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ROOSTING AND DIURNAL MOVEMENTS OF RADIO-TAGGED AMERICAN CROWS

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ABSTRACT.—Cooperatively breeding birds characteristically defend territories in which they forage and roost all year. In contrast, the cooperatively breeding American Crow (*Corvus brachyrhynchos*) is notorious for large feeding and roosting aggregations during the non-breeding season. These observations suggest a pattern of fidelity to diurnal activity centers (DAC's) with daily movements to roosts and areas of superabundant food, much like the movements of communally roosting blackbirds and starlings. We radio tagged and color marked crows at a farm in central New Jersey to examine roost use and fidelity to territories during the winter. Birds exhibited two distinct movement patterns. Seven of 11 crows returned to the farm daily where they maintained stable territories in groups of 4–5. These "DAC-based" crows left the farm early in the afternoon and travelled to large communal roosts 14–18 km from the farm. The largest roost (>5000 crows) was 4.5 km from a landfill where thousands of crows fed daily. DAC-based birds sometimes stopped at landfills in transit to roosts. Although they were almost always together at the farm, crows from the same group usually did not travel together or make the same stops between the farm and the roost. In contrast to DAC-based crows, the other birds rarely returned to the farm and were difficult to find during the day. These "vagrant" crows were most often found at landfills and probably were not part of stable groups, although they used the same roosts as DAC-based birds. Vagrants disappeared during the middle of the winter, suggesting that they were not permanent residents in the study area. *Received 16 Oct. 1990, accepted 3 April 1991.*

American crows (*Corvus brachyrhynchos*) live in groups that breed cooperatively and defend year-round territories (Kilham 1984, 1989; Chamberlain-Auger et al. 1990; C. Caffrey, pers. comm., but see Good 1952). From these studies it appears that groups are stable seasonally, but most birds were not marked, so the extent of movement between groups is not known. Crows form large communal roosts (Davis 1894, Emlen 1938, Haase 1963), but the roosting patterns of marked individuals has not been examined. Thus it is not clear if crows remain faithful to stable diurnal activity centers (DAC's) but travel daily to distant feeding areas (DFA's) and roosts. Such a pattern is typical of communally roosting European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quisculus quiscula*; Morrison and Caccamise 1985, 1990). Alternatively, crows in permanent groups may roost on their territories, and large roosts may be comprised of vagrant birds that range widely without fidelity to DAC's, as in Common Ravens (*C. corax,* Heinrich 1988). Large roosting aggregations of territory holders in cooperatively breeding species have not been reported.

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Groups in most cooperative species defend territories that contain all the resources necessary for the group (see discussion in Brown 1987, Chapter 2).

We investigated roosting and social organization in crows, using individually marked and radio-tagged birds. Our intent was to link diurnal observations of known individuals with use of roosts and distant feeding areas. We conducted the study in the winter because crows are known to roost communally then and because bird movements are not constrained by the need to tend eggs or nestlings. Specifically, we asked the following: are crow groups stable in the winter? If so, do individuals from groups use communal roosts? Do crows use DFA's in transit to and from roosts? Do groups remain associated at DFA's and roosts?

STUDY AREA AND METHODS

We studied crows using the agricultural fields at Rutgers Univ. in New Brunswick, New Jersey. The farm has approximately 2 km^2 of horse pastures, turf, corn, and vegetable fields. It is bordered by a suburban residential area to the east and south, Rutgers Univ. campus to the north, and the expansive lawns of several corporate complexes to the west. Small woodlots rim the farm except to the west.

Crows foraged in the pastures and harvested fields at the farm. We captured foraging crows by baiting with chicken eggs dosed with the sedative alpha-chloralose (Stouffer and Caccamise, in press). We kept sedated crows overnight to allow them to recover (Stouffer and Caccamise, in press). We outfitted crows with radio transmitter packages mounted with backpacks (Morrison and Caccamise 1985). The total weight of the transmitter package was 8–15 g, less than 3% of body mass. Although the transmitter and battery combinations that we used had effective ranges of up to 6 km and expected lives of 4–6 months, their effectiveness in the field was determined by the extent to which the birds damaged their antennas (see below). In addition to radio-tagging, we also bleached a pattern on the primaries or secondaries of each bird so we could visually identify individuals (White et al. 1980).

