DISPERSAL AND ASSOCIATION AMONG COMMON RAVENS¹

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Abstract. We examined the dispersal and gregariousness of 10 ravens from one feeding flock through daily and nocturnal monitoring for 70 days and nights over an area of approximately $5,000 \text{ km}^2$. One of the birds took a mate and established residency within this area. Another passed through the area on infrequent intervals having an apparently much larger range. Two stayed only a day or less. All but one bird wandered widely, taking up residency lasting for one to several weeks in ranges from $190-3,100 \text{ km}^2$. The 10 birds from the feeding flock did not stay together, although up to two occasionally overlapped at nocturnal roosts. The birds roosted and dispersed independently of one another with no indication of any "flock" cohesiveness. There was a great variation of response from "vagrants" to "residents", with one grading into the other through temporary residences and periods of wandering.

Key words: Corvus corax; ravens; dispersal; flocks; gregariousness; roosting.

INTRODUCTION

In numerous bird species, adults return year after year to established breeding territories that they defend against conspecifics. However, except in those species living in social flocks, little is known about the movements of the juveniles and nonbreeders (Greenwood and Harvey 1982). Do they also live in established ranges where their presence is cryptic because they vocalize little and do not return to a conspicuous nest site? Do they wander without observing fixed boundaries?

The behavior of the Common Raven, *Corvus* corax, may be additionally complex because juveniles and non-breeders are often gregarious and said to associate in flocks (Coombes 1948, Young 1949, Mylne 1961, Coombs 1978). Breeding pairs of *C. corax* live in established territories both winter and summer (Knight and Call 1980, Heinrich 1989). The young, however, disperse in late summer and early fall (Dorn 1972, Stiehl 1978, Skarphédinsson et al. 1990) to destinations that are so far largely unknown.

Non-resident juvenile ravens gather at animal

carcasses and at food bonanzas such as refuse dumps and near these food sites they establish communal nocturnal roosts (Heinrich 1988). In the forests of New England, most ravens' roosts are temporary, often lasting only a few days. When not returning to roosts from feeding sites or vice versa, birds usually fly singly or in pairs (Heinrich 1988), but after a food source is depleted they commonly engage in social soaring displays and then leave as a group (Marzluff et al., unpubl.). Nevertheless, despite apparent social behavior, the ravens (except pairs) at any one feeding site appear to come and go independently of one another (Heinrich 1988). Apparent independence of birds one from another near a carcass, however, does not exclude possible social behavior away from it, such as at roosts. We examined these topics by monitoring 10 radiotagged individuals.

METHODS

We captured a group of 10 ravens at a feeding station baited with calf carcasses in the forest near Weld, Maine (Heinrich 1988, Fig. 1). Three of the birds had dark mouth linings and 7 had the pink mouth linings typical of unmated subadult birds (Heinrich and Marzluff 1992). Within

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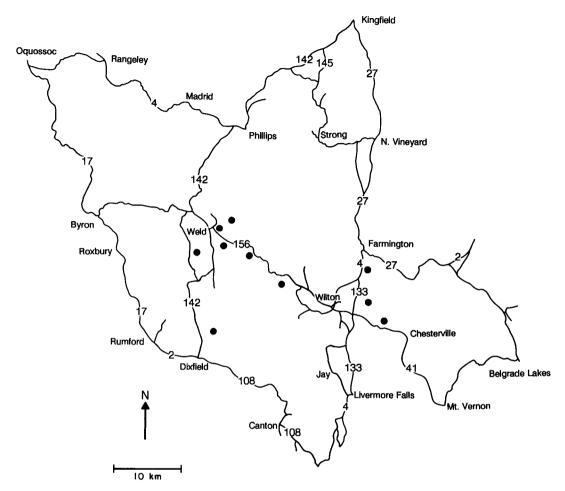


FIGURE 1. Map of the study area, showing major roads along which we surveyed. The filled circles show nest locations of ravens in 1992 and 1993 in the area near the center of the map that was surveyed for raven nests.

2 hr after capture the ravens were each equipped with a Telonics Mod-50 radio transmitter and released in the vicinity of the bait where they were captured. The transmitters were attached to the dorsal tail surfaces (the tail feathers molt in the summer) by tying them onto the main feather shafts with dental floss. Knots were reinforced with superglue.

