

ROOSTING BEHAVIOR AND GROUP TERRITORIALITY IN AMERICAN CROWS

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ABSTRACT.—Cooperative groups of American Crows (*Corvus brachyrhynchos*) maintain group territories year-round while often traveling long distances to roost communally at night. Our goal was to discover how territorial crows resolve the conflict between the cohesive nature of group behavior with requirements of dispersal to roost communally. We color-marked crows to study group composition over two years, and radio-tagged crows to study movement among roosts, territories, and feeding areas. Most crows showed diurnal fidelity to the group territory throughout the year. Yet, most birds frequently left territories during the day to forage up to 4 km away. At night, crows roosted either on their territory or 18 km away at a large roost adjacent to a landfill. Crows roosted on territories more often in spring (87%) than in winter (42%). Group cohesion was high on territories, yet we found no evidence for group behavior away from territories. Crows arrived singly both to territories in the morning and to the communal roost in the afternoon. Group cohesion for territorial crows appears to be based on decisions of individuals to return to territories from distant roosting and foraging sites. Group cohesion on territories is tied to retention of breeding sites, whereas dispersal for communal roosting likely is linked to benefits derived from foraging away from territories, particularly in winter when physiological stress is greatest and territorial food supplies are lowest. *Received 10 May 1996, accepted 9 April 1997.*

COOPERATIVE BREEDING AND COMMUNAL ROOSTING in large aggregations have attracted considerable recent attention (e.g. Allen and Young 1982, Brown 1987, Caccamise 1993). Cooperative breeding and communal roosting are forms of group behavior, yet we know of no studies that have simultaneously examined relationships between these behaviors. Occurrence of both behaviors in a single species apparently is uncommon and may explain the lack of attention from researchers. American Crows (*Corvus brachyrhynchos*) offer the opportunity to examine relationships between cooperative breeding (Chamberlain-Augur et al. 1990) and communal roosting (Stouffer and Caccamise 1991a) because crows frequently travel to large communal roosts, yet they live in stable groups that breed cooperatively and defend year-round territories.

In the northeastern United States, large com-

munal roosts of American Crows form each evening from late summer through early spring. The largest aggregations develop in winter (Goodwin 1976). Cooperative breeding and communal roosting have what appear to be conflicting requirements in that group territorial behavior requires group cohesion on territories, whereas communal roosting requires travel to distant sites with long absences from territories. It is not known how stable groups occupying territories during the day are related to large assemblages that form communal roosts at night. Nor is it known why individual crows that belong to stable groups abandon territories to join distant aggregations at communal roosts.

Our goal was to understand how crows resolve apparent conflicts between the group cohesion required for cooperative breeding and territory defense with the temporary abandonment of territories necessary to join communal roosts. We used color-marking to study group composition and radiotelemetry to study movements of individuals among roosts, territories, and feeding areas.

METHODS

Our study area was centered on the Cook College campus of Rutgers University, New Brunswick, New

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Jersey. It included the open areas on the southern part of campus and adjacent agricultural fields (hereafter "Cook"). We also worked at Edgeboro Landfill and Middlesex County Yard and Vegetative Waste Composting Facility located about 4 km east of Cook. A third study area was at a communal roost located 18 km ENE of Cook on Staten Island.

We captured crows either with the sedative alpha-chloralose (Stouffer and Caccamise 1991b) or with a WinnStarr rocket net. We used sedatives to capture only one crow because rocket nets were more reliable (22 crows). We attached transmitters (L. L. Electronics) to all captured crows using a backpack (Stouffer and Caccamise 1991a). Transmitters were two-stage (16 to 19 g) or one-stage (9 to 12 g) that weighed $\leq 3.5\%$ or about 2% of each crow's body mass, respectively. We also marked birds individually using hair stripper (Romanowski et al. 1993) to bleach unique patterns on the wing and tail feathers.

In 1990–91, we captured, marked, and radio-tagged 12 crows from five territories. Crows were aged using mouth and covert coloration (Pyle et al. 1987). One crow disappeared the day after release and was seen only periodically during the next two months. It was considered a vagrant and was not included in the analysis (Stouffer and Caccamise 1991a). The remaining 11 crows included five adults and six subadults (to second year) from five group territories. We banded seven nestlings from nests in two of these territories.