We attempted to locate each crow during the daylight hours 4–5 days a week from the time of capture through the end of March. For DAC-based birds (see below), one location sample was taken each day at a random time during the period that crows used the farm (about 08:00–13:00 h EST). We located birds at night 3–4 times a week by checking known roosts or by following bearings of birds as they left the farm. We attempted to find birds at DFA's by following bearings of birds as they arrived and departed from the farm and the roost, or by checking sites known to have been used by crows from the same roosts.

We quantified the activity of crows at the farm by continuously sampling focal individuals for three minute intervals (Altmann 1974). These data were entered on a portable computer in the field. We subsampled the data at 30 second intervals to generate discreet, independent samples. For this analysis, behaviors were combined into four categories: forage, which included walking with head down as well as handling food items; perch, including preening as well as terrestrial and arboreal perching; locomotor, which included walking with head up and flying; and other, primarily vocalizing and social interactions.

RESULTS

We captured 13 crows from 6 November through 15 February (Table 1). All were over one year old (AHY/ASY: Pyle et al. 1987). Crows captured on 17 December, 6 February, and 15 February were part of groups that we had observed for several days before capture, and which we suspected to be stable groups of permanent residents of the farm. Radio-tagged birds from these groups returned to the farm nearly every day and are referred to as DAC-based crows (see below). The birds captured on 6 November and 16 January did not regularly return to the farm and did not remain in stable groups. These birds are referred to as vagrant crows (see below).

Two crows are not included in Table 1 nor in any subsequent results. The first bird, captured on 16 January, was found dead near the farm on 18 January. From the remains, we could not determine if it was killed by a predator or dismembered by scavengers. The second bird had massive damage to primaries and secondaries on both wings when it was captured on 15 February. This bird probably was a member of the group captured that day, since we had repeatedly noticed a bird with damaged feathers in the same area. We attached a transmitter, but we did not locate the bird again.

Territories of DAC-based crows.—DAC-based crows returned to the farm nearly every day throughout the winter. We successfully located these seven birds at the farm on 88.6% of attempts (242 of 273). Because they were often foraging in fields or perched at the periphery of fields, we usually located birds visually. It was necessary to use radio signals to find birds when they ranged deeper into woodlots or into residential areas. We relied almost entirely on visual locations for birds 13 and 15; both birds damaged their antennas, drastically reducing transmitter range. The signals from these birds became increasingly poor until they could not be received at all by two weeks after release. The other birds also damaged their antennas, but we could still receive weak signals.

Plots of daily locations show that territories of DAC-based birds overlapped only slightly (Fig. 1). Based on a minimum convex polygon estimate (e.g., Anderson and Rongstad 1989), territory sizes were 0.26 to 0.49 km^2 (group A ≐ 0.49 km^2, B = 0.38 km^2, C = 0.26 km^2), although groups B and C used additional areas to the north where we were unable to follow and delineate territorial boundaries. We usually observed five individuals in each group, but at times we were unable to see all members at once. Birds from adjacent territories often foraged 50–100 m apart in the same fields, but we saw no disputes at territorial boundaries until late March. On four occasions, one or two apparently vagrant crows foraged in the same fields with territorial birds, but we never saw these birds chased away by residents. The territories of groups A and C overlapped slightly near the intersection of the lake and Ryder's Lane (Fig. 1); twice we saw chases between the two groups in this area.

TABLE 1

CAPTURE DATES AND GROUP SIZES AT THE TIME OF CAPTURE OF RADIO-TAGGED CROWS. DAC-BASED CROWS WERE MEMBERS OF TERRITORIAL GROUPS AT THE FARM; VAGRANT BIRDS WERE NOT (SEE TEXT)

Capture date	Bird number[a]	Group size	Territorial status	Group
6 November	1	>100	Vagrant	—
	2	>100	Vagrant	—
17 December	4	5	DAC-based	A
	5	5	DAC-based	A
	6	5	DAC-based	A
16 January	7	>7	Vagrant	—
	8	>7	Vagrant	—
6 February	11	5	DAC-based	B
	12	5	DAC-based	B
15 February	13	5	DAC-based	C
	15	5	DAC-based	C

[a] Bird numbers correspond to the last two digits of the USFWS series beginning with 685-65101.

