Behav Ecol Sociobiol (1988) 23:141–156

Behavioral Ecology and Sociobiology

Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*

B. Heinrich
Department of Zoology, University of Vermont, Burlington, VT 05405, USA

Received August 17, 1987 / Accepted February 21, 1988

Summary. Large animal carcasses provide a highly clumped rich source of food for ravens that should be worth defending, yet in the forests of Maine and Vermont ravens commonly feed in groups. Ravens discover baits flying singly or in pairs, but after a bait is discovered they usually arrive in groups. In contrast, the maximum number of blue jays and crows eventually attending a bait is close to those discovering it. Unlike in crows and jays, two patterns of bait use are seen in ravens: baits are used by mated resident pairs or by large crowds (sometimes exceeding 40 individuals). This pattern is unrelated to bait size from at least 9 kg to 400 kg. Eightytwo of 91 individually marked ravens from 4 feeding crowds were juveniles and/or nonbreeders. Observations of the marked ravens for parts of two winters indicate that the non-breeders are vagrant and/or they range over at least 1800 km^2 in their foraging. Most of the over 135 baits (totalling nearly 8 t of meat) distributed over 50 km were discovered by ravens within a week, and most were consumed by crowds of ravens. The vagrants coming in crowds have (unlike the territorial adults) specific vocalizations in the bait vicinity that are a powerful recruitment stimulus in playback experiments. Vagrants sometimes feed alone, but in the presence of territorial adults they feed only in groups. Resident adults chase or attack vagrants, but mildly tolerate them (and even join them) when they come in large groups. I conclude from my observations that the feeding crowds of ravens consist primarily of juvenile non-breeding vagrants who (unlike some resident adults) roost communally and who vigorously recruit each other in part to neutralize the aggressiveness of resident adults defending prized food bonanzas. The ravens' recruitment results in a sharing that reduces the temporal patchiness of extremely rare food bonanzas, and it permits the non-territorial vagrants to specialize on carcasses in the winter.

Introduction

In the winter throughout the taiga forests the raven, *Corvus corax*, feeds on a rich and highly clumped food resource – the carcasses of deer, elk and moose. Especially in areas of dense forests and frequent snowfalls, such food occurs unpredictably and is difficult to locate. Furthermore, daylight hours for foraging are reduced, and the metabolic demands in the often extreme cold are high (Schwan and Williams 1978). Any one carcass, if found, should therefore be an extremely valuable resource that merits defending vigorously (Myers et al. 1981). However, although ravens breed solitarily in large territories (Knight and Call 1980) aggregations commonly feed at carcasses (Hauri 1956; Mylne 1961; Harlow et al. 1975; Dorn 1972) which the inexperienced birds fear (Heinrich, in press).

Birds vulnerable to avian predators may aggregate in flocks, thereby gaining vigilance or protection (Pulliam 1973; Kenward 1978; Caraco 1981; Elgar 1986). However, ravens are among the largest passerine birds of the world, and once past the nestling stage they are relatively immune to predation from hawks, eagles and falcons (Hutson 1945; Bent 1946; Williamson and Rausch 1956; Cade 1960). It would therefore not be expected that they would share a rich, rare, and clumped defensible resource for mutual protection. Nevertheless, my preliminary observations in Maine and Vermont indicated that ravens not only shared such resources, they also appeared to recruit others to them (Heinrich 1988b). In contrast, the smaller and presumably more vulnerable corvids in the same area and at the same baits tolerated others and did not recruit (American crows, *Corvus brachyrhynchos*), or neither tolerated nor recruited others besides their mates (blue jays, *Cyanocitta cristata*).

I here provide evidence that ravens do, indeed, recruit and in part through comparative data on the other two corvids I present an ecological perspective for the evolution of the sharing behavior.

Methods

The primary observations here reported were made during the winters (Sept. to March) of 1984–1988 near Mt. Blue State Park, in Franklin County in western Maine. This is a heavily wooded area with numerous lakes and mountains, containing populations of white-tailed deer (*Odocoileus virgianus*), moose (*Alces alces*), bear (*Ursus americanus*) and coyotes (*Canis latrans*).

During the first two winters I used a cabin in the forest as a blind. I entered and left it only before dawn or at dusk when no ravens were near. The windows were covered, except for a viewing window equipped with a one-way mirror. The birds were apparently not afraid of the cabin, since they routinely perched in the trees next to it, and walked within several meters of it. Baits were generally placed at least 30 m distant. Additional observations were made directly in the forest, using temporary blinds. In the third winter I observed directions of arrivals to baits from an hour before daybreak until 2 h later while concealed (only a very few birds flying directly near me after daylight veered in their flight path) in the thick branches near the top of a tall spruce on a hill from which I had a panoramic view. A total of over 135 baits were used. They consisted of 3 road-killed deer and 5 moose (obtained from local game wardens), 3 cows, 12 calves, 2 sheep, 3 goats and numerous smaller mammal carcasses (rabbits, squirrels, raccons, beaver, skunk, fox, etc.) and approximately 2500 kg of slaughter-house offal (usually excluding intestines). A total of 1520 h of observations were logged at or near the primary study site in Maine from September 1984 to March 1988. Most baits were scented with human urine to discourage coyotes from taking them.

