neither sex nor age significantly affected the risk of dying (among age classes: juveniles: 48.3%; 1–3 years: 33.3%; 4–13 years: 41.7%; logistic two-factor analysis: sex: $F$ = 1.65, df =1, $P$ = 0.20; age: $F$ = 1.67, df = 2, $P$ = 0.19; juveniles vs. all older birds: 48.3% vs. 34.9%; $\chi^2$ = 0.96, df = 1, nonsignificant; see Figs. 1 and 2). There was also no effect of social status in the family: the proportion of deaths among breeders (37.0%), auxiliaries (33.3%), and juveniles (48.3%) did not differ significantly ($F$ = 2.01, df = 2, $P$ = 0.138), nor was there any significant interaction between sex and social status ($F$ = 0.49, df = 2, $P$ = 0.62; Fig. 3).

Breeder and auxiliary samples contained more unbanded birds than the group of juveniles, which were almost all banded. Unbanded birds were probably less likely to be reported to us if found dead by the public and harder for us to document as missing, so it was possible that breeder and auxiliary rates were underestimated. However, the proportion of deaths among banded core breeders ($n$ = 24) and banded auxiliaries ($n$ = 37) was only slightly and nonsignificantly higher than those for all birds in these categories: 41.6% versus 36.9% and 40.5% versus 33.3%, respectively.

At the family level, losses were spread across the 23 core families; only one family did not lose at least one member during this period, and 18 lost more than one. Nine lost at least one breeder, and both breeders disappeared from six families. Where juveniles survived and both breeders disappeared, juveniles variously remained on territory with helpers (two cases) and an unrelated adult (one case; see below) or left the territory and were seen only in communal foraging areas (one case).

Following these losses, 7 of the 23 families were no longer on their territories. Either all had died (two cases), or the remaining birds vacated the territory (five cases). No vacated territory was filled during 2003 nor, two years later, had any been filled with a completely new family, though the space was gradually used by adjoining families and their "buds" (former
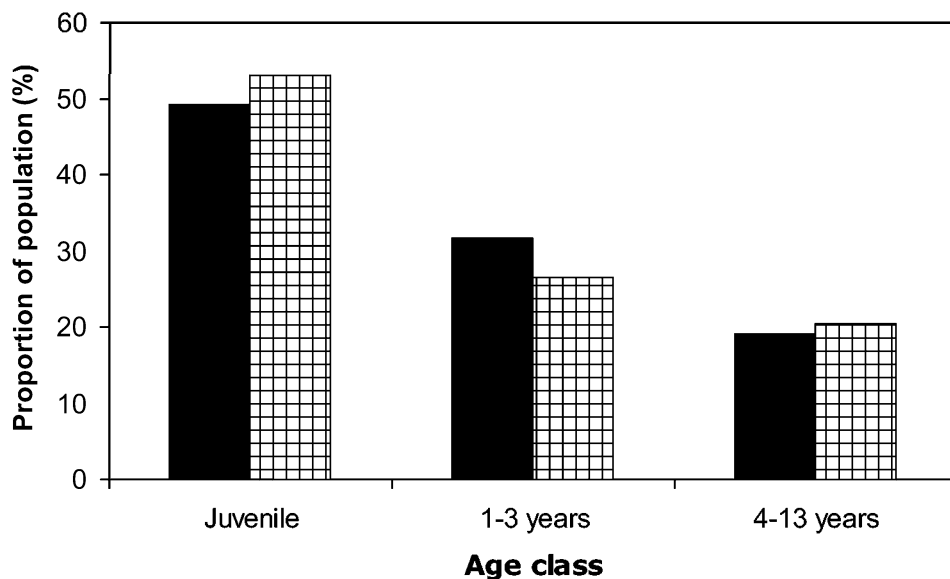
FIG. 1. Distribution of WNV deaths by American Crow age. The relative proportion of known-age, banded American Crows in three age classes from 23 families in Ithaca, New York, that were known to be alive as of 1 August 2003 (black bars) did not differ from the relative proportion among those that had died or disappeared as of 8 October 2003 (hatched bars; $\chi^2$ = 0.44, df = 2, nonsignificant). Note that ages 1–3 years represent birds likely to be helpers, whereas both sexes age 4 and older are of an age to breed (McGowan 2001).
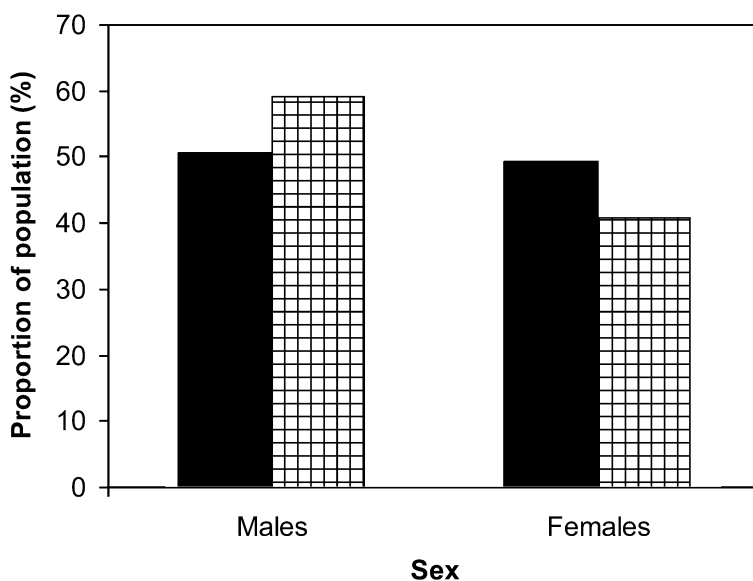


