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COOPERATIVE BREEDING OF AMERICAN CROWS

By Lawrence Kilham

Observations on the cooperative breeding of the Florida race of the American Crow (*Corvus brachyrhynchos pascuus*) were made by my wife and I at the Hendrie cattle ranch, 24 km south of Lake Placid, Florida. That more than two crows may attend a nest during incubation is mentioned by Good (1952) and at times of nest-building and feeding nestlings by Forbush (1927). Helpers feeding nestlings have been recently described by Verbeek et al. (1981) for the Northwestern Crow (*C. caurinus*). Both Good and Verbeek found, by means of banded individuals, that yearlings maintain a close association with breeding adults, presumably their parents.

STUDY AREA AND METHODS

We used two methods of confirming that helpers at nests were yearlings. One was that, when seen together, the yearlings had a brownish and adults a purplish black cast to the feathers of back, wings, and tail (Good 1952, Dwight 1975). Of greater value was the finding of Emlen (1936) that whereas adult crows have rectrices that are generally intact, with truncated ends, and form a rounded tail, those of yearlings are frayed, pointed at the ends, and form a tail that is square. These differences were seen to best advantage when an individual spread its tail, either on landing or performing leg-wing stretch. Our main method of identifying helpers (Table 1) was the presence of 3 (or more) crows at a nest at one time or, if one of these had just left to perch where it could be watched, the arrival of another. Identification of the sexes of the parent crows, although not possible on all occasions, was possible at times by the fact that the female did all of the incubating and brooding, and the males, in weeks of their greatest sexual activity, spent much time either guarding the nest or driving other crows away from it. The adults of pair B were individually marked—the male by the absence of a rectrix and his mate by her bill, smaller than that of other crows coming to the nest.

The crows at the ranch were tame due to a program of protecting wildlife and feeding corn that had gone on for 25 years. We observed nests at distances of 40–60 m without the use of blinds and frequently watched crows at distances of 7–8 m. We did not capture individuals for banding or venture close to nests in a belief that procedures of any kind might destroy the approachability of the birds. To avoid disturbing the crows, we always sat in the same places when watching nests, and scattered corn in two places (one for each family group) to make the birds familiar with us. The terrain of the ranch (area 64 km^2) is flat, with pastures surrounding groves of live oaks (*Quercus virginiana*) where

TABLE 1. Summary of observations of nests A and B of American Crows.

Stage of nesting	Nest	No. of days: In stage	No. of days: Nest under observation	Total observation times (min)	Visits to nest: Totals	Visits to nest: Rate/h (averages)	Number occasions helpers identified
Egg-laying, incubation	A	20	19	2981	316	6.00	57
	B	21	17	1093	87	4.50	12
Early nestling (brooding)	A	14	11	1762	548	19.00	170
	B	12	7	660	154	14.00	41
Mid-nestling	A	13	13	1990	319	9.00	62
	B	14	14	1740	322	11.50	56
Last week	A	7	7	1290	123	6.00	6
	B	7	7	780	83	6.25	11
Totals	A + B	55[a]	50	12,296	1952	9/h	415

[a] Length of total nesting period.

the crows nested. Grazing and passage of cattle made walking and visibility good in all directions. We were the only people walking about the ranch. Our total, joint observation time was 846 h, of which 205 h were spent watching nests.

COMMUNAL GROUPS AND TERRITORY

I witnessed 19 territorial conflicts in January and February of 2 years. In nearly all I heard a sudden burst of cawing, then saw one crow pursuing and attacking another, the two being followed by 5–6 other crows all cawing. Several times, when participants came overhead, I heard harsh *karrs* and once a whack as the attacking crow struck the intruder. All attacks moved toward a cattle drive, bordered by fences, that formed the boundary between territories A and B. Once it was reached, the pursuing crows turned back the way they had come. Due to swamps and open prairies, there were no rival crows in other directions.

Groups A and B consisted of 8–10 individuals, countable at times of scattering corn. The crows cooperating in nestings, from nest-building through to the end of brooding, consisted of the breeding pair plus 4 yearlings in family A in 1981 and 3 in families A and B in 1982. The extra crows, that were all adult and conceivably 2-year-olds, stayed away from nests until the nestling period when at least some of them, too, became helpers. I believed that their initial isolation was due to attacks made on them largely between the start of nest-building and that of egg-laying. Those that I witnessed (n = 9) were within the main territorial border and never extended to it. This suggested that the breeding crows established a smaller territory within their larger (ca 50 ha) group

territories. Seven of the 9 attacks were aerial. On 23 February the 5 crows of family A were bunched near the limit of a pasture where it reached an oak grove. When a sixth crow joined them, one crow attacked it and the two jumped into the air like fighting cocks. As the sixth crow ran away, the 5 ran after it, then all took to the air. The location of the conflict was on the boundary of the nesting territory, 190 m from nest A. In addition to these encounters, we watched two where an intruder actually reached a nest. The one at nest B, on 11 February, was driven away by two crows and the one at nest A, on 2 March, by the family of 5.