Using a Telonics TR-2 receiver and a TS-1 scanner we then surveyed for the birds every day and every night for 70 days (starting 5 February, the day of capture and marking). We logged approximately 160 km per 24 hr, stopping every 3–4 km to scan all frequencies of the 10 birds along the roads indicated (Fig. 1). Each day consisted of two shifts, a day and a night shift. We considered "day" readings those taken after day-

light and an hour before dusk. Night readings (for roost locations) refer to those taken after sundown.

Our study area encompassed the southern part of Franklin County with parts of Androscoggin, Kennebec and Somerset counties of western Maine, for a total area of approximately 5,000 km² (Fig. 1). The area comprises primarily wooded hills up to 600 m in elevation. Due to the brokenness and steepness of the terrain the range of our radios was often limited to less than 2 km. On some occasions we logged up to four readings on a single location. On many occasions, however, due to the movements of the birds and the ruggedness of the terrain, we had only one reading, relying on the topography and the strength of the radio signal to interpolate the birds' ap-

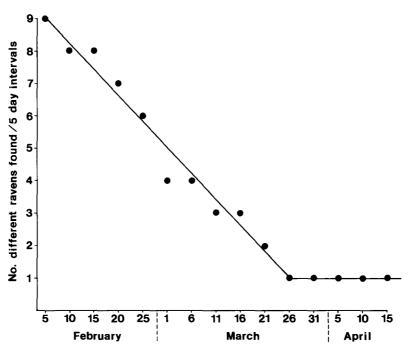


FIGURE 2. The number of different individual birds (out of the 10 radio-tagged) that were found over fiveday intervals from February 5 (the day of capture, marking and release) and until April 14. Note that only one bird (the same one) remained after mid-March.

proximate (to within 2 km²) location. Due to the wide-ranging movements of our birds, radio-locations within this resolution were sufficient to answer our questions about the birds' large-scale movements in the 5,000 km² area and about their possible associations with each other.

Throughout most of the study we kept two feeding stations available. These included the bait station where the birds had been captured and another one within 1 km where no birds had ever been captured. Ravens fed sporadically at both of these stations throughout the duration of this study, as well as at the various nearby town landfills (Wilton, Strong, Weld, and Rumford).

RESULTS

DISPERSAL

Six of the birds were still within 3–4 km of the bait where they were captured and released the next day, and two more were observed within 5–10 km when sampled in the next four days. Two birds, however, were not observed anywhere for the remainder of the study.

In general, birds either steadily left the area or

occurred further and further from the point of capture (Fig. 2). After 20 days, only five were still present in the survey area, and by another month only two, an adult and a subadult, remained. Throughout the next month the adult was found near the same location every night. On 14 April, we found the bird flying in company with another bird and then roosting at night with one other bird. On the day when the pair was flying together, we also saw a soaring aggregation of 11 ravens nearby. The pair did not join them, and since they did not follow them to their communal roost (see Marzluff et al. 1993) we presume that this black-mouthed adult bird had found a mate and was a resident. However, we found no nest *here* the following spring.

The above adult did not establish a roosting site until 20 days into our study. Our two other black-mouthed adults remained in the survey area only one and eight days, respectively. We found only one of the nocturnal roosting places of the latter bird that stayed eight days, and it roosted there only one night and was never located again.

Different temporal patterns of apparent residency emerged (Fig. 3). For example, 8151 and

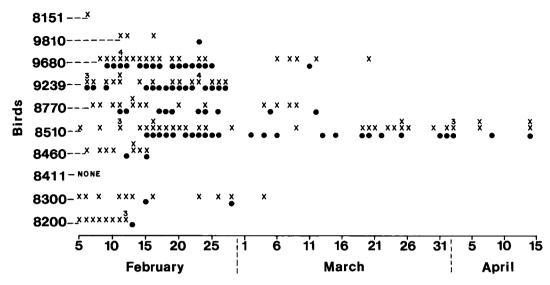


FIGURE 3. Temporal pattern of radio contacts of the 10 birds over the course of the study in the study area. Crosses indicate diurnal, and dots indicate nocturnal contacts. Note that some birds (9239, 9460, 8200) were consistently located for a limited time and then not at all. One bird (8510) was located consistently throughout the whole time. Another two (9810, 8300) were sporadically found, and two (8151 and 8411) dispersed almost immediately.

