SHORT COMMUNICATIONS

The Condor 107:128–132
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WEST NILE VIRUS DEVASTATES AN AMERICAN CROW POPULATION

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Abstract. In its spread west across North America in 2002, West Nile virus (WNV) reached a population of marked American Crows (*Corvus brachyrhynchos*) in Stillwater, Oklahoma, in late summer. Within two months, 46 of 120 individuals were missing or known to be dead, 39 of which (33% of the population) are estimated to have died for WNV-related reasons. In 2003, 56 of 78 marked crows disappeared or were found dead between June and November. Five of the 28 juvenile losses were possibly unrelated to WNV, thus we estimate that 65% of our population died because of this pathogen in 2003. The total loss of 72% of population members, including 82% of juveniles, in a single year of WNV exposure raises concern for precipitous declines in American Crow populations in coming years.

Key words: American Crows, mortality, population, West Nile virus.

El Virus del Nilo Occidental Devasta una Población de *Corvus brachyrhynchos*

Resumen. En su diseminación hacia el oeste de América del Norte durante 2002, el Virus del Nilo Occidental alcanzó a fines del verano una población marcada de *Corvus brachyrhynchos* en Stillwater, Oklahoma. En menos de dos meses, 46 de los 120 individuos registrados desaparecieron o murieron, 39 de los cuales (33% de la población) estimamos que murieron por causas relacionadas con el virus. En 2003, 56 de los 78 cuervos marcados desaparecieron o fueron encontrados muertos entre junio y noviembre. Cinco de las 28 pérdidas de juveniles posiblemente no estuvieron relacionadas con el virus, por lo que estimamos que el 65% de nuestra población murió a causa de este patógeno en 2003. La pérdida total del 72% de los miembros de la población, incluyendo el 82% de los juveniles, en un solo año de exposición al virus plantea preocupaciones en cuanto a la posibilidad de una disminución precipitada de las poblaciones de *C. brachyrhynchos* en los próximos años.

In the five years since West Nile virus was first detected in the Western Hemisphere (New York City in 1999), it has spread west to the Pacific Coast of the United States, north and west through seven Canadian provinces, and south to the Caribbean and Central America. Efforts to document the impacts of the virus on North American birds have been hampered by the lack of information from the field; preliminary data on population responses to exposure are available only for American Crows (*Corvus brachyrhynchos*, Caffrey et al. 2003) and Greater Sage-Grouse (*Centrocercus urophasianus*, Naugle et al. 2004, Walker et al. 2004).

American Crows are extremely vulnerable to West Nile virus under laboratory conditions; mortality approaches 100% (McLean et al. 2001, Komar et al. 2003, Brault et al. 2004). Data collected fortuitously suggest that crows also suffer high mortality in the wild; more than 57 000 dead crows were reported to authorities in the United States from 1999 through 2002 (Eidson, Komar et al. 2001, Marfin et al. 2001, CDC 2002a, 2002b). Because of their susceptibility to the virus, their tendency to occur in habitats occupied by humans, and their large size (compared to other birds), crows have become the sentinel organism for the spread and degree of prevalence of West Nile virus; dead crows portend human risk (Eidson, Komar et al. 2001, Eidson, Miller et al. 2001, Watson et al. 2004). Yet the relationship between the number of carcasses found and the actual number of crows that have died is not known, nor are the impacts of this epizootic on crow population organization and function.

As part of a long-term study investigating social organization, dispersal patterns, and details of cooperative nesting attempts, we had been observing a population of American Crows since the fall of 1997. Other than the relatively high loss of juveniles through early fall each year, survivorship of crows was quite high;

Manuscript received 20 June 2004; accepted 22 October 2004.

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from 1998 through August 2002, only 1%–3% of second-year and older crows disappeared between the months of June and November. In August 2002, 120 of 145 crows in 28 family groups were marked. West Nile virus arrived in our study area by early September, and by November, 46 of the 120 crows were missing or known to be dead (Caffrey et al. 2003). We estimate, based on disappearance data for September and October in years prior to the arrival of West Nile virus (Caffrey et al. 2003), that seven of the 46 crows may have disappeared for reasons unrelated to West Nile virus. Thus approximately 33% of our marked crows died within two months of exposure to West Nile virus in 2002. We continued to monitor members of this population through the end of the West Nile virus season of 2003.