Defense against interspecific intruders.—The vicinity of each nest was defended, with yearlings participating, against Red-tailed (*Buteo jamaicensis*) and Red-shouldered (*B. lineatus*) hawks, Bald Eagles (*Haliaeetus leucocephalus*), Black (*Coragyps atratus*) and Turkey (*Cathartes aura*) vultures, and gray squirrels (*Sciurus carolinensis*). The only actual intrusion observed was when a Red-tailed Hawk twice made its way onto just completed nest A. The hawk was driven out by the parent crows giving harsh rattling cries. They pursued the hawk on the first occasion but left the pursuit to the yearlings on the second, while they remained by the nest. When the hawk was on the nest, the parents drove the yearlings down into the tree, seemingly to get them out of the way when conditions were crowded.

NEST-BUILDING

Nest A.—The first evidence of interest in nesting was on 19 January when female A tried to lay several sticks in a bay tree. I watched crows carrying sticks to various places in the next week. On 1 February the members of pair A began carrying sticks from the ground into an oak growing by itself in the large pasture that formed most of their breeding territory. When I went to look, I could see nothing, the sticks laid being too few. I assumed, therefore, that this was day 1 of nest-building. The adults appeared to do all of the building at first, and it was not until 6 February that we noted 3 crows on the nest, located 30 cm within the canopy of the oak and 8 m above the ground. We became more aware of helpers on the next day when we twice saw 3 and once 4 crows at a time carrying material to the nest. On the same morning 3 crows flew not far over my head, each carrying a lump of black mud or turf in its bill. All entered the tree. On 8 February we twice noted 4 crows on the nest. The nest was completed on the following day.

Nest B.—The members of pair B tried several sites before settling on a final one on 5 February. This was located against the trunk of a slanting oak, 7 m above the ground and 15 m within a grove. Being below the canopy, I had a clear view. On 6 February I watched 90 min of almost constant activity as crows brought crooked sticks that took time to work into a structure. This meant that incoming crows had to wait, with sticks in their bills, for up to 3–4 min, for a chance at the nest. It was apparent that yearlings were taking part, for I noted 3 crows by the nest on 3

occasions, 4 crows on two, and the entire group of 5 by the nest on one. The yearlings often left their sticks for an adult to work in.

The situation changed in the next few days when, with the crows bringing mud and sod, or finer material for lining that could be easily placed, the crowding ceased. From where I sat 40 m from the nest, however, I had a view of the 5 members of the group as they walked about the floor of the grove, sometimes within 7 m of me, searching the fallen leaves of cabbage palms for fibers or decayed bits of leaves to carry to the nest. The yearlings worked in the same manner as the adults. On 9 February, the last day of building, within 90 min I observed 3 crows on the nest on 5 occasions and 4 on one occasion. With an active use of helpers, nest B was completed in 5 days and nest A in 9. These are shorter times than those encountered by Emlen (1942), in a much larger series, who found that it took crows 13 days on an average to complete a nest.

YEARLING INTERFERENCE WITH COPULATIONS

Nests A and B were both completed by 10 February. Male B had been on the nest for 11 min when his mate arrived with tail quivering. A copulation followed but was seemingly cut short by a yearling flying to the nest and pushing its lowered head under the two parents. The 3 remained silent and motionless a few moments, then flew off. Female B arrived at the nest with tail quivering a week later. I thought a copulation about to begin when two yearlings suddenly piled into the nest in a confusion of 4 crows that soon left. Another intrusion took place on the first day of egg-laying, 27 February. Pair B appeared to have completed a copulation, but only barely. Two yearlings arrived in much the same confusion as 10 days previously. Gatherings on the nest were, however, not limited to copulations. Four crows suddenly came to nest B on 11 February, with no seeming provocation. In sum, interferences took place in 3 of 7 copulations or copulation attempts witnessed on nest B. Coombs (1978) found that only 17% of copulations by Rooks (*C. frugilegus*) were not interfered with by other males.