In 1991–92, we captured, marked, and radio-tagged 10 crows from seven territories, including eight adults and two subadults. Two adults were radio-tagged the previous year, and one juvenile had been banded as a nestling the previous year. In addition to radio-tagged birds, we identified six individuals with unique physical characteristics that allowed visual identification. These included five previously marked birds and one crow that consistently had a drooping wing. We banded 29 nestlings from 10 nests in 1992. Five nests were located in territories with crows that were radio-tagged the previous winter.

In 1990–91 (1 November 1990 to 7 October 1991), we attempted to locate each crow once a day, six days a week, on a fixed schedule such that each bird was located twice between 0800 and 0930, twice between 0930 and 1100, and twice between 1100 and 1230. In 1991–92 (20 December 1991 to 1 December 1992), we attempted to locate crows once a day, six times a week. We blocked times into five periods (0800 to 1000, 1000 to 1200, 1200 to 1400, 1400 to 1600, and 1600 to 1800) and sampled each period sequentially on successive days. This resulted in approximately equal samples for each time interval. In both years when we could not locate birds on their territories, we searched for approximately one hour before considering them absent. Search areas included all sites at which radio-tagged crows had occurred previous-

ly during the day as well as novel sites that we considered potentially attractive to crows.

Our telemetry studies were divided into one spring and two winter seasons. We defined the beginning of the winter season as the date we initially released radio-tagged birds (1 November 1990 and 20 December 1991). The winter season extended until we first discovered an incubating female (9 April in 1991 and 1992). We continued spring observations through the field lives of individual transmitters (12 July to 22 September).

In both years, we located all birds roosting on their territories six nights a week. In 1990–91, this included determining the exact trees occupied by the birds and the number and identity of roost mates. In 1990–91, we located the radio-tagged crows at their communal roost on Staten Island four to seven nights a week, and in 1992 we sampled the Staten Island roost once a week during spring, and once every other week during summer. On roost visits we determined direction and time of arrival of radio-tagged birds. We determined the time and direction of departure of tagged birds from the distant roost at dawn once or twice a week. We also determined the time birds left from or arrived at their territories.

RESULTS

Diurnal activity in relation to group behavior.—Over the two years of study we attempted to locate our 21 radio-tagged birds 2,208 times during daylight hours (Table 1). On most attempts we found the birds within the same small area. We refer to these areas where individuals were reliably located during the day as the diurnal activity center (DAC). DACs were characteristic for individual birds, but when combined for group members (see below) they formed the territory for the cooperative group. We used the rate of our success at locating individuals on their DACs as a measure of fidelity. DAC fidelity ranged from 54 to 96% ($\bar{x} = 84 \pm \text{SD of } 10.2\%$) and did not differ between adults and juveniles (arcsine transformation; $t = -0.88$, $df = 19$, $P > 0.39$).

Radio-tagged crows were absent on 16% (350 of 2,208) of our scheduled field surveys. For 31% (110 of 350) of these absences, we located the birds at a landfill (Edgeboro Municipal Landfill) used by many crows from the area. Our radio-tagged crows were seen an additional 139 times at the landfill during other phases of our study. We found all but two of our radio-tagged crows at this site at least once. We associated the 11 radio-tagged birds with five different groups in 1991 and the 10 radio-tagged

TABLE 1. Fidelity to diurnal activity centers (DAC) by radio-tagged American Crows.

