

FEMALE-BIASED DELAYED DISPERSAL AND HELPING IN AMERICAN CROWS

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ABSTRACT.—Observation of a resident population of Western American Crows (*Corvus brachyrhynchos hesperis*) over five years revealed a social structure that deviates from that of a majority of cooperative breeders, including other corvids. Breeding density was unusually high (0.8 pairs/ha). Core areas occupied by pairs and families were small, overlapped extensively with those of neighbors, and were not defended against conspecifics. A nonbreeding flock was resident on the study site. Juvenile dispersal patterns were highly variable; individuals dispersed at various ages after two months postfledging. They either joined the nonbreeding flock or left the study area. Some individuals delayed dispersal for one or more years, while some returned home after extended absences. As yearlings, more females than males were resident in their natal core area during the breeding season. Most, but not all of those at home served as helpers. More females than males assisted their parents in breeding. The female bias in dispersal and helping is unusual. It suggests that the costs and benefits associated with these behaviors differ between the sexes, and may be different from those postulated for many other cooperative breeders. Received 28 January 1991, accepted 13 January 1992.

ALTHOUGH MUCH diversity exists in life-history traits among avian cooperative breeders, a majority of species share a number of ecological, demographic and social characteristics. Most species are primarily monogamous with helpers at the nest (Brown 1987, Smith 1990). Breeding groups tend to be permanent residents on all-purpose territories (e.g. Lewis 1981, Brown et al. 1983, Rabenold 1985, Curry and Grant 1990); colonially breeding species are uncommon (Brown 1974, 1978, Heinsohn 1987, Emlen 1990). Delayed dispersal by offspring rarely occurs if dispersal and floating are an option and, therefore, within-population nonbreeding flocks are uncommon (Brown 1978, Koenig and Pitelka 1981, Koenig et al. 1992). Dispersal in most cooperative breeders is female-biased (e.g. Gaston 1978a, Mumme and de Queiroz 1985, Marzluff and Balda 1988, Reyer 1990), as in most birds (Greenwood 1980). The majority of helpers across species, therefore, are sons from previous broods (e.g. Rowley 1981, Austad and Rabenold 1986, Lennartz et al. 1987, Curry 1988, Rowley and Russell 1990).

Here I describe the social organization of a cooperatively breeding population of Western American Crows (*Corvus brachyrhynchos hesperis*). I found that breeding pairs regularly were assisted by nonbreeding auxiliaries, as in other cooperative breeders. However, their social structure deviates in several ways from that

common to many cooperatively breeding species, including other corvids. I use patterns of space use, dispersal, settlement, and breeding to characterize the unusual social organization in this population.

STUDY AREA AND METHODS

I studied a resident population on the Balboa Golf Course in Encino, California, from March 1985 to March 1990. The habitat consists of tracts of grass separated by rows of trees, with additional clumps of trees scattered throughout the site. The tree flora is dominated by conifers and eucalypts, but also includes sycamores, oaks, and several exotics. The course is watered and mowed regularly, and is surrounded by parkland, cornfields, and residential areas. The climate is southern Californian Mediterranean, with hot, dry summers and occasional winter rains between December and February.

I captured 173 free-flying individuals (63 males, 54 females, 56 unsexed) using large walk-in traps ($n = 52$) and a cannon net ($n = 121$). Trapped crows were weighed, measured and marked. I took five morphological measurements: weight; total head length (from back of head to tip of bill = THL); culmen length; bill depth at anterior end of nares; and tarsus length (TL), measured as distance between intertarsal joints bent at right angles. Each individual received two identical, 3.5 × 6.5 cm patagial tags bearing two letters, a U.S. Fish and Wildlife leg band, and a unique combination of colored leg bands. Nestlings ($n = 97$) also were weighed, measured and marked between

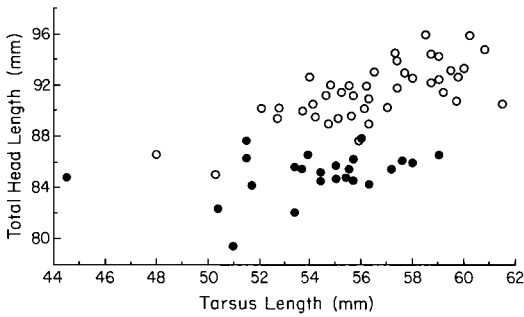


Fig. 1. Relationship between tarsus and total head length for individuals older than two months postfledging. Females and males represented by solid and open circles, respectively.

32 and 38 days posthatching (mean nestling period = $41.0 \pm \text{SE of } 0.9$ days, $n = 17$; unpubl. data).

I distinguished yearling crows from adults by the following characteristics: yearlings have a dull brown cast to their plumage in contrast to the glossy black of adults; yearling retrices and remiges are pointed or rounded in shape, in contrast to the more truncated feathers of adults; yearling tail shape is squared compared to the rounded appearance of adult tails (Emlen 1936). Marked individuals were sexed behaviorally or by using a discriminant function based on morphological measurements. Thirty individuals were sexed from observation of breeding behavior—females performed all incubation and brooding and were fed on and off the nest by males, as in other crows (Good 1952, Goodwin 1976). A discriminant function was generated based on the measurements of these individuals plus those of 42 found or obtained dead from local rehabilitation facilities and sexed by dissection. The best discriminant function, obtained by a stepwise procedure, correctly classified the sex of 96% of these 72 individuals based on total head and tarsus length (Fig. 1; $F = 102.74$, $df = 2$ and 76 , $P < 0.0001$). This discriminant function ($Z = 1.782\text{THL} - 0.503\text{TL}$) was then used to sex 17 individuals caught at least two months postfledging. Overlap in body size was too great to distinguish the sex of nestlings and young juveniles.