EGG-LAYING AND INCUBATION

Following an interim of 15–17 days after completion of nests, females signaled egg-laying by calling *caas* from their nests. They made no efforts, from this time on, to feed themselves. Table 1 gives the number of times helpers were identified in feeding them during incubation. Female A left her nest 1–4 times an hour, staying away 2–9 min to rest or preen. She was 86% attentive from days 5–18. Although we could not see details at nest A, we could detect feedings by the sound of gulping, i.e., the female's vocalizing and swallowing at the same time. When crows came to feed her when she was away, they sometimes waited on trees nearby, then flew, 2 or 3 together, to the nest on her return. We only saw her fed away from the nest once.

Crows coming to the nest frequently paused to disgorge the contents

of their mouth pouches on the pasture, then tear up larger pieces by way of preparation. When male A did this early in incubation, a yearling, seeing an opportunity, flew down to beg. MA emptied his bill at once into that of the subordinate. Female A then alighted to follow the yearling with her wings out and making nest calls. The yearling, instead of feeding her, flew with her to the nest where, in a roundabout way, she got the food intended for her originally. I witnessed 11 allofeedings during the nesting period, 8 of which were on the rim of the nest B. I twice saw MA drive yearlings that begged away from nest A.

Nest B.—I had closer views of feedings at nest B. As throughout nesting, some crows arrived with mouth pouches bulging and others did not. Female B held up her open bill and sometimes tried to seize the bill of the incoming crow. When she left the nest on 15 March, two crows remained on the rim for several minutes. This was the longest I saw any crow remain by the nest in her absence. Her periods away ranged from 2–12 min during the latter part of incubation (days 7–18) when her attentiveness was 81%. During the first 6 days it was only 46%. Due to this lesser attentiveness, she was fed away from the nest more than female A.

NESTLING PERIOD

Hatching was marked at both nests by an increase in visits. At nest B this was from an average of 4.5/h in the latter part of incubation (Table 1) to 14.6/h, and at nest A, from 6 to 19/h. In our first hour of watching, there were 38 visits, the highest record for either nest. It seemed unlikely that all of these were feeding visits. I recorded all visits to nests (Table 1) without knowing how many resulted in food being passed. Many visits, in the days of hatching, may have been without food.

At nest B, where I could see clearly, FB might open her bill and take all of the food brought in, or pass some or all of it on to the nestlings. Many visitors, after feeding nestlings, made motions as if they had picked up feces. When nestlings became larger, some crows left with mouth pouches bulging. One such, an adult male, disgorged 2–3 cc of white, liquid feces after leaving. Both Good (1952) for the American, and Wittenberg (1968) for the Carrion (*C. corone*) crow, describe nestlings as ejecting fecal matter over the nest rim, with a soiling of the outer nest and adjacent branches. I never saw this. Once, when a nestling positioned itself to do so, a waiting adult was quick to seize the excreta. Yearlings, as helpers, both fed nestlings and attended to sanitation. As we could only identify a fraction of crows coming to nests as helpers, it was impossible to estimate what portion of the total work was done by them.

After FB had ceased brooding, she spent up to 45 min, in the mid-nestling period, in sessions of tending the young and digging into the bottom of the nest. It seemed likely that this latter activity, observable in other corvids (Goodwin 1976), is to reduce populations of blood-sucking ectoparasites. Among these, with crows living in mud-con-

structed nests, a type which Boyd (1950) considers favorable, the crow flea (*Ceratophyllus rossitensis*) (Holland 1954) and blow fly larvae (*Protocalliphora*) (Good 1952) are ones to be considered.

Not all crows coming to nest B fed young. I noted in the 34 days of the nestling period that some (n = 22), being met with no begging responses from the young, left without feeding. Sometime after brooding ceased we became aware at both nests that the unmated adults or extra crows that had stayed or been driven away during nest-building, egg-laying, and incubation, had joined in feeding nestlings. It now seemed that there was an excess of help, considering that only a single nestling was fledged at nest A, and only 2 at nest B. This may have explained why yearlings were less obvious at nests in the last few weeks. It should be emphasized that we were not able to determine the status of every crow visiting the nests. We were trying primarily to determine the extent of cooperative breeding. What we found was that during the 55 days of the nesting period, 3 or more crows were at nests, either at one time or close to it, on 415 occasions. This, as shown in Table 1, was among 1952 visits made to two nests in our 205 h of watching.