Bird number	Age ^a	Date radio-tagged	Date last observed	Diurnal observations attempted	Successful diurnal observations	Fidelity to DAC (%) ^b	% of time found ^c	Group membership
115	AHY	10 Dec 90	21 May 91	94	90	95.7	97.9	TF 91
117	HY	10 Dec 90	30 May 91	97	76	78.4	92.8	TF 91
118	HY	10 Dec 90	7 Oct 91	155	129	83.2	87.8	TF 91
119	AHY	23 Dec 90	14 Jun 91	89	77	86.5	86.5	PG 91
120	AHY	23 Dec 90	30 Apr 91	83	78	94.0	96.4	PG 91
121	HY	24 Dec 90	19 Jun 91	94	79	84.0	84.0	FS 91
122	HY	24 Dec 90	12 Jun 91	92	68	73.9	81.5	FS 91
123	AHY	7 Jan 91	28 Jun 91	96	87	90.6	90.6	PA 91
124	AHY	7 Jan 91	29 Jul 91	112	103	92.0	93.8	PA 91
125	HY	28 Jan 91	22 Apr 91	57	47	82.5	82.5	HB 91
126	HY	28 Jan 91	17 Jul 91	90	77	85.6	87.8	HB 91
117	AHY	18 Dec 91	27 May 92	96	65	67.7	80.2	TF 92
120	AHY	8 Apr 92	9 Oct 92	127	107	84.3	94.5	PG 92
130	HY	31 Dec 91	7 Oct 92	132	121	91.7	92.4	PA 92
135	HY	10 Feb 92	13 Oct 92	172	164	95.3	95.9	GB 92
137	AHY	2 Jan 92	4 Aug 92	155	134	68.5	91.0	FS 92
138	AHY	31 Dec 91	30 May 92	105	57	54.3	68.6	PA 92
139	AHY	20 Jan 92	30 May 92	87	64	73.6	83.9	RT 92
141	AHY	10 Feb 92	18 Jul 92	116	94	81.0	92.2	GB 92
143	AHY	3 Mar 92	22 Jul 92	101	95	94.1	95.0	PO 92
144	AHY	3 Mar 92	9 Jun 92	58	46	79.3	79.3	PO 92

^a HY, hatching year; AHY, after hatching-year.

^b Percent of total attempts successful in locating radio-tagged bird on its territory.

^c Includes birds absent from territory but located at distant sites.

birds with seven groups in 1992. Additionally, we were aided in evaluating group composition by having six birds with unique physical characteristics (i.e. our color marks or physical attributes) associated with four different groups. We have seen these unique individuals in the same groups for as long as three years.

Each time we located a radio-tagged crow, we counted the crows in its group and identified any unique individuals. Counts of group size often varied on our successive encounters (Table 2). We estimated the number of birds in each group based on several factors including: (1) our analysis of group-size frequencies, (2) observations of unique individuals, and (3) our familiarity with patterns of group movements and spatial organization. Our estimates of group size ranged from three to seven individuals (Table 2).

We used overlapping spatial distribution of DACs for individual birds in combination with our familiarity with associative behavior of group members to deduce boundaries of group territories (Fig. 1). Group territories were cooperatively defended throughout the year (Kilham 1989). Conflict between neighboring

groups varied seasonally but was never common. Aggression was minimal except in late winter and spring, when we occasionally saw vocalization and patrol flights, particularly in early mornings.

We have evidence from nine individuals that crows remained on the same territories in successive years. In addition to the six crows with unique marks, we recaptured three birds in two consecutive years, each on the same territory in which they were originally caught. One bird initially was captured as an adult, the second as a hatching-year bird, and the third was banded as a nestling and then captured and radio-tagged the following winter.

Roosting behavior.—Radio-tagged crows roosted either locally on their territories or at a large roost 18 km from our study area (Fig. 1). Aggregations at local roosts always were small, usually from one to four birds. At most, only one or two individuals in a local roost were radio-tagged, but occasionally we counted up to four birds when we witnessed the arrival of crows or when the crows were flushed before they had settled in for the night.

Crows roosting away from their territories

TABLE 2. Frequency of group sizes for cooperative groups of American Crows.