FIG. 2. Distribution of WNV seasonal deaths by sex. The relative proportion of male and female American Crows from 23 families in Ithaca, New York, known to be alive as of 1 August 2003 (black bars) did not differ from the relative proportion among those that had died or disappeared as of 8 October 2003 (hatched bars; $\chi^2$ = 0.57, df = 2, nonsignificant).
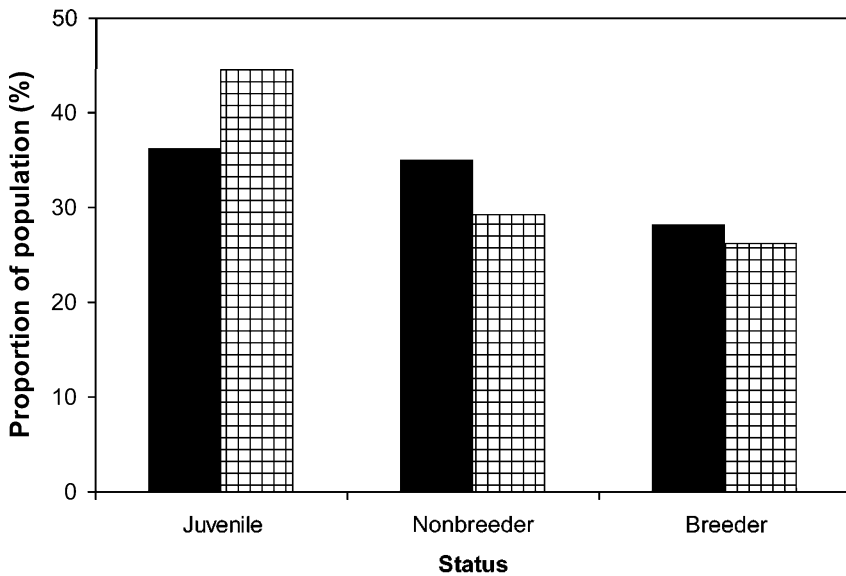
Fig. 3. Distribution of WNV seasonal deaths by status. The relative proportion of three status groups of American Crows from 23 families in Ithaca, New York, known to be alive as of 1 July 2003 (black bars) did not differ from the relative proportion among those that had died or disappeared as of 8 October 2003 (hatched bars; $\chi^2 = 0.96$, df = 2, nonsignificant).

auxiliaries newly breeding on contiguous areas; Woolfenden and Fitzpatrick 1978; see below).

*Patterns of mortality in 2004.*—In contrast with 2003, 2004 brought few deaths and no known cases of WNV in the Ithaca crows. The New York State Department of Health recorded only one WNV-positive bird for all of Tompkins County in 2004 (Table 1). In the study population, only five dead and three sick birds were encountered from late June through October and there were few disappearances. Three of the five dead were juveniles. One of the three sick birds tested negative for WNV, recovered, and was released after treatment at the Cornell Wildlife Clinic. The other two died of bacterial infections (Cornell University Wildlife Clinic Pathology reports to A.B.C.).