METHODS

For this study, we observed crows in the residential community of Stillwater, Oklahoma, during the months of June through October 2003. Second-year and older crows had been captured with a rocket net or a Netlauncher (Caffrey 2002a), or had been marked as nestlings (Caffrey 2002b). These crows had been marked with patagial tags and colored leg bands (Caffrey 2002c). No additional free-flying crows were caught for this study, and nestlings in 2003 were marked with only colored leg bands. Blood samples were taken from the brachial vein of all crows, from which we determined the sex of individuals (Griffiths et al. 1998).

Crows were observed with binoculars and spotting scopes, usually from automobiles. We monitored members of this population continuously for the six years 1997–2003. Monitoring crow groups 2–12 times per month (the differences being seasonally- and habitat-based) in the years 1997 through the beginning of 2003 allowed the detection of crow deaths or dispersal out of natal groups and out of our population. During June–November of 2003, we looked for crow groups 2–4 times per week.

American Crows are cooperative breeders—breeding pairs are assisted in reproductive attempts by nonbreeding individuals—and many of their assistants are offspring from previous years that have delayed dispersal (Verbeek and Caffrey 2002). Crows in Stillwater lived in family groups, each of which included a pair of breeders and from 0–10 ''auxiliaries'' (ostensibly nonbreeding individuals). At the beginning of the breeding season of 2003, our study population consisted of 53 crows in 18 breeding groups; 44 of these crows were individually marked, including 34 breeders (territory-owning, nest-building pair members) and 10 auxiliaries (six second-year, and four third-year, birds). Forty-six nestlings from 14 broods were marked in April and May. Of these, seven nestlings were never seen alive outside their nests, and five juveniles moved into areas where they could not be observed. The sex was not determined for two of the 34 juveniles in our data set.

We provide ''disappearance dates'' as the last dates that individuals were seen alive, thus these dates are approximations. Throughout this paper we often use ''disappearance(s)'' in lieu of ''disappearance(s) and death(s).''

Crow carcasses were submitted to the National Wildlife Health Center (USGS, Madison, WI) and tested for West Nile virus presence by virus isolation (Docherty and Slota 1988) and using a Polymerase Chain Reaction (RT-PCR) assay with West Nile virus-specific primers (Lanciotti et al. 2000).

Mortality of males and females was compared with a 2×2 contingency table and a G-test of independence. The distribution of disappearances by group size was compared, with a chi-square test, to an expected frequency calculated from the binomial distribution. We used a significance level of $\alpha = 0.05$.

RESULTS

In 2003 crows began disappearing in early June, at about the same time West Nile virus was first confirmed in Oklahoma in that year (a horse in Sequoyah County tested positive on May 28; K. K. Bradley, Oklahoma State Public Health Veterinarian and Interim State Epidemiologist, pers. comm.). By November, 56 of 78 marked crows (72%) had disappeared or were known to be dead. We found four carcasses, all of which tested positive for West Nile virus antigen.

The temporal pattern of individual disappearances (Fig. 1a) was manifested at the population level as an increase in mortality rate as the summer progressed (Fig. 1b). Juvenile crows appeared to suffer the highest mortality (Table 1), yet young crows often disappear or are found dead during the months of May and June. Disappearance data indicate no sex bias in mortality across the population ($G = 0.2$, $P = 0.63$; Table 1).

Within pairs, there was no sex bias as to the order of disappearance. There were 13 cases in which both members of a pair were marked and at least one disappeared; males and females disappeared at approximately the same time in three pairs, females disappeared first in five pairs, and males disappeared first in five pairs.

We examined patterns of disappearances within groups for evidence of horizontal transmission, but did not find strong support for crow-to-crow contagion. The distribution of disappearances did not differ from random ($\chi^2_8 = 15.3$, $P > 0.10$; Fig. 2), and the temporal data also suggested that disappearances within groups were independent events. If group members had infected other group members, subsequent deaths would have been within one week of preceding deaths (Komar et al. 2003), and disappearance dates should be similarly spaced. In eight groups where both breeders disappeared, the second to disappear did so at approximately the same time ($n = 2$), from 17–30 days later ($n = 3$), or at least two months later ($n = 3$). There were 14 groups that lost at least two members (including those that lost two breeders) and for which we had complete disappearance data. Of the 39 ''subsequent'' disappearances in those groups, 12 were within 10 days of preceding disappearances.