Year	Group	Group size								Estim. size ^a
		1	2	3	4	5	6	7	>7	
1991	TF	15	47	30	13	6	1	0	0	4
1992	TF	9	12	16	3	0	1	0	0	4
1991	PG	2	22	42	6	1	0	0	0	4
1992	PG	16	14	6	1	2	0	0	0	3
1991	FS	19	9	19	23	17	1	0	0	6
1992	FS	9	21	17	8	5	2	1	2	5
1991	PA	11	12	30	30	5	1	1	2	5
1992	PA	14	25	29	23	12	3	3	4	6
1991	HB	7	5	10	9	15	11	1	1	7
1992	GB	22	15	19	17	6	0	1	0	5
1992	PO	11	10	16	9	3	2	0	3	5
1992	RT	11	6	9	2	5	3	3	3	6

^a Estimated sizes of groups based on group-size frequencies and interpretation of group dispersion and intergroup interactions.

always flew to the same large roost on the southern end of Staten Island. We estimated the size of this winter roost at 10,000 to 15,000 crows. In winter, crows left their territories beginning in mid-afternoon ($\bar{x} = 1452 \pm \text{SE}$ of 11.4 min, $n = 38$, range 4 h 47 min), but generally they arrived at the communal roost within an hour of sunset ($\bar{x} = 1653 \pm 4$ min, $n = 95$, range 3 h 28 min). Group cohesion ended once

the birds left their territories. Individuals from a group often left the territory at about the same time in the afternoon. The average separation time (interval between departures or arrivals of radio-tagged crows of the same group) for territory departures was 7.1 ± 4.42 min ($n = 8$, mode = 0), but the arrival interval at the distant roost was nearly twice as long (15.2 ± 2.6 min, $n = 27$, mode = 1). Separation times

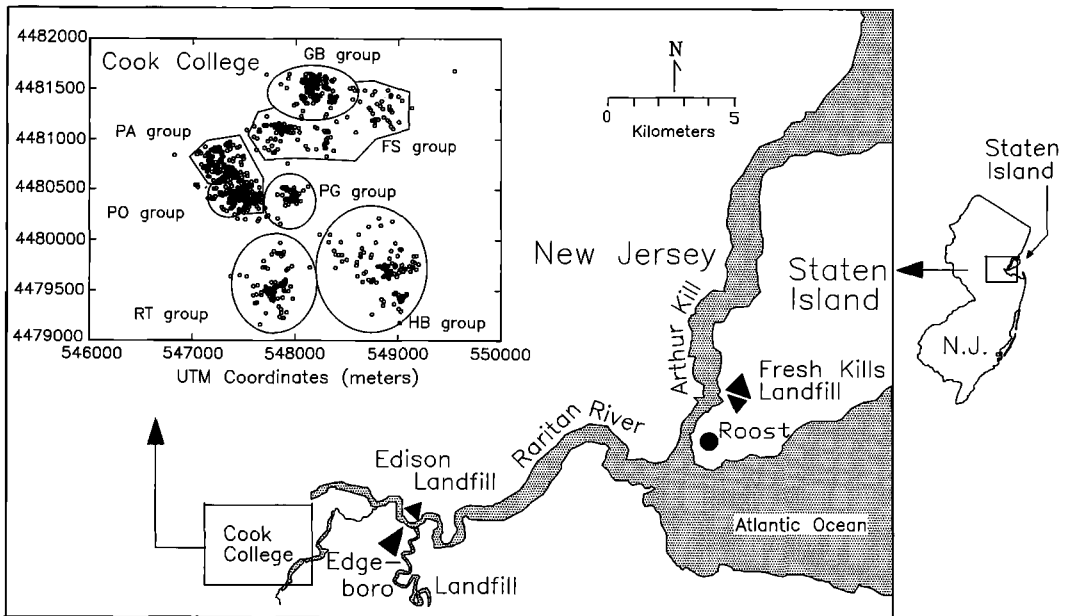


FIG. 1. Map of study area showing point locations of radio-tagged birds in 1991-92 field season (dots); distant roost on Staten Island, New York (filled circle); and off-territory foraging sites (filled triangles). Areas enclosed by solid lines in Cook College inset show approximate borders of groups territories based on point locations and visual observations of marked birds.

were significantly longer for roost arrivals than for territory departures (Mann-Whitney U -test, $U = 55.5$, $P < 0.038$). After members of the communal roost had settled for the night, we located the position of radio-tagged crows and found that crows from the same group roosted at separate locations.