Since 2002, mosquito populations have been monitored in areas where crows were actually roosting; levels of *C. pipiens* and *C. restuans*, the two species implicated in WNV transmission to birds, were about an order of magnitude lower in 2004 than in 2003 (L. Patrican pers. comm.). In 2004 in New York, the summer was cool and unusually wet. Extremely high rainfall in July–August (37.3 cm in 2004 vs. 27.1 cm in 2003; normal 18.1 cm; source of data: Ithaca Climate Page; see Acknowledgments) appeared to have

washed many *Culex* eggs and larvae out of the small, stagnant pools they prefer (L. Patrican pers. comm., A. Clark pers. obs.), and cool temperatures with highs averaging 1.1–1.6°C below normal (source: Ithaca Climate Page; see Acknowledgments) may have slowed maturation rates (see McLean 2006).

*Social and spatial change with West Nile virus 2001–2005.*—Decreases in family size in the year following such an outbreak of disease might be expected for two reasons: losses among the juvenile and yearling age classes should reduce the number of auxiliaries remaining on territories in the next year, and losses among the breeders should offer breeding openings for birds that would otherwise have stayed and probably helped. However, family size did not differ significantly between years (Fig. 4). For those families breeding in any two consecutive years, we compared the changes in family size from one year to the next across all pairs of years (2001–2002, 2002–2003, etc.). The prediction was that change in family size would be most negative for the 2003–2004 pair. Change in family size did not, however, vary significantly between pairs of years ($F = 0.964$, df = 3 and 70, $P = 0.415$).

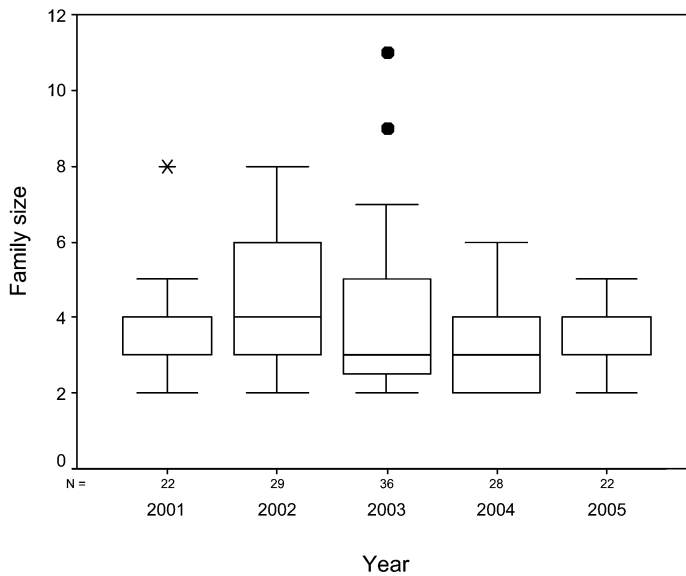If breeder openings resulted in birds finding breeding positions at a younger age, one

Fɪɢ. 4. American Crow family sizes in Ithaca, New York, during 2001–2005 breeding seasons (April–June). Average family size did not differ between years ($F$ = 1.794, df = 4 and 132, $P$ = 0.134). Boxes represent interquartile values (middle 50%), bars equal outerquartile values, thickened horizontal line through box represents the median, outliers (✶) and extreme cases (●) represent values 1.5–3 and >3 quartiles beyond the outerquartile boxes, respectively.

would predict a decrease in average age of both breeders and auxiliaries, as the latter class became more restricted to immature yearlings. Males were significantly older than their female counterparts in both status categories ($\bar{x}$ ± SE: male vs. female breeder: 7.95 ± 0.31 vs. 5.28 ± 0.36; male vs. female auxiliary: 2.38 ± 0.17 vs. 1.39 ± 0.09; Fig. 5). However, for neither sex were there significant differences in average age among years 2001–2005 for either breeders or auxiliaries (Fig. 5).