8411 were not observed at all after the first day. On the other hand, 8200 and 8460 were found 11 and 10 times for eight and 10 days respectively, and then not at all for the remainder of the study (some two months). No 9239 was found 36 times in 23 days, and then not at all for the following 47 days. In contrast, 9810 was contacted only four times in the first 23 days, then not at all for 28 days, then again four times in two days, and then only once in the following 22 days. This pattern of sporadic appearances suggests that some birds may have been only infrequently encountered because the area we sampled was at the periphery of their range.

AREA OF RESIDENCY

We attempted to amass as many locations as possible in order to determine the size of the area the birds used while they were in our study area (Fig. 4 gives a sample of four of the eight birds). However, these areas are obviously underestimates; with more readings the individual birds' foraging areas that we ascertained could undoubtedly have been much larger. For example, for bird No. 8510 (Fig. 4A) we accumulated 32 daytime locations with a spread of 46 km across east-west, and 34 km north-south (or up to 26 km north of its roosting place and 30 km west). If we assume a 40 km average diameter of a circular foraging area, then the birds' range encompasses about 1,250 km², which is near the mean for the eight birds that stayed eight or more days. On the other hand, if we assume that the nocturnal roost constitutes the center of the foraging area and our sampling represents a bias due to topography and terrain, then the birds' foraging domain has a diameter of about 56 km and its area is closer to 1,540 km².

The birds showed a great diversity of response. For example, No. 9239 (Fig. 4B) used one roost location more than other roosts. Bird No. 9810 (Fig. 4C) did not use one roost location more than others. No. 9680 (Fig. 4D) was logged over a 53 km east-west range from February 5-25 when it was repeatedly (at least two weeks) at the same location at night. After a 10 day absence the bird suddenly reappeared in the center of this range, where it now roosted for the night at a new location. It was not detected until eight days later when it appeared once more some 32 km north of where it had been found before. Its apparent foraging range of some 32×53 km was not, however, due to a gradual wandering, because the bird traversed the entire area in a single day (see Fig. 4D, 2/11 and 2/12). For example, on 11 February we found it four times with a

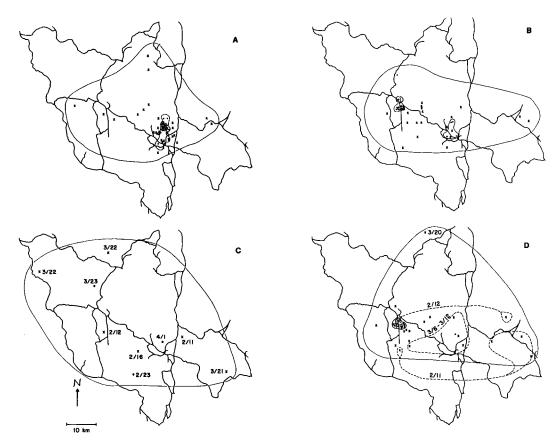


FIGURE 4. Radio-locations of a sample of four of the eight birds that we monitored. Crosses indicate diurnal and dots indicate nocturnal contacts. Light lines surround diurnal and/or nocturnal roosting areas, as well as some dates of occupancy or movements. (A = bird No. 8510, B = 9239, C = 9810, D = 9680).

maximum distance of 45 km apart. On the next day the same bird was observed in the afternoon 38 air km to the east of where it roosted that night.

Although the ravens often flew at least 32 km in a single day between foraging sites and roosts and/or between different foraging sites, they tended to stay within areas bounded by about 16 \times 32 km (Nos. 9770, 9239, 8460, 8200, 8510, 8300) over at least 2–3 week periods. Therefore, these data, given the daily possible flight ranges, indicate at least temporary, though consistent, residency.

ASSOCIATIONS?

Our 10 birds, although originating from one feeding flock, roosted in at least nine different locations. On eleven occasions two of the radio-tagged birds were found at night in the same general area, suggesting they occupied the same roost. However, most of the other (52) records of roosting birds were without one of the other ten birds. Nevertheless, the tagged birds still roosted communally. On two occasions we tracked birds (that repeatedly came back to the same area at night) to their roosts in the forest, and in both cases the marked bird was accompanied by 30–40 other birds.