The roost emptied quickly in the morning, resulting in similar departure times for group members (\bar{x} separation time = 6.1 ± 3.02 min, $n = 21$). However, individual crows probably returned to their territories independently because arrival intervals averaged 17.8 ± 13.02 min ($n = 20$). Separation times were significantly longer for territory arrivals than for roost departures ($U = 83.5$, $P < 0.001$).

We determined seasonal patterns in use of roosts by locating radio-tagged crows in roosts. We checked the local roosts more often than the distant roost because of difficulties in traveling to the distant site. As a result our data take two forms: (1) on some nights we confirmed the location of each individual by checking both the distant and local roosts; (2) at other times we were able to check just the local roosts, allowing us to confirm the location only of those individuals present. On these nights the location was unknown for individuals roosting away from their territories. We report our data as bird-nights, which represent an observation of a radio-tagged individual on a single night (i.e. 10 birds on one night would yield 10 bird-nights). We confirmed the locations of our radio-tagged birds (type 1 above) for a total of 1,492 bird-nights (775 in winter, 717 in spring). We failed to locate birds only about 1% of the time on these nights (0.9% in winter, 1.6% in spring). These values overestimated actual absences because some of our failures occurred as transmitters began to fail. The risk of missing a bird increased as radio signals became weak due to aging batteries or damaged antennas.

We recorded 669 bird-nights (572 in winter, 97 in spring) when we could determine only that radio-tagged birds were absent from their local roosts (type 2 above). On these nights we were unable to travel to the distant roost to confirm that absences from local roosts indicated use of the distant roost. Nonetheless, we believe that these absences represented use of the distant roost because on at least 99% of the bird-nights when we confirmed the location of our birds, they occurred at only two locations,

the roosts on their territories or the distant roost on Staten Island.

Radio-tagged crows roosted away from their territories more frequently in winter than in spring ($\chi^2 = 409.7$, $df = 1$, $P < 0.0001$). Crows spent only 42% of bird-nights on their territories in winter (prior to 10 April), but they used local roosts 87% of the time during the spring season. Juveniles roosted locally more often than adults in winter (51% vs. 36%; $\chi^2 = 30.5$, $df = 1$, $P < 0.001$) and during spring (97% vs. 85%; $\chi^2 = 23.1$, $df = 1$, $P < 0.001$).

Patterns of use for local and distant roosts varied among individual crows (Fig. 2). Some birds roosted exclusively at the distant roost until the end of winter (e.g. crow 117), and others alternated between the distant and local roost (e.g. crow 118). In all cases, use of the distant roost declined from winter to spring (e.g. March and April; Fig. 2). By mid-April, most crows either stopped going to the distant roost, or made individual forays to it after a series of successive nights at a local roost.

Foraging activity away from the territory.—Most of the radio-tagged crows left their territories during the day (Table 1). In nearly all cases, we located these birds at known foraging sites. Crows foraged away from their territories in three circumstances. First, they used foraging sites near their territories (i.e. within 500 m). One such site was located at a harvested corn field adjacent to the southwestern side of our study area. In fall, abundant post-harvest waste grain attracted what appeared to be migrant flocks of crows as well as many of our marked crows from the study area. Second, we found a foraging site 4 km from our study area that was used during brief diurnal forays, usually by individual crows. This site was at the landfill consisting of a vegetative waste-composting facility and a large municipal landfill and was in an area of filled marshland adjacent to the Raritan River (Fig. 1). Third, foraging areas near or along the way to distant roosts were used when crows commuted between their territories and the Staten Island roost. These sites were not exclusive of the other two types, but we considered them distinct because crows used them after they left their territories in the afternoon and/or before they arrived at their territories in the morning. The landfill was the most frequently used site. In 110 of 125 (88%) times that we observed radio-tagged crows at