The combined losses of juveniles and older, established auxiliaries were predicted to reduce the number of families with associated auxiliaries in the following year. As shown in Figure 6, the percentage of families (64.3%) with auxiliaries in 2004 was the lowest value in the five years, significantly different from 2001 ($\chi^2$ = 4.82, df = 1, $P \leq 0.05$), but not from 2002 ($\chi^2$ = 2.76, df = 1, $P \leq 0.10$) or any other single year.

We expected that the loss of breeders and whole families would affect the size of territories, but exactly how would depend on the birds' responses to the newly unoccupied space. For an area of 3.724 km² in which we knew the total number of families breeding during

2002–2005, family density averaged 8.33 families per square kilometer. Densities dropped by six families (17%) from 2003 to 2004, and by two more in 2005 (Table 3).

No new pairs of breeders arrived to take over vacant territories. Adjoining families gradually encroached on the space. Some territories where birds bred successfully in 2003 became undefended boundary areas between remaining families. The one source of new breeding pairs (five in 2004) were auxiliaries from existing families that found mates and bred independently in areas adjacent to their natal areas. Most of these continued to share space with a natal family (see below).

*Budding, breeding, and helping after outbreaks of West Nile virus.*—Following the loss of birds and opening of territories, several unusual social changes occurred, including female budding, merged families, and a case of adoptee helping. "Budding" refers to a former nonbreeder attracting a mate and settling in part of the territory on which it had been an auxiliary (Woolfenden and Fitzpatrick 1978). For Florida Scrub-Jays (*Aphelocoma coerulescens*), at least, it is a male behavior (Woolfenden and Fitzpatrick
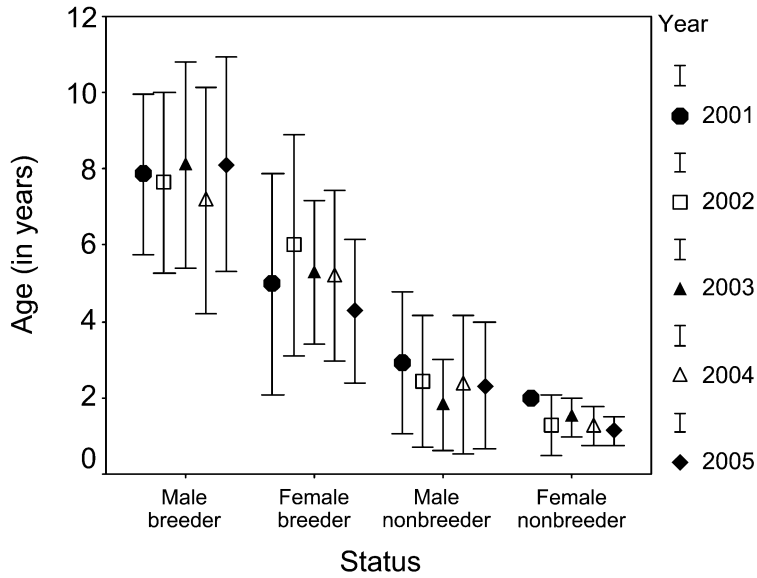
FIG. 5. Ages of different classes of family members in cooperatively breeding American Crow families during 2001–2005 breeding seasons (April–June). Status classes differed significantly in age ($F$ = 151.293, df = 3 and 243, $P$ < 0.001). Also, males were significantly older than females within each status class (breeders: $F$ = 27.007, df = 1 and 98, $P$ < 0.001; nonbreeders: $F$ = 14.781, df = 1 and 142, $P$ < 0.001). Bars represent $\bar{x}$ ± SE.
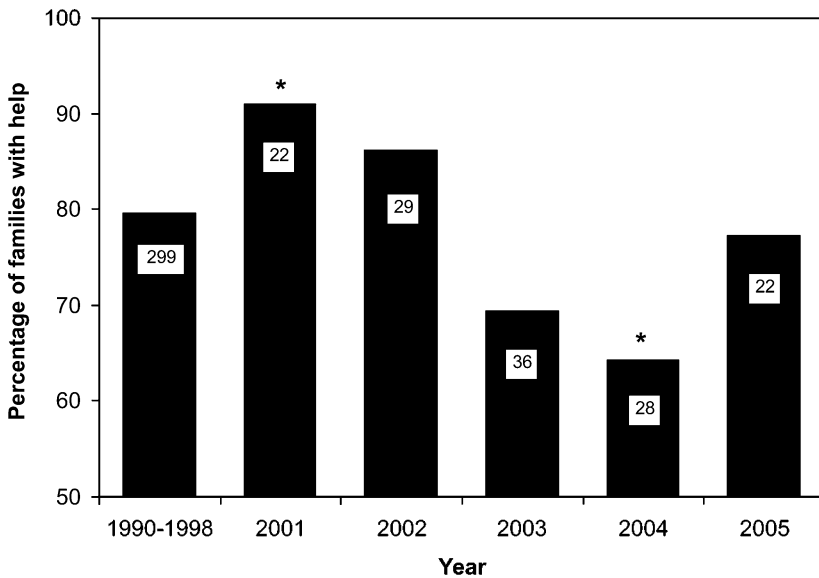