DISCUSSION

The breeding of American Crows is of interest in the extent to which yearlings join in nest-building, feeding the female in incubation, caring for the nestlings when they appear, and in sanitation of the nest. Part of the attraction seemed to be a wanting to be with the parents. It was this, we felt, that explained 3 to 5 crows arriving at a nest at a time as well as the frequency of allopreening (Kilham unpubl. data). The crows of all ages seemed drawn to close contact at times. I have read of no accounts of such inclusive family bonds in the cooperative breeding of other birds (Rowley 1976).

In spite of American Crows being among the least and Scrub Jays (*Aphelocoma coerulescens*) among the most (Woolfenden 1975, 1976) studied of cooperative breeders, a few comparisons are worth making.

The jays are restricted to a limited habitat, the one in which their cooperative breeding presumably evolved. Conditions under which American Crows originally lived in North America, on the other hand, no longer exist. It is difficult, therefore, to theorize on what the selective advantages of their cooperative breeding were originally. Crows have, however, certain attributes which suggest what some of these may have been. Among these is intelligence. Intelligence may have been selected for as an accompaniment of their social organization, adaptability, omnivorous habits, resourcefulness, curiosity, and sense of play (Kilham 1984). Intelligence and adaptability, whether among primates or birds, puts a premium on offspring staying with parents. The educational experience gained, by the yearlings we watched, included all phases of nesting as well as territorial and nest defense.

If yearlings benefit, parents and nestlings appear to do so as well. As Woolfenden (1976) points out, active defense of nests is linked with

cooperative breeding. The bills of crows are weapons strong enough to repel many predators, especially when the crows are acting in concert. Other advantages, aside from bringing food to the nest, are also conceivable. Yom-Tov (1974) has discussed, for Carrion Crows, the value of crows nesting synchronously to minimize the danger of intraspecific egg predation. In watching pair B of our crows, I noted that it was 4 days behind pair A in starting its nest. With the aid of 3 active helpers; pair B finished its nest in 5 days, catching up with pair A that took 9. Other survival advantages of helpers may be that parents, under less pressure to bring food, will have more time for special activities, the female to probe for ectoparasites in the nest bottom, the male to guard the nest, and both to keep the nest clean. This latter function would seem important if the nest and its surroundings are not to be spattered with excreta, as noted by Good (1952) and Wittenberg (1968) for the nests they studied.

An important question is whether the behavior we observed in Florida was local and exceptional. Conceivably crows elsewhere, long shot at and persecuted, may, like coyotes (*Canis latrans*) under similar conditions (Ryden 1979), have changed their breeding habits. This cannot be ruled out. Certainly conditions at the ranch were exceptional. The crows there were sedentary, and the ones we watched lived in all-purpose territories, both situations being among those listed by Woolfenden (1976) as favoring cooperative breeding. Possibly in the north, with crows migrating south in winter, family groups and territories are less stable. Yet, as mentioned by Forbush (1927), 3 crows aided in building a nest in Boston and 3 were seen feeding nestlings at a nest in Connecticut, while Good (1952), without seeming to appreciate what he was observing, noted yearlings as present at various stages of nesting in Ohio. To these observations might be added those of Verbeek et al. (1981) on the Northwestern Crow that was, for a time, regarded as a subspecies of *C. brachyrhynchos* (Bent 1946).

SUMMARY

Advantage was taken of a ranch where, thanks to a policy of protecting wildlife and scattering corn for many years, American Crows were relatively tame. Observations on two family groups, that consisted of a breeding pair and 3–4 yearlings, revealed that the latter participated in all phases of nesting from nest-building to feeding the female in incubation and brooding and caring for the nestlings. Unmated adults assisted only in the latter activity. All helpers participated in the defense of nests and territory. The theoretical benefits of the cooperative breeding, as well as selective pressures that may have led to its evolution are discussed.

Addendum.—Since writing the above, my wife and I have spent another breeding season at the ranch. Although only a single yearling was present, the total number of crows in each group remained the same as in the year before, with 8 in group A and 10 in group B. In spite of the

non-breeding crows being all adults, with one exception, cooperative breeding took place at all stages of nesting. Why so many adults should remain on the territories of single breeding pairs is a puzzle that may be difficult to solve. One hypothesis is that, with considerable changes in land use in Florida in recent times, there is not enough suitable habitat for American Crows in the breeding stage to move into a situation with parallels to that described by Woolfenden (1975) for Scrub Jays.

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