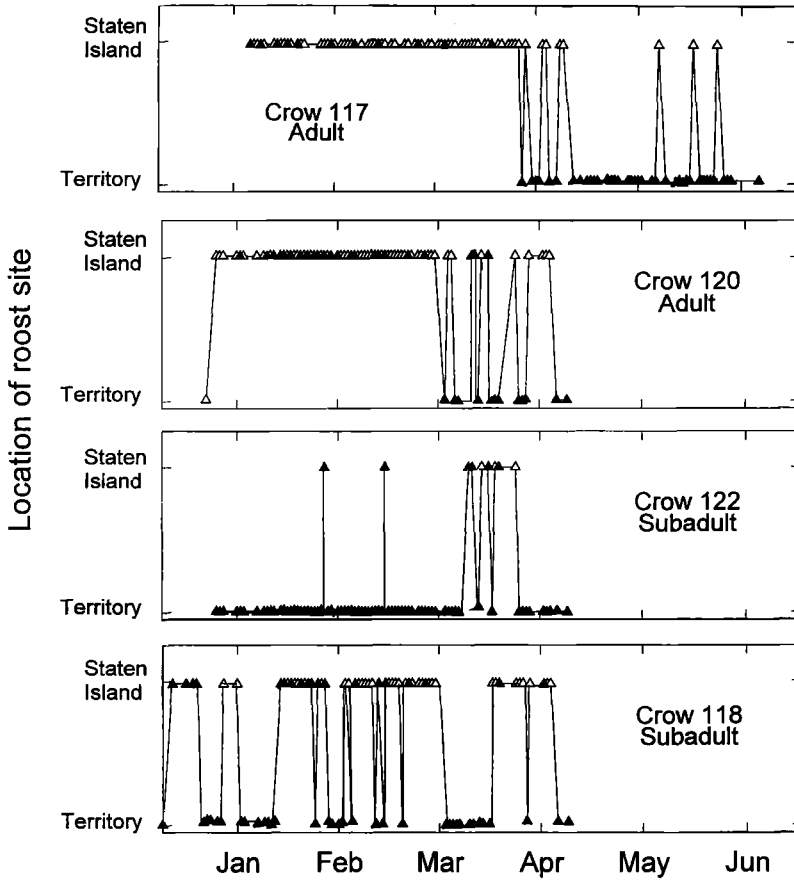


FIG. 2. Seasonal patterns of use of local and Staten Island roosts by radio-tagged American Crows. Solid triangles indicate confirmed use; open triangles represent occasions when presence of crow at distant roost was presumed but not confirmed (see text).

the landfill in the afternoon, individual crows roosted at the distant Staten Island roost. On only 10 occasions did crows forage at this site in the afternoon and then return to roost locally on their territories. Another site frequently used by our radio-tagged birds was west of the roost across the Arthur Kill waterway. Difficulties of getting to and working in this area precluded our successful identification of the precise site used by the birds. Nonetheless, commuting radio-tagged crows regularly stopped at this site as well as at other sites near the Staten Island roost.

Additional evidence suggests that crows usually stopped during their commute between the territory and the distant roost. This is based on travel times between territories, distant roosts, and foraging sites. In the morn-

ing, crows took an average of $50 \pm \text{SD of } 30.9$ min ($n = 43$) to travel from the distant roost to their territories. In the evening, they took more than twice as long ($t = 2.90$, $df = 10$, $P = 0.008$), averaging 126 ± 85.8 min ($n = 11$) to travel from their territories to the distant roost.

DISCUSSION

Diurnal movements relative to group behavior.— Each crow consistently used its own DAC despite frequent trips to a distant roost in the evening. This pattern occurs in many communally roosting species (e.g. European Starlings [*Sturnus vulgaris*], Caccamise and Morrison 1988; American Robins [*Turdus migratorius*] and Common Grackles [*Quiscalus quiscula*], Morrison and Caccamise 1990; and Red-winged

Blackbirds [*Agelaius phoeniceus*], Johnson 1979, Caccamise 1990). For crows, the individual nature of the spatial distributions that form DACs easily could be overlooked because of the prominence of their group-based behavior on territories. Nonetheless, DACs for each of the radio-tagged crows had unique features, even among members of the same cooperative group.