I conducted approximately 5,300 h of observation, concentrated during the breeding season (March through June). I made observations using 10 \times binoculars and a spotting scope, and my car as a blind. The roads throughout the course provided access to all areas. I censused the study site and noted the location of individuals four to six times per week during the breeding season and one to three times per week at other times of the year. Nest locations were plotted on a map of the study site each year. I calculated internest distances using a GTCO Digitizer. Residents ranged widely both on and off the course; however, during the breeding season pairs concentrated their activity in a specific core area. I defined two types of

core areas based on their location: interior core areas bordered on all sides by golf course; peripheral areas in which nests were placed in trees along the edge, so that one side of the nest tree faced off the course (e.g. a street or the driving range).

Individuals were classified as breeders, auxiliaries, or members of the nonbreeding flock. Breeders engaged in courtship activities, remained in close contact during the egg-laying stage, and were never assisted in nest building. For 31 of 59 breeding pairs observed over five years, at least one member was marked. Auxiliaries were nonbreeders regularly associated with a breeding pair and their core area. Of 45 individual auxiliaries, 28 were marked. Members of the nonbreeding flock often were with each other, and were not tied to a particular core area. Fourteen nonbreeding flock members were marked. Of marked nestlings, 12 males and 9 females either were caught after two months postfledging or eventually were observed breeding. These individuals are included in the above sample sizes.

I defined helpers as auxiliaries that fed nestlings. Determination that nonbreeders associated with breeding pairs were not acting as helpers was based on at least three 4-h periods of observation at nests after hatching. Individuals were classified as having dispersed once they no longer concentrated their activity in their natal core area.

Survivorship of nestlings and juveniles was measured at four stages: fledging, two weeks postfledging, two months postfledging, and one year. Two weeks is the approximate time before fledglings first come down to the ground successfully; before this time they cannot generate enough lift to return to trees. Two months was the earliest observed age of independence. For the group classified as having survived to one year, I included only those individuals alive at two months whose subsequent fates were known.

Survivorship, dispersal and settlement patterns, and sex-related behavior were analyzed only for marked individuals. I used ANOVAs and *t*-tests to analyze relationships between dispersal behavior and individual characteristics. Sex biases in dispersal and helping were analyzed using only yearlings so that each individual was included only once. All statistical tests used are two-tailed. In all cases the most powerful test, appropriate for sample size, was used. For variables where no significant between-year differences were found, data were pooled across years. Descriptive statistics are presented as means and standard errors.

RESULTS

SPATIAL DISTRIBUTION

During the breeding season, crows were members either of breeding groups or a resident nonbreeding flock.

Breeding groups.—Breeding groups occupied core areas distributed throughout the course (Fig. 2). Breeding density on the course as a whole remained relatively constant over the five years at approximately 0.8 pairs/ha. All core areas contained large trees and parts of fairways, and overlapped widely with those of neighbors. Interior core areas appeared larger and less overlapping than peripheral ones. Nearest-neighbor distances for interior nests were significantly greater than those for peripherals, and nests in interior core areas had fewer other active crow nests within 110 m (the furthest nearest-neighbor distance measured; Table 1). Rows of trees along the edges of the course therefore supported a higher density of nests than in the interior. The core areas of many peripheral pairs were almost completely overlapped by those of others. Some peripheral pairs even nested in the same tree; in each of three years, one tree was shared by two different pairs.

Occupancy of interior core areas was more stable than that of peripheral ones. All interior pairs bred in the same location for as long as they were monitored (2–5 years). Four pairs breeding for their first time also established themselves in the interior. Peripheral core areas contained both long-term residents and several pairs each year that “squeezed in” to these areas. Some of the “squeezer” pairs were resident in the area but nested off the study site in some years (e.g. in a park across the street). Some of the long-term peripheral residents had nearby off-the-course foraging areas where they could be found regularly. Three pairs breeding for their first time established themselves on the periphery over the five years.

Core areas did not appear to be defended against conspecifics. Neighbors often foraged together, members of breeding groups were regularly observed in others' core areas, and breeders rarely prevented others from entering their nest tree or landing on or near their nest.

Vacancy and establishment of core areas.—In two different years, an interior male died after previously having bred successfully. One death oc-

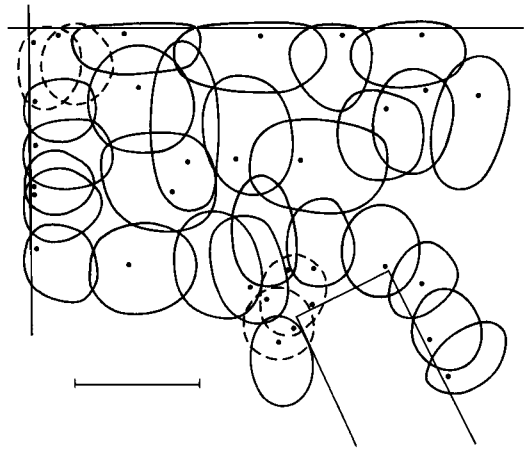


Fig. 2. Core areas and nest locations (•) of pairs observed in 1989. Core areas subjectively drawn. North (top) and west borders of study plot (indicated by fine lines) are boundaries of golf course. Lined area near southeast corner is driving range. The golf course extends to both the east and south. Broken lines indicate approximate core areas of pairs not part of study. Scale bar on bottom left represents 200 m.

curred during the breeding season; his mate went on to fledge one of the four nestlings alive at the time of his death. The other occurred in November. In both cases, the core areas of these males remained unoccupied for the following two breeding seasons. One was still vacant four years later. Neighbors did not expand into the available space and prevent new pairs from settling; adjacent core areas remained approximately the same, and there were conspicuous vacancies where the former pairs had resided. In three other years, two females (and presumably their mates) and one family of three “disappeared” for the breeding season and then returned to the course and their core areas early in the summer of the same year. In all three cases, these interior core areas also remained unoccupied for the duration of the breeding season.