One bird switched groups for a few days but later returned to its original group. Bird 5 was with birds 4 and 6 in group A 91% of the times it was found, but we also located it in a second, adjacent territory (the four points north of Rt. 1 in Fig. 1). Although bird 5 foraged and perched within a few meters of the two crows in the adjacent territory, we saw no aggression directed toward it.

Activity varied slightly over the course of the day while crows were at the farm (Fig. 2). Perching was the most common activity for most of the day, accounting for 29 to 66 percent of hourly observations. Locomotor activity varied between 17 and 43 percent. Both perch and locomotor varied significantly among hours, probably as a result of the high frequency of perching at the expense of locomotor at 1300 and 1400 h (log-likelihood test, both $G > 19.9$, $df = 6$, both $P < 0.003$). Time spent foraging remained relatively constant between 15 and 21 percent. The apparent decrease in foraging as the day progressed was not significant by regression ($R^2 = 0.47$, $P = 0.09$).

Roosting by DAC-based crows.—By the second night after release all DAC-based crows joined communal roosts. Until late December most birds used a roost in Perth Amboy about 14 km NE of the farm. This roost had a maximum of about 500 crows through December but was abandoned by 12 January. For the rest of the winter, all locations of roosting birds were from a roost on Staten Island, about 18 km ENE of the farm. This roost contained at least 5000 birds through the end of March. Both roosts were in secondary forest dominated by red maples

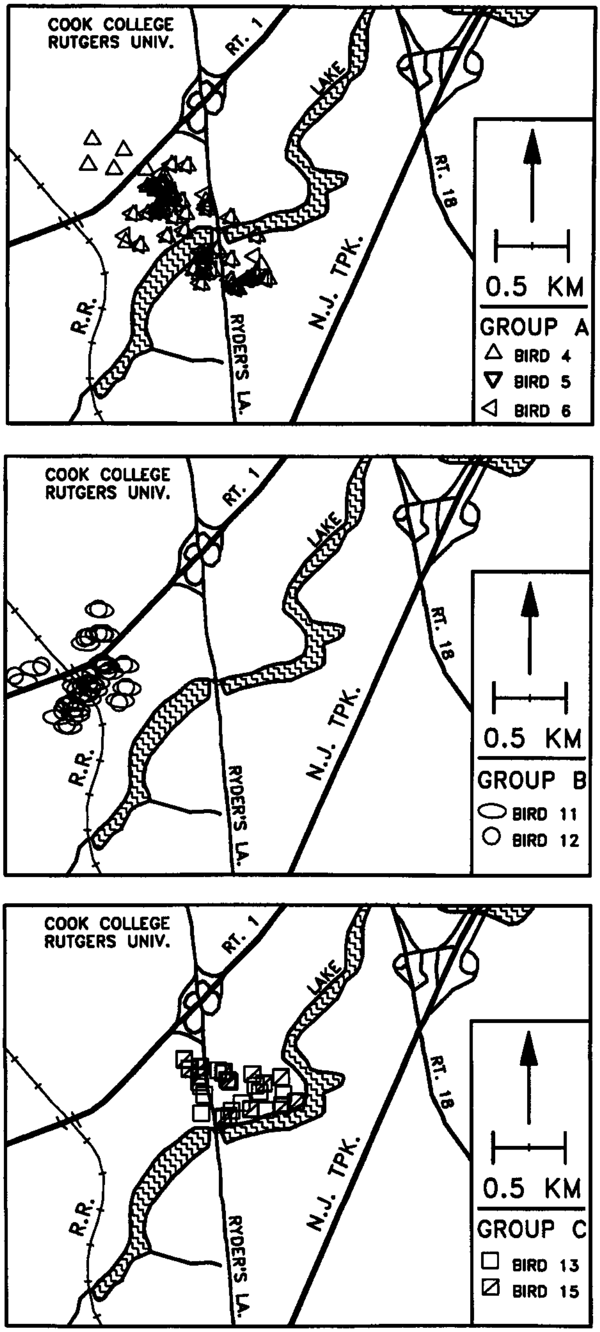

FIG. 1. Territories of DAC-based crows. Plots show daily locations of marked individuals from the indicated groups.