Crows were faithful to their DACs even in winter when they frequently traveled to distant roosts at night. The high level of DAC fidelity is most easily explained by group cohesion. However, such a clear relationship is not apparent in other roosting species with high levels of DAC fidelity. This is because other roosting species are not known to actively defend territories outside of the breeding season. Nonetheless, continued presence in the breeding area probably contributes to long-term occupancy of a breeding site even when territories are not maintained in the nonbreeding season. For example, in winter European Starlings regularly spend the night in cavities that they will later use for nesting (Lombardo et al. 1989).

The variation in our counts of group size was unexpected. We identified three sources: (1) one or more group members were absent at the time of the count, (2) group composition actually changed, or (3) nongroup members were present on the territory (these were either individuals from nearby territories or groups of vagrants). The absence of group members at the time of field surveys was the most frequent cause for the variation. Absent birds often were at nearby foraging sites (see below). In addition, group membership for some individuals seemed somewhat labile in that certain crows were absent for extended periods (i.e. days to weeks), only to return at varying intervals without any apparent resistance from the more stable group members. Similar observations were made by Caffrey (1992), where dispersion of juvenile crows ranged from leaving the area entirely to remaining with the family group. The only actual changes in group composition that we saw occurred when groups increased in size as young of the year took up residency on the natal territory. Chamberlain-Auger et al. (1990) concluded that increases in size of crow groups were due to young remaining on natal

territories. We documented this three times in our study.

Despite variations in group size, the stability of groups was evident based on consistent group composition for the marked crows. Some individuals remained with the same group on the same territory throughout the three years of our study. This stability likely minimized strife among groups. Overt aggression was rare among groups, only becoming apparent for short intervals in March and April.

Roosting behavior.—Radio-tagged crows were very consistent in their selection of roost sites, occurring either: (1) alone or in small groups on their territories, or (2) at the large communal roost on Staten Island. Nonetheless, the social behavior related to group membership and territoriality differed markedly depending on where the crows roosted. When roosting on the territory, crows maintained strong group ties, often interacting with other group members throughout the day and up until the time they settled for the night.

When crows roosted at Staten Island, we found no evidence for group cohesion once individuals left the territory. The considerable differences among group members in the timing of arrivals at their territories and departures from the distant roost suggest that departure decisions were made independently. Similarly, we found no evidence of group cohesion when several group members were present at the distant roost. We detected no coordinated group activity nor any tendency for group members to roost near one another.

Foraging activity away from the territory.—Radio-tagged crows frequently left their territories to forage. Most often this occurred in mid- to late afternoon when crows left for the day. However, individuals also left earlier in the day for intervals ranging from about 10 min to 2 h. Brief absences (10 to 30 min) generally occurred when crows traveled to foraging sites away from their territories but within the study area at Cook College. However, individual crows sometimes were absent from their territories for longer intervals (1 to 2 h). These absences resulted mainly from travel to more distant foraging sites. We cannot confirm that every such absence was a foraging trip, but our evidence suggests that travel to off-territory foraging sites accounted for a large proportion of the absences. Once we identified the forag-

ing sites used most frequently by radio-tagged crows, we generally checked these sites whenever a crow was missing from its territory. We located radio-tagged crows at the landfill 31% of the times they were absent during territory checks. During the remainder of absences crows probably used at least one other distant foraging site. Despite extensive searches within a radius of 6 to 8 km around the study area, however, we never located an additional foraging site.

The landfill was an important foraging site, both during the day and in the evening before crows went to roost. Foraging was the most frequent behavior observed at the landfill, particularly when crow numbers increased late in the day. We found that 88% of the radio-tagged crows that visited the landfill late in the day roosted at Staten Island that night; only 12% returned to their territories to roost. These observations suggest that the evening visit to the landfill was a regular practice of crows before they undertook the long commute to the roost at Staten Island.

Why do cooperative breeders leave the group territory?—The American Crow is the only species known to breed cooperatively on a group territory but leave the territory at night to attend a distant communal roost. The typical pattern among other cooperative breeders is for all group members to remain on the territory both day and night. Some species leave the territory as a group to forage elsewhere for short intervals (e.g. Green Woodhoopoes [*Phoeniculus purpureus*], Ligon and Ligon 1990). However, this is quite unlike our crows that leave territories individually and show no group-related behavior at distant foraging areas or at communal roosts.

