BREEDING BIOLOGY OF AMERICAN CROWS

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ABSTRACT.—The breeding biology of cooperatively breeding American Crows (Corvus brachyrhynchos) was studied on Cape Cod, Massachusetts, from 1983–1987. The study site consisted of habitats ranging from a remote barrier beach to populated suburban areas. Family groups ranged in size from two to 10 members, the latter including an adult pair with their one- to four-year-old offspring. Territories were defended year-round and the mean territory size was 42.1 ha. The mean distance between nests of bordering territories was 0.86 km. Most (88%) nests were built in pitch pine (Pinus rigida) trees. Mean nest depth was 24.1 cm, mean total diameter of the nests was 40.7 cm, and the mean diameter of the nest cups was 23.8 cm. Nest height averaged 9.7 m; mean tree height was 10.9 m. Incubation occurred between March and June over an average of 22.3 days. The mean number of days until fledging was 30.1. Reproductive success was measured through the mean number of surviving fledglings. The total mean was 2.0 (N = 46). There was a trend towards increased fledgling production in family groups with six or more members (N = 10, \bar{x} = 2.6 \pm 1.7). Received 16 Oct. 1989, accepted 30 Jan. 1990.

Relatively little is known about the breeding biology of North American Corvus with the exception of Northwestern Crows (Corvus caurinus) (Butler 1974, Verbeek and Butler 1981, Verbeek 1982, Butler et al. 1984). We report here the demographics and breeding biology of a population of American Crows (C. brachyrhynchos) located on Cape Cod, Massachusetts. Accounts that exist on American Crows have described the natural history of populations in other regions of the United States (Good 1952, Graber et al. 1987) and of the Florida race (C. b. pascuus) (Kilham 1984a, b, c; 1985a, b; 1986a, b).

STUDY AREA AND METHODS

The study was conducted continuously from 1983 through 1987. The data presented here are part of a long-term study of reproductive success and life history patterns of crows in two disparate habitats. One area, a seven km-long barrier beach (Sandy Neck, Barnstable, Massachusetts), was bounded by a 3200 ha salt marsh to the south and Cape Cod Bay to the north. The barrier beach was characterized by dunes on the north and south and interior patches of maritime forest (approximately 100 ha or 17% of the barrier beach). The barrier beach was subject to seasonal human recreational activities, primarily along the beach front. In contrast, the other study site was located in the developed areas of Barnstable, Massachusetts, which included residential, business, and recreational locations. This area was approximately 150 ha, consisting entirely of broken habitat. Data were collected using binoculars (7 × 35), spotting scopes (30×), and recorded through field notes, 35 mm pho-

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tography, and audio and video recordings. Group sizes were standardized for comparison by determining the number of territorial adults at the onset of incubation. We delineated territories on an U.S. Geological Survey Map (scale 1:24,000) by connecting the locations of displays and fights between neighboring groups. The territory sizes were measured with a planimeter. In areas where there was a tidal flow we measured the territory size during high tide.

Nests were located by following crows carrying sticks and observing nest building or by tracing a unique vocalization made by the incubating female breeder (Kilham 1986b). Nest distances were determined by marking their locations on the U.S. Geological Survey Map and then measuring the distances between them with a ruler. We measured nest dimensions while the nestlings were being banded or at the time of nest failure. Nestlings were banded with U.S. Fish and Wildlife aluminum leg bands and unique combinations of colored, plastic leg bands.

RESULTS

Group sizes.—Crows in our study site usually bred cooperatively (94.4%, N=54) and the offspring remained within the family units throughout the year. Group sizes ranged from two to 10 members (Table 1). The mean group size was 4.4 ± 1.9 birds (N=54, range = 2-10 birds). In all instances where an unassisted breeding pair successfully raised young (N=3), the young remained with the parents and helped in the following years. In groups that have been observed for more than one year, all offspring have remained on natal territories and actively assisted the breeders. Therefore, the composition of a group includes the breeding pair and offspring aged one to several years old.

Territories. — The mean territory size was 42.1 ± 33.6 ha (N = 49, range = 9.4–104.0 ha). There was a significant difference between the sizes of territories located in the two study sites (Chamberlain-Auger, unpubl. data). The mean distance between nests in bordering territories was 0.86 \pm 0.6 km (N = 12, range = 0.2–2.29 km).

Nests.—The mean nest depth was 24.1 ± 5.6 cm (N = 18, range = 10–38 cm). The mean nest diameter was 40.7 ± 6.6 cm (N = 19, range = 17–48 cm) and the mean nest cup diameter was 23.8 ± 4.5 cm (N = 17, range = 16–36 cm).