I observed the establishment of seven core areas by pairs breeding for the first time (four males and two females tagged as nestlings, one

TABLE 1. Nest spacing in interior versus peripheral core areas. Values are $\bar{x} \pm SE$ (n). P -values based on t -tests.

| | Interior | Peripheral | P |
|---------------------------|----------------------|----------------------|--------|
| Nearest neighbor (m) | 63.6 \pm 3.6 (47) | 47.4 \pm 4.5 (38) | <0.01 |
| Active nests within 110 m | 2.64 \pm 0.21 (33) | 4.33 \pm 0.38 (33) | <0.001 |

TABLE 2. Percentage of breeding groups containing auxiliary birds (helpers and nonhelpers) and with only helpers.

| | 1985 | 1986 | 1987 | 1988 | 1989 | All years |
|--------------------------------|------|------|------|------|------|-----------|
| Breeding groups observed | 7 | 16 | 26 | 40 | 26 | 115 |
| Percent with auxiliary present | 57 | 56 | 39 | 28 | 31 | 37 |
| Percent with helper | 29 | 47 | 28 | 25 | 26 | 30 |

male caught when two years old and a member of the nonbreeding flock). Whether in the interior or on the periphery, settlement by all pairs appeared to involve simply squeezing into already occupied areas, accompanied by the

slight shifting of neighbors. Overt aggression was never observed. All six individuals tagged as nestlings (regardless of sex, dispersal behavior, or helper experience) settled within two core areas of their natal one.

Nonbreeding flock.—Each year this flock consisted of 20 to 30 birds. Members of the nonbreeding flock often were seen in one particular area of approximately 4 ha; no pairs bred at the center of this area, but the periphery merged into the core areas of several breeders. Nonbreeders were not restricted to this area. They were also regularly seen in the core areas of breeding pairs. The flock included individuals from four months to several years old. One male who bred from at least 1986 through 1988 joined the nonbreeding flock for the breeding season of 1989 when at least seven years old. His mate had been unmarked and her fate unknown. Of 14 birds known to have spent at least one breeding season in the nonbreeding flock, 11 were male and 3 were female. The nonbreeding flock may have served as a focus for pair formation. At least seven individuals of both sexes paired, settled, and attempted to breed the year after their tenure in the flock.

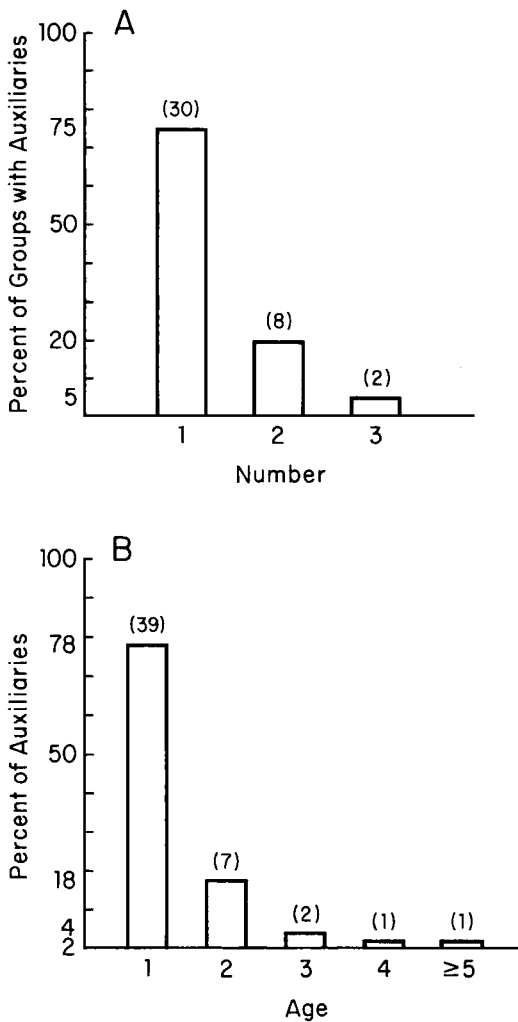


Fig. 3. (A) Distribution of auxiliary birds among breeding groups with auxiliaries, 1985-1989. (B) Age distribution of known-age auxiliaries.

COMPOSITION OF BREEDING GROUPS

In each year a substantial proportion of breeding groups contained nonbreeding, auxiliary birds. The proportion of groups with auxiliaries ranged from 28 to 57% annually, averaging 37% over all years (Table 2). The majority of groups contained only one auxiliary, although up to three were sometimes present (Fig. 3). Of known-age auxiliaries ($n = 50$), most (78%) were yearlings (Fig. 3B). Across all years of the study, 61% of auxiliaries of known sex were female. Significantly more female than male yearlings were at home during the breeding season. Of 15 females, all were present in their natal core areas; of 14 males, 9 were at home ($P = 0.0169$, Fisher's exact test). This sample in-

TABLE 3. Sex differences in helping by yearlings resident on golf course. (A) All individuals of known sex. (B) Individuals tagged as nestlings or members of whole broods caught postfledging. Chi-square test for part A significant ($P < 0.001$), as was Fisher's exact test for part B ($P = 0.0198$).

| | | Acted as helper | |
|----|--------------------|-----------------|----|
| | | Yes | No |
| A. | All individuals | | |
| | Females | 10 | 1 |
| | Males | 3 | 10 |
| B. | Tagged individuals | | |
| | Females | 6 | 1 |
| | Males | 3 | 9 |

cludes all individuals tagged as nestlings and those caught postfledging where all members of the brood were known to be marked.