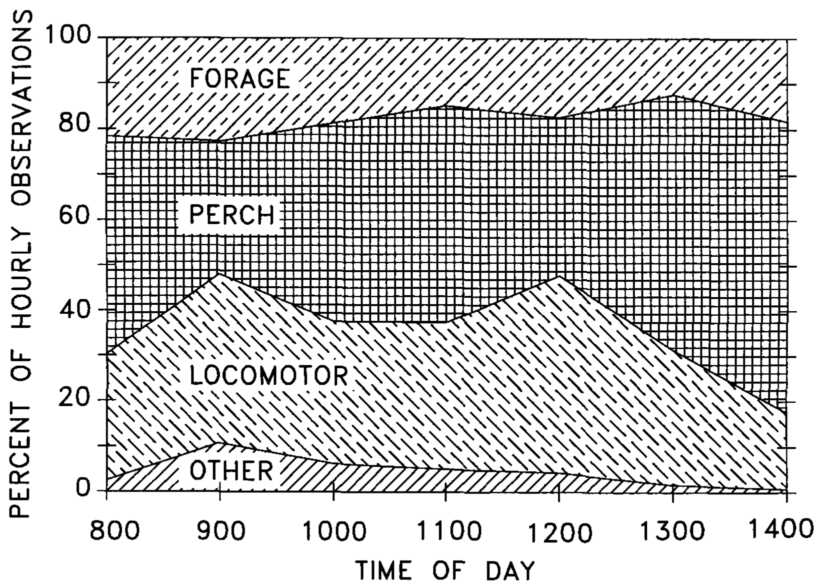

FIG. 2. Activity budget of DAC-based crows on their territories.

(*Acer rubrum*) 3–8 m tall. In addition to American Crows, a smaller number of Fish Crows (*C. ossifragus*) used the roosts. Crows usually assembled at several locations within 0.5 km of the roost site, then coalesced at the roost by dusk.

Six of the seven DAC-based crows roosted at the farm on the night they were released. Birds 4, 5, and 6 roosted together in a tall white spruce (*Picea glauca*). Birds 11, 13, and 14 roosted in woodlots but could not be precisely located. None of the DAC-based crows roosted at the farm after the first night, although we did observe DAC-based birds roosting at the farm in April, after the conclusion of this study.

We successfully located DAC-based birds at communal roosts on 84.1% (122 of 145) of attempts. Some absences were probably related to weather. January 25 was rainy and foggy, and no DAC-based birds used a communal roost, although they did leave their territories. Other absences may have been due to poor radio performance; the Staten Island roost was sufficiently spread out that we may not have been close enough to detect the weak signals from some birds.

Travel to roosts by DAC-based crows.—Our measurements of commuting time between the farm and roosts indicated that birds stopped in transit. Stops were shorter in the morning than in the afternoon. Birds left the roost between 06:17 and 07:10 h and arrived at the farm between

07:10 and 07:54 (Fig. 3). They remained on their territories until 13:00 to 14:40, and arrived at roosts between 15:39 and 17:08. Based on an average body mass of 521 g, we calculated the velocity of maximum range for our birds to be 51 km-h^{-1} (Caccamise and Hedin 1985). Thus the commute to the Perth Amboy roost (14 km) should have taken 16 min and 21 min to the Staten Island roost (18 km). There was only a 50 min difference between mean departure time and mean arrival time in the morning, leaving about 30 min for a stop. In the afternoon, however, the 135 min difference between mean departure time from the farm and mean arrival time at the roost allowed at least 100 min for a stop.

On 11 occasions we found DAC-based birds at a landfill in Edison about 4 km from the farm between the farm and both communal roosts. We found two DAC-based crows at the Edison landfill in the morning. They continued on to the farm before we returned by 07:50 and 08:05. On nine other occasions we found DAC-based crows at the same landfill between 13:30 and 16:20. These birds were present at roosts the same evening. We never found DAC-based birds at landfills between 08:05 and 13:30, the period when we were searching for vagrants (see below).

Based on counts of birds flying into and out of landfills, hundreds of crows at a time used the Edison landfill, and thousands used a giant landfill on Staten Island north of the roost. We never located DAC-based birds at the Staten Island landfill, but it was logistically difficult to find birds there. There were several good vantage points from which to watch birds and receive signals near Edison, but most of the giant complex on Staten Island was inaccessible.