Of 18 crow groups, only one (of three crows) survived intact; the group of two with zero losses in Figure 2a was a breeding pair that produced at least one fledgling, which we were unable to identify before it/they disappeared. Eight groups lost the majority of

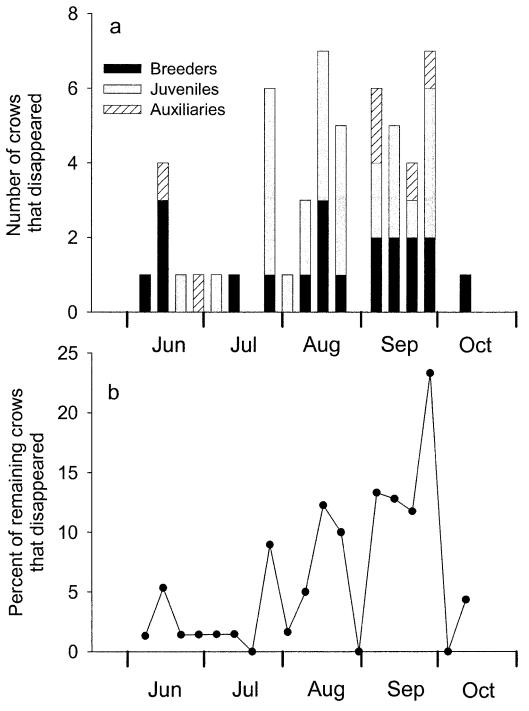

FIGURE 1. Fifty-six of 78 marked crows disappeared from June through October 2003; two breeders for whom ''disappearance dates'' could not be determined are not included. Tick marks on X axes indicate the first day of the month. (a) Number of crows that disappeared during each week. Breeders were members of nest-building pairs, juveniles were crows hatched in 2003, and auxiliaries were second-year and older nonbreeding group members. (b) Percent of the remaining population that disappeared each week.

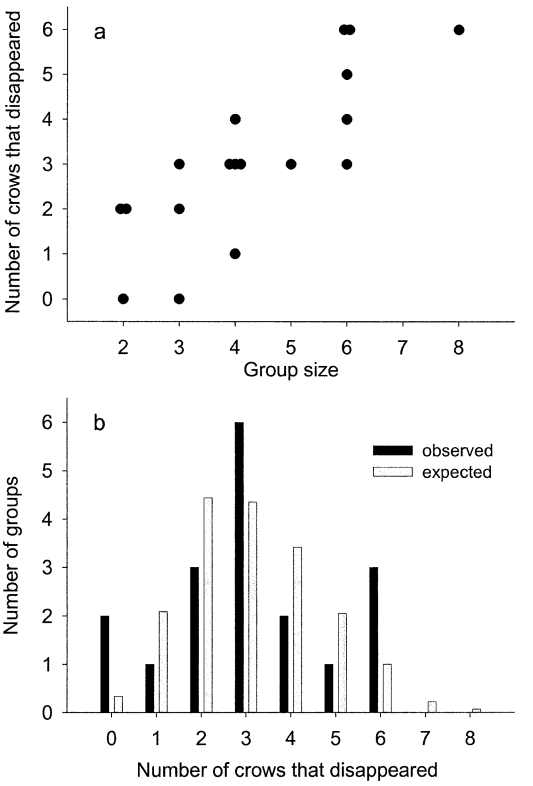

FIGURE 2. Fifty-six of 78 marked crows disappeared from June through October 2003. (a) Number of crows that disappeared from groups of different sizes. (b) Observed and expected (binomial) distributions of crow disappearances.

their members, four juveniles were orphaned (of which three didn't survive), and six whole groups disappeared. As crows disappeared, we observed lone group survivors wandering and calling from around their territories, unmarked individuals moving in to replace lost breeders, and the remnants of neighboring groups joining together to come undone, again, by more disappearances.

DISCUSSION

We followed the devastation of an American Crow population we had been observing for five years, as West Nile virus arrived and the majority of the population disappeared. We found only four carcasses in 2003, but crows tend to seek out quiet, protected places when they begin to succumb to West Nile virus infection (A. B. Clark, D. A. Robinson, and K. J. McGowan, pers. comm.). Almost all territories of crows in this study included wooded and densely veg-

TABLE 1. Numbers of marked crows alive on 1 June 2003, and numbers (%) of those that disappeared through 31 October 2003. Breeders were members of nest-building pairs, auxiliaries were second-year and older nonbreeding group members, and juveniles were crows hatched in 2003. Two juveniles of unknown sex are included under ''Total.''

	Females		Males		Total	
	Alive 6/1	Gone 11/1	Alive 6/1	Gone 11/1	Alive 6/1	Gone 11/1
Breeders	16	11 (69%)	18	11 (61%)	34	22 (65%)
Auxiliaries	3	2 (67%)	7	4 (57%)	10	6 (60%)
Juveniles	17	14 (82%)	15	13 (87%)	34	28 (82%)

etated areas used by crows but not by humans; areas impossible to search efficiently. Avian carcasses generally last less than a week on the ground (Osborn et al. 2000), and one of the four carcasses we found had been scavenged. In addition, dying crows are more vulnerable to predation, and predators may carry their bodies elsewhere. For these reasons, and those below, we do not believe that the lack of more carcasses suggests our crows disappeared for reasons unrelated to West Nile virus.