Auxiliaries were prior offspring of the breeding pair. All 27 auxiliaries marked as nestlings or juveniles associated with their parents ($n = 17$) or, if both parents were unmarked, they were in their natal core areas ($n = 10$). The other marked auxiliary was a widowed female who in 1989 joined another pair and acted as a helper. She was at least five years old and had bred on the study site in 1988. Her genetic relationship with the breeding pair she helped was unknown.

HELPING

Most auxiliaries (82%) acted as helpers. In addition to feeding nestlings, helpers also fed the breeding female during incubation and brooding, fed fledglings, guarded nestlings and fledglings, and attended to nest sanitation. Non-helping auxiliaries continued to associate with breeding pairs and to be based in their core areas throughout the breeding season, but were never observed at active nests. All helpers and most nonhelping auxiliaries begged from and were fed by one or both breeders, particularly the male.

Across all years of the study, 72% of helpers of known sex were female. Among yearlings resident on the golf course, helpers were primarily female (Table 3A). To control for the possibility that females were more likely to be caught after fledging, I also analyzed the relationship using only those resident yearlings

TABLE 4. Annual mortality of breeders from March to March. Sample sizes larger for males because they were trapped more frequently than breeding females.

| | Males | | Females | |
|-----------|-------|----------------------|---------|----------------------|
| | No. | Percent disappearing | No. | Percent disappearing |
| 1985-1986 | 6 | 0 | 1 | 0 |
| 1986-1987 | 7 | 14 | 2 | 0 |
| 1987-1988 | 9 | 0 | 5 | 20 |
| 1988-1989 | 17 | 12 | 9 | 0 |
| 1989-1990 | 23 | 4 | 12 | 0 |
| Total | 62 | 7 | 29 | 3 |

tagged as nestlings or members of whole broods caught and marked between fledging and the following breeding season. Again, significantly more females than males acted as helpers (Table 3B). This was not simply a function of delayed dispersal by females; I also analyzed the difference between the sexes in their likelihood to help if at home for the breeding season. Ten of 11 females, but only 3 of 8 males assisted their parents. This difference is significant (Fisher's exact test, $P = 0.0408$). I excluded individuals who were home for the breeding season but whose helper status could not be determined because nest failure occurred before feeding began.

Three marked females and two marked males remained home with their parents for an additional one to three years after their first. In every case, these individuals helped in some years but not in others.

SURVIVORSHIP

Table 4 summarizes the annual disappearance rates of breeders by sex from one breeding season to the next (March to March). Survivorship over the five years was 93% for males and 97% for females. This is an exact figure for females; the single elimination was hit by a golf ball. Of the four males, three were found dead. The fourth, at least eight years old and an interior resident for the first four years of the study, disappeared and was presumed dead.

Table 5 summarizes survival of nestlings and juveniles. In total, 71% of fledglings survived two months. Approximately 68% of all fledglings survived to age 1. Known causes of death

TABLE 5. Nestling and juvenile survivorship between four life stages. Survival from two months postfledging to one year excludes nine individuals of unknown fate.

| | Total | Survived | |
|-------------------------|-------|----------|---------|
| | | No. | Percent |
| Fledging | 97 | 68 | 70 |
| Two weeks postfledging | 68 | 54 | 79 |
| Two months postfledging | 54 | 48 | 89 |
| One year | 39 | 37 | 95 |

of fledglings and juveniles included falling to the ground before they could fly, predation by Great Horned Owls (*Bubo virginianus*) and Red-shouldered Hawks (*Buteo lineatus*), disease (lung tumors found upon dissection), and injuries sustained from golf balls. No carcasses showed any indication of starvation.

JUVENILE DISPERSAL

Young crows exhibited variable dispersal patterns after two months old. Figure 4 summarizes the first-year histories of 43 individuals alive two months postfledging (early August). Of individuals known to be alive the following January, 18% had dispersed from their natal core areas in their first fall and either joined the nonbreeding flock or left the golf course. One-half of these individuals returned home as yearlings the following breeding season. I found that 82% of the juveniles remained home until at least January. In February, prior to the beginning of the breeding season, 12% of those at home left to join the nonbreeding flock or disperse off the course. I found that 55% of all juveniles remained at home throughout their first year and at least into their second summer. A few remained for one or more additional years, as indicated above.

I examined the relationship between first-year dispersal behavior and several characteristics of individuals, but found no significant patterns. Dispersal patterns were statistically unrelated to: (1) incubation date; (2) prefledging size (weight, THL and TL); (3) brood size at fledging, two weeks, and two months; and (4) whether or not individuals were members of helped broods. Some of the above sample sizes were small. However, pooling data into home/not and golf course/not categories for January and March did not alter the results.

For two- and three-year-olds, preliminary data

suggest there was no effect of dispersal behavior on survivorship or the outcome of first breeding attempts. For individuals alive as yearlings whose subsequent fates were known, 1 of 11 males and 2 of 11 females died. The first breeding attempts of eight males and six females all were unsuccessful.

DISCUSSION

In social organization, Western American Crows depart from the few generalizations that apply to a majority of cooperatively breeding species. Within this dense population, historically successful breeding areas were available and unoccupied, and a nonbreeding flock was present. Nonbreeding individuals of both sexes dispersed from home for the breeding season, delayed dispersal and acted as a helper, or delayed dispersal but did not help. Females delayed dispersal and assisted their parents more frequently than males. These characteristics combine with other aspects of space utilization to distinguish these birds as unusual among both cooperative breeders and corvids.