Crows from the same group rarely travelled together between the farm and the roost, and in some cases even used different roosts, although they were nearly always together at the farm. Birds in the same group arrived at or departed from the farm or the roost within two minutes of each other in only 29% (2 of 7) of observations in which we knew exact arrival or departure times. Similarly, on only 11% (1 of 9) of observations of DAC-based birds at landfills did we find more than one bird from the same group.

Vagrant crows.—We saw behavioral differences between vagrants and DAC-based crows beginning before the birds were captured. Birds 1 and 2 were captured together at the farm on 6 November as a part of a group of about 150 crows foraging in a recently harvested corn field. The birds in that group fought over access to the eggs we provided, and birds had to pick up the eggs and fly away in order to avoid harassment. The group of vagrants from which birds 7 and 8 were captured did not fight over eggs, although seven birds were eating the eggs at the same time. Other crows vocalized from nearby trees, but those birds may have been the

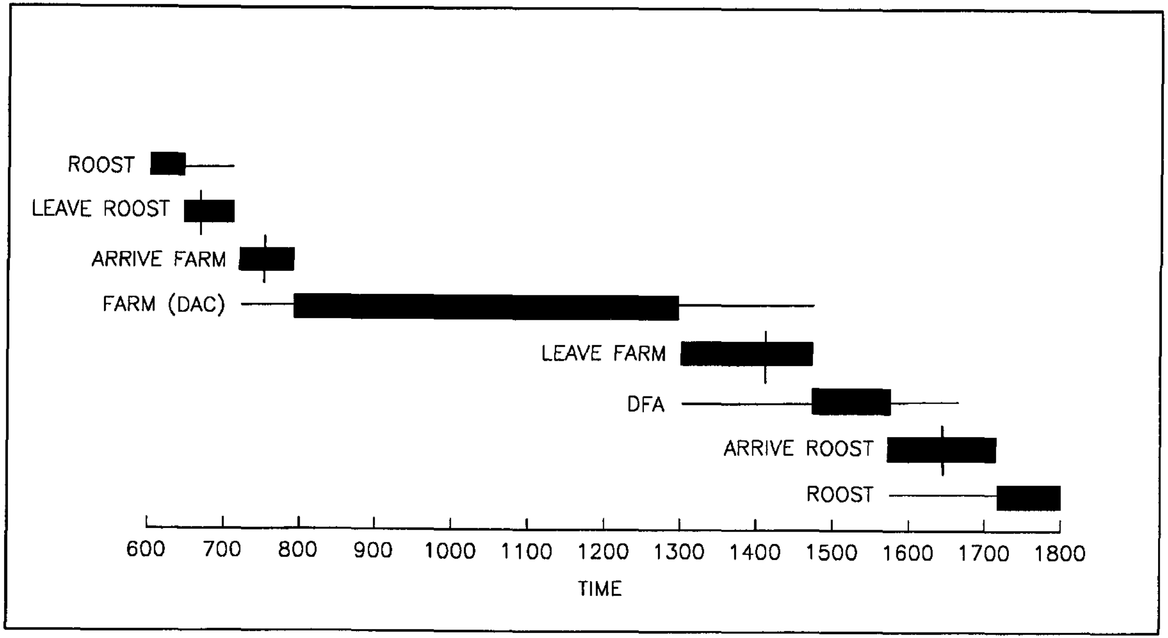

FIG. 3. Pattern of daily movement for DAC-based crows using distant feeding areas (DFA's) and communal roosts. For arrival and departure times, horizontal bars show ranges and vertical lines show means. For roost, farm, and DFA, horizontal lines show ranges and horizontal bars show times when birds were most likely to be present.

residents that we later captured at the same site. We also saw conflict over food at landfills and at roosts. In contrast, DAC-based birds took turns eating eggs, with two or three eating at a time while the others perched nearby on the ground or in trees. The first group to eat would then move off to the side and other individuals would descend, although it was not unusual for at least one member not to eat eggs at all.

The four vagrants were not faithful to the farm or to the individuals with whom they were captured. For example, bird 1 returned to the farm in a large flock four times, then switched to the Edison landfill. Bird 2 did not return to the farm, but was twice located at the Edison landfill, and later began to leave the roost in the direction of the Staten Island landfill. In general, vagrants were very difficult to locate during the day, although they used the same roosts as DAC-based birds. We spent over 90 hours searching the study area for diurnal locations of vagrants, but we only found them on 31.8% (21 of 66) of attempts. We stopped systematically searching for these birds during the day after they disappeared permanently from communal roosts.