In addition to the primary study site, I also provided a "permanent" meat station in the woods within visual range (40 m) of my home in Richmond, Vt. I observed ravens there informally for approximately 150 days throughout 3 winters, primarily in the early mornings.

Most of the 300 km between the Vermont and Maine study sites is suitable raven habitat, and I routinely saw ravens (0.6 per 100 km) when travelling between sites, with no apparent differences in frequency of sightings toward one or the other end of this transect. Baits provided along the transect were also visited by ravens.

During the first two winters of the study, I provided bait(s) at the Maine study site only once every two weeks, and observed each bait and the birds coming to it continuously for 2–7 days or until the food was eaten. Food remaining after each set of observations was removed. During the third and fourth winters I also simultaneously provided 10–14 baits over areas spanning 10 to 50 km. The baits were checked once or twice per day to count birds and/or to observe tracks in the snow to determine bait utilization. When 1 or 2 ravens fed they left distinct tracks next to the bait. However, when a crowd of at least 15 birds fed for one day they trampled even deep fluffy snow into a solid mat at least $20\ m^2$ near the bait.

In addition to the wild birds, I observed from 2–7 birds through a large window in an aviary attached directly to my home. These birds originally consisted of 2 from one nest, 4 from another, and one hunger-weakened adult captured by hand at the Maine study site. These birds were kept in 3 separate aviaries until September, when all were simultaneously released to observe possible interactions. Within several days the birds started to leave the area, and I then recaptured 2, which I observed for another 6 months at my home.

Voice recordings of ravens were made in the field from a blind with a P-200 E.P.M. parabolic microphone, and recorded on cassette tape with a super ANRS portable stereo cassette deck (KD-1636 Mark II). Playback in the field was with an Electro-Voice Inc. PA12F loudspeaker. Playback volume was 62–66 db at 75 m (as determined with a Type 1565-A General Radio Co., portable sound-level meter), equivalent to the birds' own vocal output. Sonograms were prepared from the cassette tapes with a Kay Electronics Digital Sono-Graph 7800, using an analysis filter of 150 Hz.

The ravens used for marking and radio tagging were captured (on 4 occasions) in an aviary (6 m × 4 m × 3 m) built out of chicken wire and tree poles into the forest the previous summer. One side of the aviary was lifted and supported by a strut, with a wire from the strut leading to a nearby (15 m) blind built out of densely woven fir and spruce saplings and branches from which the strut could be yanked to close the case within 1 s. A large quantity of meat (100–300 kg) was continually provided within and around the cage, while the cage was left open. When the birds no longer showed any apparent hesitation in feeding within the cage, I hid in the blind before dawn, waited until all of the birds in the vicinity were inside, and then sprung the trap. No birds escaped. All of the birds ($n = 10$ to 43) were temporarily put into individual burlap bags before being weighed, measured and marked.

Patagial wing markers of approximately 10 cm × 5 cm (see Dorn 1972) were cut from differently colored TXN-18 vinyl coated nylon (manufactured by Cooley, Inc., Anaheim, CA). They were attached onto the left wing surface with knobby rivets, and the attachment reinforced with super-glue. Different colors were used to denote different age classes and years of capture. Juvenite birds (from previous spring) have dull brownish feathers while sub-adults (2 year old) and adults have glossy blue-black plumage. Age was also determined by mouth and tongue colors (pink = juvenitles, mottled = subadults, black = adult, see Kerttu 1973). Numbers (approximately 4 cm tall) were painted onto all of the vinyl wing markers with black vinyl screen ink (manufactured by Naz-Dar Co., Chicago, Ill.). Birds with patagial wing markers were also provided with U.S. Fish & Wildlife aluminum leg bands.

Two birds (one adult and one juvenile) were equipped with Telonics "mod 70" radio transmitters. The transmitters, each weighing 22 g, were attached in a back-pack fashion using a harness of 6.4 mm tubular Teflon ribbon, sutured with dental floss and sealed with super-glue.

Results

Patterns of bait use

During the four winters of this study, all 28 large mammalian carcasses left in the forest were consumed by large crowds of ravens. Similarly, almost all of the other 106 baits (of approximately