All of the nests were built in trees. The species of trees which were used were: pitch pine (*Pinus rigida*, N=42), white pine (*P. strobus*, N=2), spruce (*Picea* sp., N=2), and eastern red-cedar (*Juniperus virginiana*, N=2). The mean tree height was 11.0 ± 3.2 m (N=44, range = 5.3-16.4 m). The mean nest height was 9.9 ± 3.1 m (N=44, range = 4.6-15.4 m). In all cases new nests were built each year, and in some instances a second nest was built when the first failed.

We measured the distances between nests within a territory (crows remained on their territories year-round) for subsequent years and the mean intra-nest distance was 0.2 ± 0.2 km (N = 23, range = 0.0–0.6 km).

	Number per group									
Year	2	3	4	5	6	7	8	9	10	$\bar{x} \pm SD(N)$
1983	_	3	_	1	_	_	_	_	_	3.5 ± 1.0 (4)
1984	2	7	1	2	1	_	_	_	_	$3.5 \pm 1.2 (13)$
1985	1	4	4	2	3	_	_	_	_	$4.1 \pm 1.3 (14)$
1986	_	6	2	2	2	1	3	_	_	$4.9 \pm 2.0 (16)$
1987	_	3	_	1	_	1	_	1	1	$5.7 \pm 2.8 (7)$
Total	3	23	7	8	6	2	3	1	1	$4.4 \pm 1.9 (54)$

TABLE 1
GROUP SIZES OF AMERICAN CROWS

Incubation and brooding.—The mean incubation period for crows on Cape Cod (1983–1987) was 23.2 ± 6.0 days (N = 13, range = 14–33 days). We observed crows incubating during the months of March (N = 1), April (16), May (10), and June (2). The earliest date on which incubation was initiated was March 20, 1984, and the latest date on which we observed the beginning of incubation was June 17 (1985 and 1987). The months (N) during which hatching occurred or during which we observed young in the nest were: April (2), May (15), June (19), and July (1). The mean number of days until fledging was 29.6 ± 5.3 days (N = 15, range = 16–36 days). The earliest date on which we observed a nestling to fledge was May 26, 1985, and the latest was July 26, 1983.

Reproductive success.—Table 2 shows the mean number of fledglings that survived each year. Fig. 1 correlates group size with the number of surviving fledglings. There was no significant difference between fledgling survival and the number of birds in a group.

DISCUSSION

Group size.—American Crows were originally thought to have bred as pairs with the young dispersing at the end of the breeding season (Bent 1946, Good 1952, Goodwin 1976). Kilham (1984c) observed helping behaviors by auxiliaries and concluded that a cooperative breeding system was being employed by the Florida race of American Crows (C. b. pascuus). Our observations of the Cape Cod population concur with Kilham's findings. In addition our observations of particular behaviors in some of the groups suggest a trend towards communal breeding. We have observed shared incubation and brooding by breeders and helpers seven times in three years in the two largest breeding groups (unpubl. data). To date, all surviving offspring have remained on their natal territories for at least

Year	$\bar{x} \pm SD$	No. nests
1983	0.8 ± 1.1	5
1984	2.3 ± 1.8	14
1985	2.0 ± 1.7	13
1986	3.3 ± 1.3	8
1987	1.0 ± 1.3	6
Total	2.0 ± 1.7	46

TABLE 2
MEAN NUMBER OF SURVIVING FLEDGLINGS

four years and acted as non-breeding helpers; consequently the group size increased each year.

Northwestern Crows also utilized a cooperative breeding system but only one of the offspring was allowed to remain as a helper each year (Butler et al. 1984). Another North American Crow, the Fish Crow (C. ossifragus) is not known to breed cooperatively (Goodwin 1976).

Territories.—Historically American Crows were thought to be non-territorial throughout most of the year except when nesting was occuring (Bent 1946, Good 1952, Goodwin 1976, Brown and Veltman 1987). Our observations revealed that the territories of crows on Cape Cod were all-purpose and actively defended throughout the year. Territorial behavior patterns described by Kilham (1985b) were observed for all group members, but in many instances the breeders initiated the displays with the auxiliaries joining later. During the coldest winter months, the crows from observed breeding groups joined other crows in a common roost. We observed the birds leaving their territories towards dusk, joining other crows in the roost throughout the night, and then returning to their territories at dawn.

The size of American Crow territory observed in our study area ranks between that of the Black Crow (C. capensis) (60 ha, Skead 1952) and the Carrion Crow (C. corone) (26.7 \pm 10.4 ha, Wittenberg 1968). The nesting territory of the Northwestern Crow (0.49 \pm 0.2 ha, Butler et al. 1984) is considerably smaller than American Crow territories observed in our study area.