Year-round residence on breeding territories confers at least two advantages. First, it increases breeding opportunities by maintaining ties to a successful breeding group on an established territory. Individuals can maintain their social position within the group, accruing all of the benefits associated with cooperative behavior. Related to this are benefits gained by avoiding or delaying the need to establish dominance rank when contact is made with unfamiliar individuals or groups away from the territory. Young crows may be at a disadvantage compared with older, more experienced individuals in establishing their social rank (Caf-

frey 1992). The second advantage is that year-round residence in familiar surroundings likely is safer than moving to new locations during the nonbreeding season. Intimacy with the local landscape allows individuals to become acquainted with dangers (e.g. predators) and to become familiar with the location of safe havens and local food sources. The single factor that limits year-round residence on territories most often appears to be the consistent availability of adequate food supplies.

When food supplies on a territory fail to meet energetic or nutritional requirements, the territory holder(s) must leave to forage elsewhere. A common solution to the problem is seasonal abandonment of the territory, but this carries a serious disadvantage in that the territory must be reclaimed at the onset of each breeding season. This costly and time-consuming process holds the serious potential for territory loss. Short-term diurnal abandonment of the territory is another approach to deal with seasonal variation in food availability. This approach is used by other cooperatively breeding, territorial species. During the nonbreeding season, groups of Green Woodhoopoes undertake brief forays to foraging sites outside their normal territory boundaries, presumably because foraging opportunities are better at these distant sites (Ligon and Ligon 1990).

We propose that travel to distant communal roosts by crows is another form of territory abandonment based on the need to supplement the foods available on the territory. In this case, individual crows depart their territories in the afternoon, leaving sufficient time before dark to fulfill their foraging requirements at distant sites. Depending on the time of year, the territory might remain occupied by some group members, or it might be totally abandoned for the night. In either case, it is unlikely that the territory would be occupied by a nonresident group. Crows leave their territories with little or no tendency to maintain group-based behavior. Thus, territorial contests among groups would be unlikely late in the day when most crows leave their territories individually to forage at distant sites.

Caccamise and Morrison (1986, 1988) showed that when European Starlings travel long distances to forage at high-quality sites away from their DACs, they can feed there twice for the costs of a single round trip. They

do this by roosting overnight near the foraging site. Starlings use large communal roosts when food supplies are lowest on DACs (Caccamise 1991). It is more efficient to roost overnight than to return to the DAC whenever the foraging site is closer to the nighttime roost than to the DAC. Similarly, crows can accomplish the same efficiency when they travel to distant foraging sites and roost nearby. Thus, we propose that large communal roosts of crows, such as the one at Staten Island, are passive aggregations that develop when many individual crows assemble for the night at or near the same foraging areas.

Similar patterns of movement between DACs and distant roosts are known for at least five communally roosting species (European Starlings, Morrison and Caccamise 1985; Common Grackles, Caccamise et al. 1983; Red-winged Blackbirds, Caccamise 1990; American Robins, pers. obs.). Among these species, the American Crow is the only one that breeds cooperatively. All of the intensively studied DAC-based communally roosting species, including crows, display high levels of fidelity to their DACs. European Starlings use a series of foraging sites near the roost (Caccamise and Morrison 1988) but occasionally change roosts during a season. In contrast, our crows always used the same distant roost site. This difference can be explained by differences in stability of the foraging sites used by the two species. The sites used by crows (landfills) probably showed little seasonal change in quality, thus obviating the need for crows to change sites. On the other hand, starlings used sites that were naturally ephemeral (e.g. fruiting trees, corn stubble, irrigated turf), requiring changes in foraging sites and the associated nearby roosts when the quality of distant foraging sites deteriorated.

Roosting behavior in American Crows is similar to that in the other communally roosting species that display DAC-based roosting behavior. Cooperative breeding appears to have little direct effect on the nature of communal roosting in crows. Persistent fidelity to the same DAC is interrupted by an apparent resource-driven need to forage at distant sites. Thus, interpretations of the functional significance of communal roosting that have developed from studies of other species should apply equally well to cooperative breeding in American Crows.

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