FIG. 6. Percentage of American Crow families with three or more family members during the breeding seasons (April–June) of 2001–2005, and the mean for 1990–1998 (from McGowan 2001). Families with helpers were significantly less common in 2004 than in 2001 (difference between bars marked *; $\chi^2$ = 4.82, df = 1, $P$ ≤ 0.05), but not significantly different than in any other year. Sample sizes are shown in bars.

TABLE 3. Density of American Crow families within the central study area (3.724 km$^2$) in Ithaca, New York, and the number of those families that resulted from a "bud" of a natal territory in 2002–2005. See text for description of budding.

| Year | Number of families | Family buds | Families per km$^2$ |
|------|--------------------|-------------|---------------------|
| 2002 | 33                 | 1           | 8.86                |
| 2003 | 35                 | 0           | 9.40                |
| 2004 | 29                 | 5           | 7.79                |
| 2005 | 27                 | 0           | 7.25                |

1978, 1984). Indeed, over the past decade, female budding among crows in this population has been a very rare occurrence (K. McGowan unpubl. data). By contrast, the breeding families in 2004 included at least four cases of young female crows budding.

In one case, only two males, an unbanded adult and a banded two-year-old, remained of a family that lost multiple auxiliaries and at least one breeder to WNV. They were joined in late winter 2003–2004 by a three-year-old female helper from an adjacent territory. The trio used parts of the helper's natal territory and of an adjacent territory where both breeders disappeared in spring 2004. Relations with her family were somewhat agonistic, and the two groups regularly disputed the boundary. In spring 2004, however, their nests were only ~50 m from each other.

In a second case, a three-year-old female (a 2003 helper) joined an unbanded male in an area adjoining her family. She visited the nest of her natal group in 2004, but appeared to be nesting on her own. In 2005, the pair nested in the same location and hatched young as an unassisted pair.

In the third case, a three-year-old female ("3I") nested with an unbanded male on territory used by her natal family. Her father had died of WNV in 2003. Her mother and her mother's new mate were seen around 3I's nest before egg laying. The older pair nested only ~0.41 km away, and after 3I's mother disappeared and presumably died, the two families, both with fledged young, merged. In 2005, there were again two nests on the territory; postfledging, the family moved together as a two-pair unit in a large territory encompassing all or part of three territories of families gone since 2003.

In the fourth case of budding, the female's nesting territory adjoined that of her natal

family. In 2005, her second year of breeding "next door," she and her mate still used her natal territory and gathered sticks there for nest-building on their breeding territory.

The case of adoptee helping began when a female breeder died during WNV season 2003. She was replaced within weeks by the female breeder of the adjoining territory, who had just lost her own mate of many years. This female foraged with, but was never seen feeding or preening, the four fledglings of her new family. The male that she had joined then died of WNV, and she remained with the juveniles, a five-year-old unrelated helper, and the juveniles' one-year-old sibling. Only two juveniles, their sibling, and the female survived to November 2003. After winter 2003–2004, during which the female occupied her new territory and the juveniles often used communal foraging areas, she moved back to her original territory with a new male and the two surviving young of her adoptive family. They bred successfully in 2004 and 2005, with active help from the two young "adoptees," who stayed on the female's original territory. Thus, it appears that deaths of breeding adults may also reorganize the relationships within and between "families."