Space utilization.—The use of space by crows in this population differs from the majority of other *Corvus* species that have been studied in detail, and corvids in general. Core areas appeared to be smaller than reported territory sizes for other crows and corvids (e.g. Shank 1986, Chamberlain-Augur et al. 1990, Richner 1990), and breeding density was higher (Loman 1980, Vines 1981, Parker 1985, Davis and Davis 1986, Fitzpatrick and Woolfenden 1986, Richner 1989). The lack of any obvious area defense also contrasts strikingly with the described breeding-season space-utilization patterns of other corvids, most of which (including colonial species) maintain exclusive access to certain areas (Goodwin 1955, 1976, Antikainen 1980). Congeners such as Common Ravens (*Corvus corax*; Newton et al. 1982, Davis and Davis 1986), Hooded Crows (*C. corone cornix*; Loman 1984, 1985), Carrion Crows (*C. c. corone*; Richner 1990), and Black Crows (*C. capensis*; Skead 1952) are described as classically territorial.

Among crows in North America, space-use patterns are diverse. Northwestern Crows (*C. caurinus*) defend small nesting territories only during the breeding season (Butler et al. 1984), whereas larger, all-purpose territories are defended for at least the breeding season by Florida Crows (*C. brachyrhynchos pascuus*; Kilham

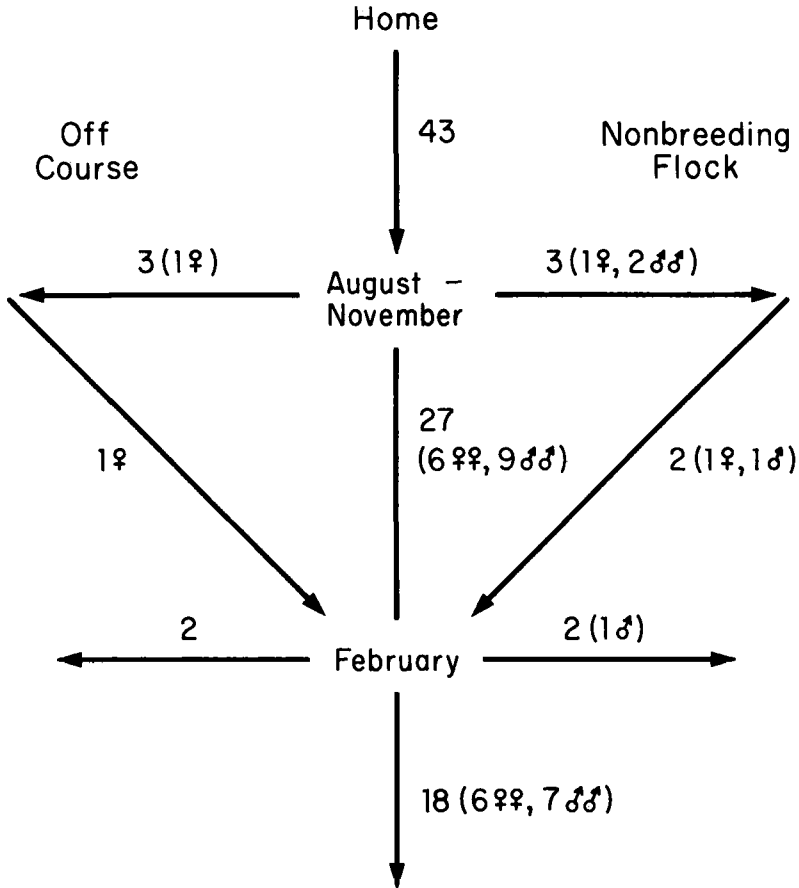


Fig. 4. Dispersal patterns of juveniles marked before or just after fledging. Numbers and sex (where known) of individuals pursuing different strategies indicated. A number of individuals of unknown fate (not shown) disappeared from study area: 10 between August and November; and 5 (including 1 male) during February.

1984) and year around by Eastern American Crows (*C. b. brachyrhynchos*; Kilham 1985, Chamberlain-Auger 1990, K. McGowan, pers. comm.). Despite the documented variation in the timing of defense and the size or type of territory, members of these populations all were observed to actively exclude conspecifics from breeding areas. However, references to the lack of overt territoriality in other populations of American Crows (Black 1941, Good 1952) and Fish Crows (*C. ossifragus*; McNair 1984) exist. The tendency for Western American Crows to nest in colonies (Emlen 1942) adds to the diversity. Breeding density in my study population was similar to that in the colony studied by Emlen (0.8 vs. 0.56 pairs/ha). Anecdotal references to breeding colonies of Western Amer-

ican Crows in Bent (1946) and Goodwin (1976) suggest that this may be a regular phenomenon.

Delayed breeding.—Breeding-habitat saturation and a shortage of mates are the limiting factors most often invoked as the basis for delayed breeding among cooperative breeders (Koenig and Pitelka 1981, Emlen 1982, Emlen and Vehrencamp 1983, Brown 1987). Each year on the golf course there were identifiable unoccupied interior areas. The density of nests and high degree of core-area overlap on the periphery indicated successful breeding did not require a great deal of space. Settlement by new pairs did not involve obvious aggressive interactions. This suggests that breeding habitat was not limited. Additionally, nonbreeders included both males and females, suggesting no short-

age of potential mates. The lack of any area-defense and high degree of sociality resulted in easy access to other obvious breeding requirements (e.g. food and water). Thus, it is difficult to argue limiting resources as the cause of delayed breeding.