Nests.—Nests of American Crows have been described in detail (Bent 1946, Good 1952). Nests were constructed by both the breeders and helpers (Kilham 1984, pers. obs.). In some cases, second nests were begun when the first failed. Renesting attempts have been reported by Emlen (1942) and Kilham (1986a). In addition to renesting, our observations

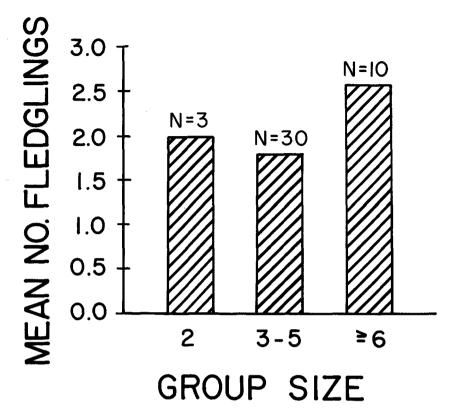


Fig. 1. Mean number of fledglings as a function of group size.

revealed the building of false nests or practice nests by both the breeders and the helpers. This was seen in 12 instances.

In some instances, Northwestern Crows build nests on the ground or in decidous trees (Butler et al. 1984) and there are reports of American Crows nesting in deciduous trees (Bent 1946, Good 1952). We found that all crow nests in our study area were in evergreen trees, with the majority of nests located in pitch pines, the most common tree in the area.

Incubation and brooding.—Reported incubation periods for American Crows vary from 16 days to 18 days (Emlen 1942, Bent 1946, Kilham 1984c). The breeding season for crows in Florida usually extends from January until May (Kilham 1985a). Good (1952) observed fledging to occur after 26 to 35 days, and Goodwin (1976) lists 35 days for C. brachyrhynchos. The average age of fledging for Northwestern Crows is 32 ± 2.5 days, and 26 ± 3.4 days (Butler et al. 1984). Incubation and brooding

in American Crows by the female exclusively has been observed by Good (1952) and Kilham (1984c), while incubation by both sexes was reported by Bent (1946). Our observations of crows on Cape Cod revealed incubation and brooding primarily by the breeding female but with assistance from the helpers (Chamberlain-Auger, unpubl. data). Feeding of the incubating bird and the young was a cooperative effort shared by the breeders and the helpers (Kilham 1984c, unpubl. data).

Reproductive success.—Emlen (1942) found 77% mortality of nestlings in a California colony of American Crows. Parental desertion and nestling competition were thought to be the causes of mortality. In our study, the known causes of mortality to eggs, nestlings, or fledglings were: predation by raccoons (Procyon lotor) (five nests containing nestlings) and Great Horned Owls (Bubo virginianus) (three nests with nestlings and one caged fledgling), automobiles (three fledglings), injury (one fledgling), infanticide (one nestling), hunting (one fledgling) (also discussed by Bent 1946 and Good 1952), starvation (two fledglings), and adverse weather conditions (one nest with nestlings). Butler et al. (1984) found a 75% survival rate of Northwestern Crow fledglings after nine weeks. Glaucous-winged Gulls (Larus glaucescens) were the primary cause of fledgling deaths.

Woolfenden and Fitzpatrick (1984) examined the effect of helpers on reproductive success in Florida Scrub Jays (Aphelocoma c. coerulescens). Their results showed a significant increase in fledgling success when a helper was present but no increase in production as helper numbers increased. In addition, they observed a trend towards increased fledgling success when an older, experienced helper was present. Similarly, Lawton and Guinton (1981) reported a significant increase in Brown Jay (Cyanocorax morio) fledgling production with experienced helpers.

In our study, there was no significant difference in fledgling production between groups without any helpers and groups with one to three helpers, although the trend was for decreased production in the larger group size. We propose that this trend can be explained as a consequence of habitat variation between territories which resulted in subsequent mortality differences. We observed an increased degree of predation on eggs and nestlings of groups living in the more rural undeveloped areas (N = 12 or 40%), i.e., the barrier beach. The result was fewer fledglings surviving ($\bar{x} = 0.6 \pm 1.4$). Two of the causes of the increased predation rate on the rural groups were lower nest heights and a lack of a food source provided by humans (garbage and road kills). We suspect that raccoons, the most common predator, were forced to search for natural foods and had greater access to crow nests (unpubl. data).

In groups greater than or equal to six birds (four or more helpers), there was a trend towards increased fledgling production. All of these groups

were found in the more urban regions of the study site, and all contained experienced helpers. In addition, our observations have revealed that in a few of the largest groups one-year-old birds, the inexperienced helpers, were permitted to watch the breeders and older helpers but not allowed to participate in the feeding of the incubator/brooder or nestlings.

American Crows were initially thought to have a simple breeding system but our observations are similar to recent studies revealing the more complex reproductive system of a highly social bird.

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