DISCUSSION

Mortality of crows in our study population in Ithaca, New York, during two years with West Nile virus was clearly elevated far above normal values. Overall mortality from the end of July through the first week of October was elevated by a factor of ~4.5 and exceeded total normal annual mortality. The size of the increase varied among the different classes of birds, however. In both 2002 and 2003, the proportion of juveniles dying or disappearing was nonsignificantly greater than loss of other age classes of birds (Fig. 1), but the normal rate of mortality for juveniles during the August–October period, computed for the decade 1990–1999, is >4× that for adults (Table 2). Juvenile losses in 2003 were about 3× greater than the previously normal level, whereas adult losses increased 10-fold. The loss of ≥36% of breeders during August–October 2003 contrasts sharply with the 8% annual breeder loss in 1990–1999 (Marzluff et al. 2001). Annual losses of nonbreeders, which include the effects of prebreeding dispersal, average 24% (McGowan 2001), in contrast with

the 33.3% losses during August–October in 2003. Thus, the change in the breeders' survival was much greater than for either juveniles or nonbreeders.

Our mortality rates during two WNV seasons are similar to those reported in the first year of WNV presence in an Oklahoma population of crows (33%: Caffrey et al. 2003), but less than occurred in the second outbreak year there (72%: Caffrey et al. 2005), or among a sample of 28 mostly juvenile crows in the first year of an Illinois outbreak (68%: Yaremych et al. 2004). The Oklahoma study, like the present one, followed banded territorial families including breeders, auxiliaries, and juveniles. For the Illinois study, Yaremych et al. (2004) captured crows mostly in a single locality, at a communal foraging area, and it is possible that these crows roosted in a single, particularly vector-inhabited location. Data from the Breeding Bird Survey (BBS; Sauer et al. 2005), however, suggest that real differences in mortality may exist between localities, and that Illinois in 2002 and Oklahoma in 2003 experienced greater crow mortality than upstate New York in either year. The trend graph for BBS data in Illinois shows a marked and frightening decline from 2002 to 2003, dropping from 28 crows per census (estimated) to 17.5 (estimated) (Sauer et al. 2005). This is the lowest value in 35 years and presumably reflects extreme losses in summer 2002. The BBS data for Oklahoma show a slight increase from 2002 to 2003, but a dramatic decline in 2004 (from 49 to 29 crows per census, estimated), reflecting the higher mortality in the WNV season of 2003 (Sauer et al. 2005). Trend lines for New York show a continuous decline since the appearance of WNV, but do not show the dramatic single-year decreases apparent in these and some other states. This contrast may reflect the twofold differences in mortality, as indicated in the studies of marked birds, or it may indicate differences in habitats and crow movement patterns between states.

West Nile virus killed all Ithaca crows without regard to age, sex, or breeding status, as it did in Oklahoma and Illinois (Yaremych et al. 2004, Caffrey et al. 2005). This pattern is somewhat surprising, given other reports on epidemics in birds. Woolfenden and Fitzpatrick (1984) found that an epidemic of an unidentified disease among their study population of Florida Scrub-Jays affected all ages and sexes,

but affected juveniles most strongly, wiping out the entire juvenile cohort for that year. Nolan et al. (1998) found that an outbreak of *Mycoplasma gallisepticum* disproportionately killed male House Finches (*Carpodacus mexicanus*).

On the other hand, although mortality was not biased by sex, age, or social status, the increase in mortality above normal rates differed by age and status, being most marked for breeding adults and least for juveniles. Such a pattern has the potential to significantly affect population demographics and social structure.

Episodes of high mortality have implications for both populations and individuals. In cooperative breeders, these are closely linked, in that individual decisions to remain in a group as an auxiliary or settle as an independent breeder may be influenced by competition for breeding resources. An unusually large loss of breeders, such as occurred in 2003, should sharply increase the available breeding opportunities. If auxiliaries are primarily constrained by a lack of breeding opportunities, the appearance of vacant territories and open breeding positions should be reflected in the degree of cooperative breeding behavior in the next years.

We expected new breeders to recruit from the nonbreeders, which are typically younger than breeders of the same sex (Fig. 5). In the two years immediately after high mortality, family sizes, ages of breeders and nonbreeders, and numbers of families without helpers did not show any significant change. It should be noted, however, that the direction of most absolute differences between 2004 and previous years were consistent with predictions: fewer groups with helpers and fewer large families. Age comparisons from one year to the next within a given area are complicated, because survivors all turn one year older each year, whereas we could not know the ages of unbanded breeder replacements.