The majority of nonbreeding auxiliaries (75%) were yearlings. Yearling American Crows retain juvenile plumage and lack full gonadal development (Black 1941). Delayed maturation appears to be a characteristic of the genus, as suggested by the lack of breeding by yearlings in American Crows (Good 1952, K. McGowan, pers. comm.), Hooded Crows (Loman 1985), Rooks (Holyoak 1971, Marshall and Coombs 1957 [in Roskaft et al. 1983]), Common Ravens (Coombs 1978, Davis and Davis 1986), and Australian Ravens (*C. coronoides*; Rowley 1969 [in Davis and Davis 1986]). Thus, a large fraction of delayed breeding may be an ancestral life-history trait in the genus *Corvus* rather than a response to immediate demographic conditions. However, delayed maturation does not explain all delayed breeding in this population. Although several individuals attempted to breed when two years old, 25% of nonbreeding auxiliaries were at least that age. All of the five marked individuals that delayed breeding for two or more years eventually bred on the golf course.

Delayed dispersal.—Yearlings of both sexes employ several dispersal options. Juveniles may disperse from their natal core areas at any time after two months postfledging. They may join the resident nonbreeding flock or disperse different distances off the course. Some dispersers never were seen in the area again, some maintained various amounts of contact with their families, and some returned after extended periods. Alternatively, individuals remained in the immediate area for one or more years. Individuals that delayed dispersal varied in their behavior: some maintained residency and family relationships but were observed regularly in other locations; some were virtually inseparable from their parents. This situation is very different from that in Hooded Crows, where essentially all offspring had left home by September and were not seen with their parents again after November (Loman 1985). The observations of Verbeek and Butler (1981) suggest that yearling Northwestern Crows also may pursue variable dispersal options.

Given delayed breeding, nonbreeders in a majority of avian species disperse and float until a breeding vacancy becomes available (Stacey and Ligon 1987, Koenig et al. 1992). Among cooperative breeders, delayed dispersal by young birds is commonly interpreted as an adaptation providing: (1) group-membership benefits (Alexander 1974, Gaston 1978b, Bednarz and Ligon 1988); (2) current access to resources (Alexander 1974, Stacey and Ligon 1987, Ligon et al. 1988); or (3) future access to breeding status (Brown 1974, Woolfenden and Fitzpatrick 1978, Koenig 1981, Ligon 1981). None of these interpretations easily explains delayed dispersal in my study population, or its sex bias. The presence of a nonbreeding flock into which young birds commonly dispersed, and the extreme tolerance displayed by individuals regarding spatial distribution makes it unlikely that dispersers sacrificed any benefits of group membership. That breeders did not prevent others from foraging in their core areas suggests that access to food also was unlikely to be affected by dispersal. These conclusions are underscored by preliminary data, which show no difference in mortality rates between individuals that did delay dispersal versus those that did not. Finally, given the extensive ranging of individuals throughout the area, it seems unlikely that birds in the nonbreeding flock sacrificed information on local breeding opportunities.

I considered two further hypotheses that might explain both delayed dispersal and its sex bias. First, delayed dispersal might provide benefits via extended parental care. For example, auxiliaries continued to beg from and be fed by the breeding pair (see results). Second, competition within the nonbreeding flock might impose costs which could be avoided by remaining home (Eden 1987). Although I did not study the social structure of the nonbreeding flock, such flocks often are the setting in which dominance relationships are established (Garnett 1981, Eden 1987). Both hypotheses predict that smaller and lighter birds should delay dispersal. Females more commonly delayed dispersal and are smaller and lighter than males, but I found no differences between dispersers and nondispersers in prefledging size and weight. However, the sample sizes for these tests were small.

Helping.—For individuals of other species that

delay dispersal, the main benefits of remaining home are often acquired through helping. Helping has been suggested to provide both indirect benefits through increased inclusive fitness (e.g. Brown and Brown 1981, Hunter 1985, Emlen 1990), and direct benefits as a stepping stone to breeding status (e.g. Koenig 1981, Kinnaird and Grant 1982, Woolfenden and Fitzpatrick 1984) or as an opportunity for socially learned breeding skills (e.g. Woolfenden 1975, Lawton and Guindon 1981, Fairbanks 1990). In this population, helpers are siblings of the nestlings they help and so would gain an inclusive-fitness benefit if their behavior increased parental breeding success. Over six years, helpers were not found to have such an effect (Caffrey 1991). It is unlikely that helping is a stepping stone to breeding status in ways that have been demonstrated in other cooperative breeders. Breeding habitat does not appear limited; therefore, helping does not function as a means of obtaining breeding space (Gaston 1978a, Woolfenden and Fitzpatrick 1984, Rowley and Russell 1990). Nor is helping a means of inheriting a mate (Reyer 1990) or producing future allies or helpers (Ligon and Ligon 1978, Rabenold 1985). Finally, it is possible that helping provides opportunities for the learning of breeding skills. I have observed helpers literally following in their parents' footsteps and manipulating discarded nesting material, sitting next to and watching their parents during nest building, being thwarted by breeders as they attempted to feed nestlings inappropriate items, and jostling with the breeding female for the opportunity to brood eggs and nestlings.

Extant theories regarding potential benefits do not offer an easy explanation for the observed sex bias in helping. Possibly, given their greater role in nest building and early brood care (pers. observ.), females may benefit more from social learning. However, there is little evidence to support this idea.

In conclusion, this study has demonstrated that Western American Crows exhibit many of the phenomena commonly observed in cooperatively breeding birds: delayed breeding, delayed dispersal, and helping at the nest by relatives. However, Western American Crows differ from other cooperative breeders by exhibiting obligate delayed breeding, by showing varying degrees of delayed dispersal, and by the strong female bias in delayed dispersal and helping.

Interpretation of these unusual patterns awaits careful study of the costs and benefits associated with delayed breeding, dispersal behavior, and helping for each sex.