Vagrants used communal roosts at Perth Amboy and Staten Island, but each disappeared permanently from roosts during the winter. Bird 1 was last located on 23 November, bird 2 on 2 January, bird 7 on 9 February, and bird 8 on 2 March. Before they disappeared permanently, we located roosting vagrants on 70.7% (41 of 58) of attempts. In addition to using communal roosts, on five nights bird 1 roosted, apparently alone, in a stand of white pines (*Pinus strobus*) 8 km NNE of the farm.

DISCUSSION

DAC-based crows.—The territorial fidelity and stability of DAC-based groups at the farm was much like that reported by Kilham (1984, 1989) from Florida and Chamberlain-Auger et al. (1990) from Cape Cod, although Good (1952) reported that crows were only territorial in the breeding season in Ohio. The groups we studied probably bred at the farm beginning in April; we saw members of each group carrying nesting material at that time. Because we only marked two or three birds in each group, we cannot be certain that the other group members were the same individuals throughout the winter, but since we saw considerable social interaction without conflicts within the groups, we suspect that groups were stable. The birds we captured were all AHY/ASY, so we cannot evaluate possible behavioral differences as a function of age.

Bird 5 divided its time between group A and a second, adjacent group, possibly in an effort to join the second group. The second group had only two other individuals, compared to four others in group A, so there may have been a better chance to breed by joining a smaller group. Similar short-term dispersal forays are common in Florida Scrub Jays (*Aphelocoma c. coerulescens*; Woolfenden and Fitzpatrick 1984:151, see also Brown 1987:104).

Daily movements of DAC-based crows, which included daily return to a group territory, use of supplemental food sources off the territory, and roosting communally is an unusual pattern for a cooperatively breeding species. Typically, cooperative species maintain family territories during the non-breeding season on which they forage and roost (e.g., Brown 1978). In several species, adjacent breeding groups combine in the non-breeding season, and the resulting larger group ranges over the area of all the smaller breeding territories (Long-tailed Tit [*Aegithalos caudatus*], Gaston 1973; Buff-rumped Thornbill [*Acanthiza reguloides*], and Striated Thornbill [*A. lineata*], Bell and Ford 1986). White-winged Choughs (*Corcorax melanorhamphos*) wander, as a group, over a wide area in the non-breeding season, foraging largely on grain stubble (Rowley 1977). Scrub Jays make short forays out of their territories to forage on grain handouts, but return promptly (Woolfenden and Fitzpatrick 1977). We know of no other cooperative species with the pattern displayed by crows, in which groups associate for part of every day and then break up to forage and roost elsewhere.

Use of supplemental food sources, especially landfills, off their territories may permit DAC-based crows to maintain their territories at times when the territories do not provide sufficient food. We believe, however, that the crows we observed were seldom food limited on their territories since they spent relatively little time foraging and most of the day loafing (Fig. 2). Further, they often cached food and they became less attracted to baits over the course of the day. We consider it more likely that crows used food sources off their territories because either (1) foraging was more efficient or safer at DFA's, or, (2) visiting supplemental sites enabled birds to know of foraging sites in the event that they were unable to find food on their DAC's, such as after a heavy snow.

It is interesting that groups did not remain together except at the farm. This suggests that the advantage to individuals of maintaining groups on territories does not persist when not on the territory. Further, this means that birds that use the same DFA or roost are essentially anonymous to each other in comparison to birds that are together during the day. This anonymity may explain why crows share food on their territories (see also Kilham 1989:22) but fight over food off their territories. Within groups, restraint from eating (or food sharing; see Taylor and McGuire 1988) may be a cooperative act maintained by a high potential for future interactions. At large roosts or DFA's, however, there is little chance to interact repeatedly with the same individuals, making reciprocity less likely (Trivers

1971, Axelrod and Hamilton 1981). Food sharing may also be important for forming and maintaining the social bonds necessary for successful cooperative breeding (see discussion in Seyfarth and Cheney 1988).