Evidence from the lab and the field suggests crows are at great risk of infection, and survivorship of infected individuals is close to zero. Unlike 24 other species of birds tested (Komar et al. 2003), American Crows have become infected through every route examined—getting bitten by infected mosquitoes, eating infected prey, drinking water containing viral particles, and being in physical contact with infected conspecifics (Komar et al. 2003). Of 40 experimentally infected crows, only one (that became infected through physical contact with infected crows) survived (McLean et al. 2001, Komar et al. 2003, Brault et al. 2004). Limited field data also suggest that few crows have survived infection; antibodies specific for West Nile virus were detected in only five of 156 crows caught in east-central Illinois from February through October 2002 (Yaremych et al. 2004).

During 1998–2002, prior to the arrival of West Nile virus in our study area, only two of 150 breeders disappeared from June through October of each year, and only four of 156 auxiliaries disappeared during those same periods. We therefore believe that all of the breeder and auxiliary disappearances from June–November 2003 reflect deaths from West Nile virus infection. However, juvenile disappearance is much more common during summer and early fall. Of 100 marked fledglings over the years 1998 and 2000–2002, 33 disappeared or were known to have died between May through mid-July, and only one disappeared between July and September. Of 84 juveniles alive in August of the years 1998–2001 combined, 18% disappeared during the months of September and October. Only two of 34 fledglings in 2003 disappeared before mid-July. If we attribute both of those disappearances to ''natural causes,'' and apply the same disappearance relationships from previous years to the 2003 cohort from mid-July through October, approximately five of the 28 juvenile disappearances between fledging and November might have occurred in the absence of West Nile virus. Thus 68% (23/34) may be a better estimate for the mortality suffered by young crows in the face of their first West Nile virus season.

We therefore estimate that in 2003, 65% of our study population (51 of 78 individuals) died because of exposure to West Nile virus. Combined with the natural losses of juvenile crows (which brought their mortality to 82% before their first November, in an otherwise above-average year for post-fledging survivorship), 72% of our population died over one West Nile virus season in Oklahoma (June through October). Mortality was similar in an examination of a smaller number of crows in east-central Illinois in 2002; 19 of 28 (68%) radio-tagged (mostly juvenile) American Crows died and tested positive for WNV infection (Yaremych et al. 2004).

Crows in Stillwater were year-round residents with complex social lives. The majority of auxiliaries were individuals that had delayed dispersal, but many groups also included individuals that had moved in from other groups. Most of the crows in our population delayed breeding until 3 or 4 years of age, and many remained home or moved within the population until they bred. We regularly saw crows spending time with groups other than their own, and some individuals that had dispersed out of our population returned occasionally to natal territories and spent time with their parents. Some individuals visited their siblings living elsewhere, and some moved in with their siblings' families. Several males established territories adjacent to their parents, and extended families of at least three generations would sometimes spend time together (CC, unpubl. data). Thus the effects of West Nile virus extended beyond the number of crows that died, to fracturing the foundation of the social lives of survivors.

Are the surviving crows in Stillwater alive because they are immune, or because they have yet to be exposed to the virus? To the extent that the latter is the case, and barring the evolution of a less virulent strain of West Nile virus, American Crow populations in North America might be expected to decline precipitously in the next few years. We discovered only four of approximately 56 dead crows, which suggests that the tens of thousands of carcasses found in North America in the last five years might under-represent the number that have died by an order of magnitude. As such, West Nile virus is likely to cause devastating disruptions to the social organization and demographics of American Crows.

We thank Mike Disney, Roy Churchwell, and the City Manager's Office of Stillwater, Oklahoma, for assistance in accessing nestlings in 2003, and Chad Powers for help in the field. We also thank the diagnostic staff at the USGS, National Wildlife Health Center in Madison, Wisconsin, for the testing of crow carcasses. We are grateful to Charlie Peterson for help of all kinds, including the production of our figures. Nick Komar, Paul T. Green, David S. Dobkin, Melanie K. Rathburn, and two anonymous reviewers provided helpful comments on earlier versions of the manuscript, and Robert M. Gibson provided binomial distribution guidance. This research was funded by grants from the National Science Foundation (IBN 0331531) and the Payne County (OK) Audubon society, and financial assistance from Jerry and Nona Wilhm.

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