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LITERATURE CITED

- ALEXANDER, R. D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5:325-383.
- ANTIKAINEN, E. 1980. The breeding success of the Jackdaw *Corvus monedula* in nesting cells. *Ornis Fenn.* 58:72-77.
- AUSTAD, S. N., AND K. N. RABENOLD. 1986. Demography and the evolution of cooperative breeding in the Bicolored Wren, *Campylorhynchus griseus*. *Behaviour* 97:308-324.
- BEDNARZ, J. C., AND J. D. LIGON. 1988. A study of the ecological bases of cooperative breeding in the Harris' Hawk. *Ecology* 99:1176-1187.
- BENT, A. C. 1946. Life histories of North American jays, crows and titmice, part II. U.S. Natl. Mus. Bull. 191.
- BLACK, C. T. 1941. Ecological and economic relations of the Crow, with special reference to Illinois. Ph.D. thesis, Univ. Illinois, Urbana.
- BROWN, J. L. 1974. Alternate routes to sociality in jays—With a theory for the evolution of altruism and communal breeding. *Am. Zool.* 14:63-80.
- BROWN, J. L. 1978. Avian communal breeding systems. *Annu. Rev. Ecol. Syst.* 9:123-155.

- BROWN, J. L. 1987. Helping and communal breeding in birds: Ecology and evolution. Princeton Univ. Press, Princeton, New Jersey.
- BROWN, J. L., AND E. R. BROWN. 1981. Kin selection and individual selection in babblers. Pages 244-256 in *Natural selection and social behavior: Recent research and new theory* (R. D. Alexander and D. W. Tinkle, Eds.). Chiron Press, New York.
- BROWN, J. L., D. D. DOW, E. R. BROWN, AND S. D. BROWN. 1983. Socioecology of the Grey-crowned Babbler: Population structure, unit size and vegetation correlates. *Behav. Ecol. Sociobiol.* 13:115-124.
- BUTLER, R. W., N. A. M. VERBEEK, AND H. RICHARDSON. 1984. The breeding biology of the Northwestern Crow. *Wilson Bull.* 96:408-418.
- CAFFREY, C. 1991. Breeding group structure and the effects of helpers in cooperatively breeding Western American Crows. Ph.D. dissertation, Univ. California-Los Angeles, Los Angeles.
- CHAMBERLAIN-AUGER, J. A., P. J. AUGER, AND E. G. STRAUSS. 1990. Breeding biology of American Crows. *Wilson Bull.* 102:615-622.
- COOMBS, F. 1978. The crows. Batsford Ltd., London.
- CURRY, R. L. 1988. Group structure, within-group conflict, and reproductive tactics in cooperatively-breeding Galapagos Mockingbirds, *Nesomimus parvulus*. *Anim. Behav.* 36:1708-1728.
- CURRY, R. L., AND P. R. GRANT. 1990. Galapagos Mockingbirds: Territorial cooperative breeding in a climatically variable environment. Pages 289-331 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, Cambridge.
- DAVIS, P. E., AND J. E. DAVIS. 1986. The breeding biology of a Raven population in central Wales. *Nature in Wales* 3:44-54.
- EDEN, S. F. 1987. Dispersal and competitive ability in the Magpie: An experimental study. *Anim. Behav.* 35:764-772.
- EMLEN, J. T. 1936. Age determination in the American Crow. *Condor* 38:99-102.
- EMLEN, J. T. 1942. Notes on a nesting colony of Western Crows. *Bird-Banding* 13:143-154.
- EMLEN, S. T. 1982. The evolution of helping. I. An ecological constraints model. *Am. Nat.* 119:29-39.
- EMLEN, S. T. 1990. White-fronted Bee-Eaters: Helping in a colonially nesting species. Pages 489-526 in *Cooperative breeding in birds* (P. R. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, Cambridge.
- EMLEN, S. T., AND S. L. VEHCAMP. 1983. Cooperative breeding strategies among birds. Pages 93-120 in *Perspectives in ornithology* (A. H. Brush and G. A. Clark, Jr., Eds.). Cambridge Univ. Press, Cambridge.
- FAIRBANKS, L. A. 1990. Reciprocal benefits of allo-mothering for female vervet monkeys. *Anim. Behav.* 40:553-562.
- FITZPATRICK, J. W., AND G. E. WOOLFENDEN. 1986. Demographic routes to cooperative breeding in some New World jays. Pages 137-160 in *Evolution of animal behavior* (M. Nitecki and J. Kitchell, Eds.). Univ. Chicago Press, Chicago.
- GARNETT, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits *Parus major*. *Ibis* 123:31-41.
- GASTON, A. J. 1978a. Demography of the Jungle Babbler, *Turdoides striatus*. *J. Anim. Ecol.* 47:845-870.
- GASTON, A. J. 1978b. The evolution of group territorial behavior and cooperative breeding. *Am. Nat.* 112:1091-1100.
- GOOD, E. E. 1952. The life history of the American Crow *Corvus brachyrhynchos* Brehm. Ph.D. thesis, Ohio State Univ., Columbus.
- GOODWIN, D. 1955. Some observations on the reproductive behavior of Rooks. *Brit. Birds* 48:97-105.
- GOODWIN, D. 1976. Crows of the world. Cornell Univ. Press, New York.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140-1162.
- HEINSOHN, R. G. 1987. Age-dependent vigilance in winter aggregations of cooperatively breeding White-winged Choughs (*Corcorax melanorhamphos*). *Behav. Ecol. Sociobiol.* 20:303-306.
- HOLYOAK, D. 1971. Movements and mortality of Corvidae. *Bird Study* 18:97-106.
- HUNTER, L. A. 1985. The effects of helpers in cooperatively breeding Purple Gallinules. *Behav. Ecol. Sociobiol.* 18:147-153.
- KILHAM, L. 1984. Cooperative breeding of American Crows. *J. Field Ornithol.* 55:349-356.
- KILHAM, L. 1985. Territorial behavior of American Crows. *Wilson Bull.* 97:389-390.
- KINNAIRD, M. F., AND P. R. GRANT. 1982. Cooperative breeding by the Galapagos Mockingbird, *Nesomimus parvulus*. *Behav. Ecol. Sociobiol.* 10:65-73.
- KOENIG, W. D. 1981. Space competition in the Acorn Woodpecker: Power struggles in a cooperative breeder. *Anim. Behav.* 29:396-409.
- KOENIG, W. D., AND F. A. PITELKA. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pages 261-280 in *Natural selection and social behavior: Recent research and new theory* (R. D. Alexander and D. W. Tinkle, Eds.). Chiron Press, New York.
- KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.* 67:111-150.
- LAWTON, M. F., AND C. F. GUINDON. 1981. Flock composition, breeding success, and learning in the Brown Jay. *Condor* 83:27-33.