Vagrant crows.—Movements of vagrant crows differed from those of DAC-based crows in four respects. (1) Vagrants left the area in the middle of the winter. (2) Vagrants probably did not have DAC's. They were not faithful to the farm or any other location and were most likely to be found at landfills. (3) Vagrants and DAC-based birds differed temporally in their use of landfills. DAC-based birds seldom or never used landfills in the middle of the day (between 08:00 and 13:30, Fig. 3), but vagrants used landfills at all hours. (4) Vagrants that were captured together did not remain together.

These patterns of diurnal movement and short-term residency in the study area suggest that vagrants may be migrants from farther north. Alternatively, they may be birds that dispersed from local natal groups but have not found new groups. We think the radio-tagged vagrants were migrants, since they were over one year old and they disappeared in midwinter. A similar pattern of irregular movement followed by disappearance was reported for vagrant Common Ravens (Heinrich 1988). Kilham (1989:44) also reported wandering flocks of vagrant crows in Florida during January. Movement patterns of vagrants differ in scale from movement within a smaller area by "floaters" in territorial species (e.g., Smith 1978). Also, vagrant crows did not form any temporary associations with stable groups, as do floaters (Smith 1978).

Roosting.—All crows used communal roosts throughout the winter. Most absences were from March, suggesting that some crows used another, undiscovered roost during that time. Based on visual observations after all radios had expired, DAC-based birds began roosting at the farm in April. Seasonal variation in roost choice is also common in starlings (Morrison and Caccamise 1985).

Crow roosts were spatially associated with superabundant food sources, as appears to be the case for roosts of other species (Caccamise and Morrison 1988). A recent explanation for communal roosting behavior, the "patch-sitting hypothesis," suggests that large roosts form as passive aggregations near superabundant food supplies (Caccamise and Morrison 1986). The largest and longest-lasting roost, on Staten Island, was near an enormous landfill used by thousands of crows. It would be interesting to examine if roost establishment follows landfill establishment on a broad geographic and temporal scale; Davis (1894) reported that "able bodied crows do not roost on Staten Island in winter, but fly as night approaches to better protected retreats in New Jersey." This is the reverse of the pattern a century later, after Staten Island became a dumping ground for the other boroughs of New York City and former agricultural land in New Jersey was replaced by urban sprawl.

For vagrants, roosting on Staten Island reduced the commute to the Staten Island landfill to only 4.5 km, supporting the patch-sitting hypothesis for roost establishment (Caccamise and Morrison 1986, 1988). Finding DAC-based crows at the Staten Island landfill would have provided support for the patch-sitting hypothesis for those birds. DAC-based crows stopped at the Edison landfill before continuing on to the Perth Amboy or Staten Island roosts, and we suspect that they also used the Staten Island landfill, although we were unable to find them there.

Roost-site selection by crows that did not use large roosts provides a comparison to the typical communal roosting pattern. Characteristics of roosts used by these crows suggest that they chose roost sites to avoid detection by predators or to reduce heat loss, but neither of these advantages was likely at large communal roosts. Birds 4, 5, and 6 roosted together in the dense cover of a spruce for one night after release. Bird 1 roosted repeatedly in a pine. We also saw birds 11 and 12 and several unidentified birds (probably the rest of group B) roost in a Norway spruce (*Picea abies*) in May. Predation deterrence is probably the greatest benefit to crows roosting in foliage, especially in May (Walsberg and King 1980). Cooperative groups in other species have been reported to roost together, huddled deep in foliage, on their territory (e.g., White-winged Chough, Rowley 1977; Buff-rumped Thornbill, Bell and Ford 1986; Green Wood-Hoopoe [*Phoeniculus purpureus*], Ligon et al. 1988).

Several crows roosting in dense foliage is a dramatic contrast to thousands of birds blanketing a woodlot of scrubby trees that offer no cover, such as at the Perth Amboy or Staten Island roosts. Since birds at large roosts space themselves out and do not seek cover, it is unlikely that these roost sites provide any thermal benefit (see also Kelty and Lustick 1977, Walsberg 1986). Although large roosts have the advantage of diffusion of risk and many eyes to spot predators (Crook 1965, Pulliam 1973), these roosts are probably easily detected by predators (see discussion in Skutch 1989, Chapter 4). Presumably the risk of a predator finding the roost is outweighed by the benefits of being in a large group.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227–265.

ANDERSON, D. E. AND O. J. RONGSTAD. 1989. Home-range estimates of Red-tailed Hawks based on random and systematic relocations. J. Wildl. Manage. 53:802–807.