During our daytime surveys our radio-tagged birds were monitored within 1-2 km of other tagged birds on 13 occasions (once with five, once with four, once with three, ten times with just one other tagged bird). However, on 96 times they were *not* in the company of one of the other marked birds. The birds were thus at least twice as likely to be found together (presumably at highly localized feeding bonanzas) than at the much less localized suitable roosting sites. The birds therefore have a tendency to be gregarious, but they apparently do not form a social group. Each of the seven birds that did not disperse after the first day intersected at the same time in our study with 4–6 other birds, either at a roost or foraging area. Of the "associations", those between 9680 and 9239 (six times) and 9239 and 8510 (five times) were most frequent. However, these apparent associations did not represent permanent relationships, because 9239 was not seen after February 27, whereas 9680 was observed until March 20 and 8510 was picked up routinely until the end of the study, on 14 April.

DISCUSSION

Studies of bird dispersal have a long and rich history (Greenwood and Harvey 1982) and numerous variables have been identified that affect bird movements. Almost nothing was known of the dispersal or associations of common ravens. Breeding common ravens occupy specific domains year-round (Haurie 1956) and they nest near or at the same location each year (Knight and Call 1980). Four to six young are usually reared per year. The young stay with their parents throughout the summer and then disperse (Dorn 1972, Stiehl 1978, Skarphédinsson et al. 1990).

In the fall and winter flocks of ravens often aggregate at food bonanzas in the forests of western Maine, and most of these birds consist of sub-adult non-breeders (Heinrich 1988, 1989). Young from the local nests rarely show up at the winter feasts, and only rarely do immatures marked in any one year show up again in the area the next year.

The above studies had centered on a relatively small area near Weld, Dixfield and Farmington, in Franklin County, in western Maine. Except for perhaps a specific population of marked birds at landfills, it was not known where the rest of the birds moved to. Do they pass through the area known to contain at least 8 traditional nest sites (see Fig. 1) or do they stay and remain unnoticed?

Rather than monitoring the presence or absence of identified birds at a specific site such as a rich food source, we radio-tagged birds and searched for them over a 5,000 km² area for a period of 70 days. In addition to learning about possible movements of birds in and/or through this area, we also hoped to learn something about possible social interactions in the presumed feeding "flocks" (Coombes 1948, Young 1949, Mylne 1961, Cooms 1978). Our 10 radio-tagged birds were captured together, allowing us to see whether or not the birds form cohesive flocks or whether the birds are only gregarious. As pointed out (Greenwood and Harvey 1982) most previous studies on bird dispersal have relied on band recoveries, which overestimate dispersal because of mortality. However, there were also limitations to our methods. First, our study area consists of large tracts of nearly unbroken forests in very hilly country that is, however, conveniently criss-crossed by roads. In our daily and nightly surveys we were limited by these roads. In general, we surveyed for radio-signals from elevated ground, but the topography and sheer size of the area nevertheless limited our ability to provide a day-by-day record of the presence/absence of marked birds. We could only ascertain presence, not absence. Furthermore, since we on occasion found birds to move over 40 km in one day, any one reading per day provided little information about size of area used. However, a minimum foraging area could be deduced by plotting contacts over consecutive days. We could monitor no more than one quarter of the study area per day/night, therefore, a bird that was continuously present for four days in one area might not necessarily be located by us more than once per week. We presumed, however, that over the period of 70 days it would, on occasion, be found if present during that time.

Our results showed that some birds are indeed highly vagrant. They disappeared in a few days, not to be found anywhere, on any survey. However, other individuals were repeatedly encountered for several weeks, and sometimes several times on the same day. Eventually most of these birds, too, disappeared. Some of our birds returned nightly to specific communal roosts. However, roost shifts were frequent. There was no tendency for the ten marked birds from the one feeding aggregation to roost together, although ravens in captivity develop a social hierarchy and possibly a social group (Gwinner 1964). Up to two of our marked ravens occasionally overnighted in the same roost, but that could have been by chance alone given that the birds seek communal roosts for overnighting and the number of available roosts are likely small.

Although we kept two feeding stations available at and near where the 10 birds were captured, we attempted to first disperse the birds after the capture (by temporarily removing the bait) to determine if the 10 birds would leave together along with the rest of the feeding crowd (of over 40 individuals) and then reconvene at the next bait. They did not. Nor did they show up again as a group when crowd feeding resumed anywhere else. Instead, each bird moved independently, contrary to the deeply entrenched notion in the literature that sub-adult ravens associate in a "flock" structure.

It seems surprising that the birds left the area at all when food was available at all times. We can only speculate that vagrancy is not only the result of a search for food, but also a function of search for mates and/or suitable territories.

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