- LENNARTZ, M. R., R. G. HOOPER, AND R. F. HARLOW. 1987. Sociality and cooperative breeding of Red-cockaded Woodpeckers, *Picoides borealis*. *Behav. Ecol. Sociobiol.* 20:77-88.
- LEWIS, D. M. 1981. Determinants of reproductive success of the White-browed Sparrow Weaver, *Plocepasser mahali*. *Behav. Ecol. Sociobiol.* 9:83-93.
- LIGON, J. D. 1981. Demographic patterns and communal breeding in the Green Woodhoopoe, *Phoeniculus purpureus*. Pages 231-243 in *Natural selection and social behavior: Recent research and new theory* (R. D. Alexander and D. W. Tinkle, Eds.). Chiron Press, New York.
- LIGON, J. D., AND S. H. LIGON. 1978. Communal breeding in Green Woodhoopoes as a case for reciprocity. *Nature (Lond.)* 276:496-498.
- LIGON, J. D., C. CAREY, AND S. H. LIGON. 1988. Cavity roosting, philopatry, and cooperative breeding in the Green Woodhoopoe may reflect a physiological trait. *Auk* 105:123-127.
- LOMAN, J. 1980. Reproduction in a population of the Hooded Crow *Corvus cornix*. *Holarct. Ecol.* 3:26-35.
- LOMAN, J. 1984. Breeding success in relation to parent size and experience in a population of the Hooded Crow. *Ornis Scand.* 15:183-187.
- LOMAN, J. 1985. Social organization in a population of the Hooded Crow. *Ardea* 73:61-75.
- MARZLUFF, J. M., AND R. P. BALDA. 1988. Resource and climatic variability: Influences on sociality of two southwestern corvids. Pages 255-283 in *The ecology of social behavior* (C. N. Slobodchikoff, Ed.). Academic Press, New York.
- MCLAIR, D. B. 1984. Breeding biology of the Fish Crow. *Oriole* 49:21-32.
- MUMME, R. L., AND A. DE QUIEROZ. 1985. Individual contributions to cooperative behavior in the Acorn Woodpecker: Effects of reproductive status, sex, and group size. *Behaviour* 95:290-313.
- NEWTON, I., P. E. DAVIS, AND J. E. DAVIS. 1982. Ravens and buzzards in relation to sheep farming and forestry in Wales. *J. Appl. Ecol.* 19:681-706.
- PARKER, H. 1985. Breeding performance and aspects of habitat selection in subarctic Hooded Crows *Corvus corone cornix*. *Fauna Norv. Ser. C Cinclus* 8:1005.
- RABENOLD, K. N. 1985. Cooperation in breeding by nonreproductive wrens: Kinship, reciprocity, and demography. *Behav. Ecol. Sociobiol.* 17:1-17.
- REYER, H.-U. 1990. Pied Kingfishers: Ecological causes and reproductive consequences of cooperative breeding. Pages 529-557 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, Cambridge.
- RICHNER, H. 1989. Phenotypic correlates of dominance in Carrion Crows and their effects on access to food. *Anim. Behav.* 38:606-612.
- RICHNER, H. 1990. Helpers-at-the-nest in Carrion Crows *Corvus corone corone*. *Ibis* 132:1058.
- ROSKAFT, E. R., Y. ESPMARK, AND T. JARVI. 1983. Reproductive effort and breeding success in relation to age by the Rook *Corvus frugilegus*. *Ornis Scand.* 14:169-174.
- ROWLEY, I. 1981. The communal way of life in the Splendid Wren, *Malurus splendens*. *Z. Tierpsychol.* 55:228-267.
- ROWLEY, I., AND E. RUSSELL. 1990. Splendid Fairy Wrens: Demonstrating the importance of longevity. Pages 3-30 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, Cambridge.
- SHANK, C. C. 1986. Territory size, energetics, and breeding strategy in the Corvidae. *Am. Nat.* 128:642-652.
- SKEAD, C. J. 1952. A study of the Black Crow *Corvus capensis*. *Ibis* 94:434-451.
- SMITH, J. N. M. 1990. Summary. Pages 593-611 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, Cambridge.
- STACEY, P. B., AND J. D. LIGON. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *Am. Nat.* 130:654-676.
- VERBEEK, N. A. M., AND R. W. BUTLER. 1981. Cooperative breeding of the Northwestern Crow *Corvus caurinus* in British Columbia. *Ibis* 123:183-189.
- VINES, G. 1981. A socio-ecology of Magpies *Pica pica*. *Ibis* 123:190-202.
- WOOLFENDEN, G. E. 1975. Florida Scrub Jay helpers at the nest. *Auk* 92:1-15.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1978. The inheritance of territory in group-breeding birds. *BioScience* 28:104-108.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: Demography of a cooperative-breeding bird. *Monogr. Pop. Biol.* 20. Princeton Univ. Press, Princeton, New Jersey.