AXELROD, R. AND W. D. HAMILTON. 1981. The evolution of cooperation. Science 211: 1390–1396.

BELL, H. L. AND H. A. FORD. 1986. A comparison of the social organization of three syntopic species of Australian thornbills (*Acanthiza*). Behav. Ecol. Sociobiol. 19:381–392.

BROWN, J. L. 1978. Avian communal breeding systems. Ann. Rev. Ecol. Syst. 9:123–155.

———. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, New Jersey.

CACCAMISE, D. F. AND R. S. HEDIN. 1985. An aerodynamic basis for selecting transmitters in birds. Wilson Bull. 97:306–318.

——— AND D. W. MORRISON. 1986. Avian communal roosting: implications of "diurnal activity centers." Am. Nat. 128:191–198.

——— AND ———. 1988. Avian communal roosting: a test of the patch-sitting hypothesis. Condor 90:453–458.

CHAMBERLAIN-AUGER, J. A., P. J. AUGER, AND E. G. STRAUSS. 1990. Breeding biology of American Crows. Wilson Bull. 102:615–622.

CROOK, J. H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. London 14:181–218.

DAVIS, W. T. 1894. Staten Island crows and their roosts. Auk 11:228–231.

EMLEN, J. T., JR. 1938. Midwinter distribution of the American Crow in New York state. Ecology 19:264–275.

GASTON, A. J. 1973. The ecology and behaviour of the Long-tailed Tit. Ibis 115:330–351.

GOOD, E. E. 1952. The life history of the American Crow *Corvus brachyrhynchos* Brehm. Ph.D. diss., Ohio State Univ., Columbus, Ohio.

HAASE, B. L. 1963. The winter flocking behavior of the common crow (*Corvus brachyrhynchos* Brehm). Ohio J. Science 63:145–151.

HEINRICH, B. 1988. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the Raven, *Corvus corax*. Behav. Ecol. Sociobiol. 23:141–156.

KELTY, M. P. AND S. I. LUSTICK. 1977. Energetics of the starling in a pine woods. Ecology 58:1181–1185.

KILHAM, L. 1984. Cooperative breeding of American Crows. J. Field Ornithol. 55:349–356.

———. 1989. The American Crow and the Common Raven. Texas A&M Press, College Station, Texas.

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.

MORRISON, D. W. AND D. F. CACCAMISE. 1985. Ephemeral roosts and stable patches? A radiotelemetry study of communally roosting starlings. Auk 102:793–804.

——— AND ———. 1990. Comparison of roost use by three species of communal roostmates. Condor 92:405–412.

PULLIAM, H. R. 1973. On the advantage of flocking. J. Theor. Biol. 38:419–422.

PYLE, P. D., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

ROWLEY, I. 1977. Communal activities among White-winged Choughs (*Corcorax melanorhamphus*). Ibis 120:178–197.

SEYFARTH, R. M. AND D. L. CHENEY. 1988. Empirical tests of reciprocity theory: problems in assessment. Ethology and Sociobiol. 9:181–187.

SKUTCH, A. F. 1989. Birds asleep. Univ. Texas Press, Austin, Texas.

SMITH, S. M. 1978. The underworld in a territorial sparrow: adaptive strategy for floaters. Am. Nat. 112:571–582.

STOUFFER, P. C. AND D. F. CACCAMISE. Capturing American Crows using alpha-chloralose. J. Field Ornithol. in press.

TAYLOR, C. E. AND M. T. MCGUIRE. 1988. Reciprocal altruism: 15 years later. Ethology and Sociobiol. 9:67–72.

TRIVERS, R. L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46:35–57.

WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk 103:1–7.

——— AND J. R. KING. 1980. The thermoregulatory significance of the winter roost-sites selected by robins in eastern Washington. Wilson Bull. 92:33–39.

WHITE, S. B., T. A. BOOKHOUT, AND E. K. BOLLINGER. 1980. Use of human hair bleach to mark blackbirds and starlings. J. Field Ornith. 51:6–9.

WOOLFENDEN, G. AND J. W. FITZPATRICK. 1977. Dominance in the Florida Scrub Jay. Condor 79:1–12.

——— AND ———. 1984. The Florida Scrub Jay: demography of a cooperatively-breeding bird. Princeton Univ. Press, Princeton, New Jersey.