Somewhat surprising was the way in which the family members responded to newly available breeding positions and also whole territories. Similar to other cooperatively breeding species where vacancies are usually filled by nonbreeders in adjacent territories (Russell and Rowley 1993, Pasinelli et al. 2004), new families all contained breeder pairs of which one or both originated in nearby families. But no pairs of two completely new birds settling in were detected. Furthermore, budding as a form

of territory acquisition has been primarily a male trait even in this population (K. McGowan unpubl. data). However, during the years following WNV-related deaths, the trend was for as many or more females to obtain breeding territories that included part of their natal site (see Legge and Cockburn [2000] for another example of a shift to female budding). In addition, adjacent families only slowly used the spaces left vacant, and some previous breeding areas were unused or shared at least through 2005.

The slow use of opened space and relatively small social effects differ from the rapid responses of other bird species to experimentally produced breeding spaces (Hatchwell and Komdeur 2000). For instance, when transplanted to previously unoccupied areas, male Seychelles Warblers (*Acrocephalus sechellensis*) rapidly adjusted their dispersal strategies to compete for high-quality territories rather than budding off part of their natal territories. They then switched back to budding when habitat was saturated and budding again resulted in greatest fitness (Komdeur and Edelaar 2001). Carrion Crows (*Corvus corone corone*) breed cooperatively in some populations and not in others. Experimental transplanting of young from a noncooperative population to a cooperative one resulted in philopatry and helping by transplanted birds (Baglione et al. 2002), demonstrating that cooperative breeding resulted from sensitivity to local conditions rather than from genetic constraints and past selection. Not all populations of American Crows are cooperative breeders (Verbeek and Caffrey 2002), and one would expect crows to show flexibility in the face of local conditions. The question remains, however, what conditions would reduce the current benefits of philopatry and induce a switch.

There may well be benefits of philopatry and of maintaining local social relationships that extend beyond either inclusive fitness benefits to helpers or the value of a safe place to wait for a breeding position (as in the "reciprocal altruism hypothesis" for the evolution of longevity and social queuing; Ridley et al. 2005). Indirect fitness benefits appear to be small in crows (Caffrey 2000, K. McGowan unpubl. data), and the species' normally low mortality and frequent use of communal areas for foraging and roosting suggest that individual access to resources while "waiting" is not a strong benefit. The previously unusual and opportunistic territory-budding

by young females suggests that both males and females prefer a continued association with their natal family and space. Opportunities to enlarge an area with resources that are relatively amicably shared during non-nesting periods could be one benefit of territory-budding and continued association between related families. It is notable in this regard that new breeders did not settle where families had died or disappeared in 2002 and 2003. Such rapid social adjustments that would maximize immediate productivity (e.g. recruitment of new pairs from outside the immediate area to suddenly vacant territories) may be slowed by the complex of factors that influence social decisions in long-lived birds.

On the other hand, both social and population effects are less than one might have expected, given the mortality. After two years of elevated mortality, and especially after losing >33% of our marked population in the second year, the number of breeding families within the study area declined ~17% from 2003 to 2004. This marked but not dramatic change in breeding density can be directly attributed to the cooperative breeding system: the presence of auxiliaries buffered the breeder losses, facilitating new breeding pairs through budding and recruitment to single breeder openings, and preventing a more dramatic decline in breeding units. Woolfenden and Fitzpatrick (1984) reported a similar buffering of breeding density after an epidemic in their population of Florida Scrub-Jays. It is likely that the presence of "surplus" crows existing as auxiliaries in a population can ameliorate some population effects of WNV for a while.

Despite the buffering capacity of cooperative breeding, if the severe outbreaks like those documented here and in other areas (Yaremych et al. 2003, Caffrey et al. 2005) occur repeatedly over several years, they must cause drastic population reduction unless resistance evolves rapidly. There is, as yet, little evidence of increasing resistance. Only 3% of sampled crows showed antibodies in Illinois during the 2002 WNV season (Yaremych et al. 2004; see also Ringia et al. 2004). In Ithaca and surrounding areas, our sampling of crows for antibodies since 2001 suggests that resistance is increasing extremely slowly, if at all (K. McGowan et al. unpubl. data). This being the case, subsequent outbreaks will affect a largely naïve population and will cause continuing, perhaps dramatic, population declines.

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