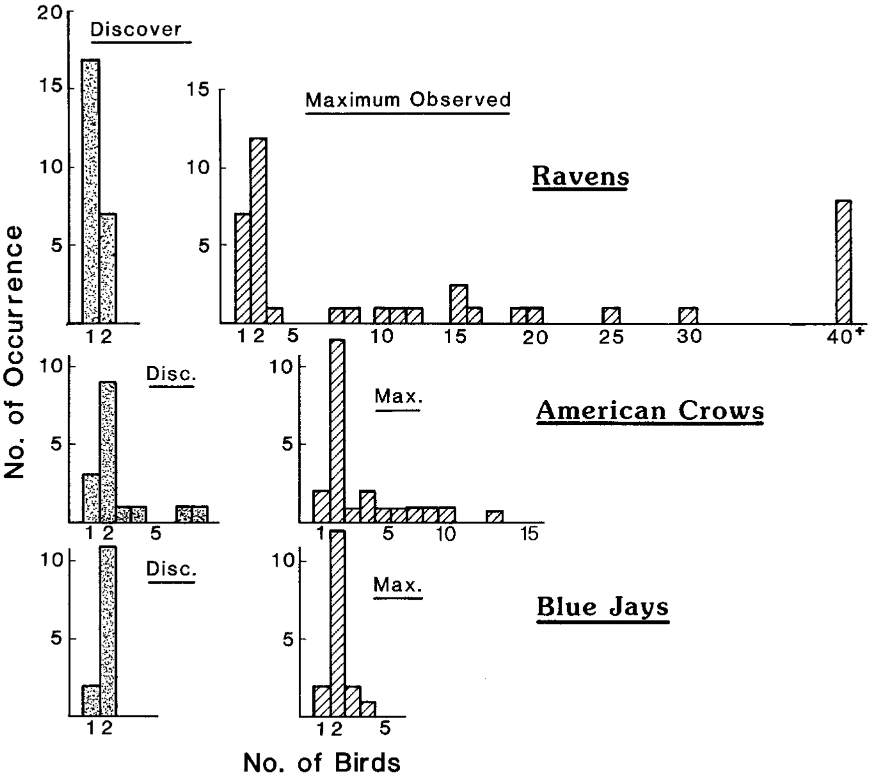

Fig. 1. Number of birds discovering a bait vs the maximum numbers that were later observed on it at any one time

2500 kg) weighing 9 or more kg each were also consumed by raven crowds. Coyotes and foxes occasionally fed on some of the baits.

The mammalian carcasses were left uneaten until opened, but after being opened they vanished quickly. For example one of two moose carcasses (unfrozen) in November was cut open, and it was then consumed in one week solely by ravens (no mammalian scavengers present) while the second carcass lying near it was left untouched. When two weeks later the second carcass was also opened, it too was consumed by ravens in one week. A cow carcass (frozen solid) was untouched through December, and then consumed within one week after it was chopped open. The meat from opened sheep and deer carcasses was totally consumed by ravens in 2 days without any other scavengers present. It is safe to conclude that ravens alone consumed most of the carcasses and baits.

Two patterns of bait use were observed in ravens. Baits/carcasses were visited by 1–2 birds at the same time, or they were visited by crowds (Figs. 1 and 2). These patterns were not a function of bait mass from 9 kg to at least 400 kg. However, the arrival of crowds was highly variable. For example, some 10 kg baits and/or large carcasses attracted crowds of ravens on the same day that they were put out (Fig. 4), while others did not have raven crowds feeding on them until two months later. Until a raven crowd finally consumed the bait, however, it was generally visited only by 1–2 birds at a time. It is possible that the ultimate size of the raven crowd is limited by the amount of bait, but this was difficult to test because of the logistic problem of providing sufficient meat. In one winter I attempted to replenish a bait at several-day intervals for two months, and up to 90 ravens fed at this bait simultaneously.

My data underestimate both the total number of baits that may attract large numbers of ravens as well as the maximum numbers of ravens possible at a bait because I usually removed the bait after a few days and before a crowd could potentially gather (see Methods). Also, the numbers seen at any one time underestimate the maximum number feeding at the site (later section). No crowds of crows or jays gathered at any time, even though both species were more common than ravens. The number of crows and jays present was usually close to the number making the bait discovery (Figs. 1 and 2). Therefore, neither crows nor jays showed recruitment (for the time being operationally defined as large increases of birds at the bait following discovery by a few).

No population estimates directly at the study site are available, but my subjective impression was that (in the absence of baits) ravens were rare and blue jays common. (The Audubon Christmas Bird

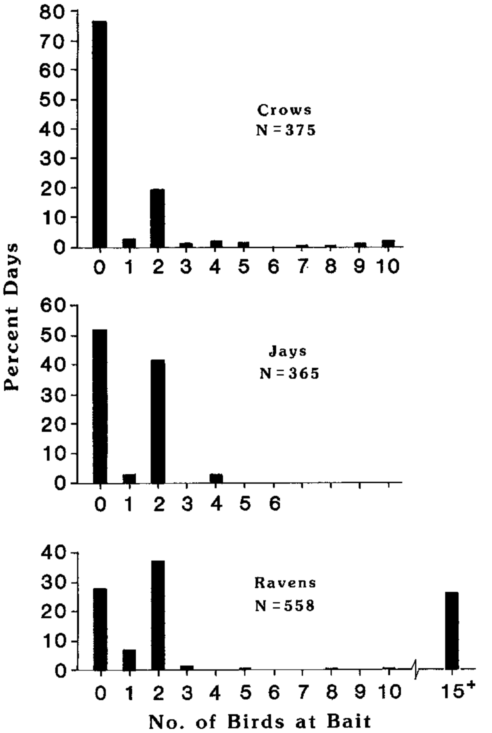

Fig. 2. The percent days baits were visited by respective no. of birds. *n* refers to no. of days the indicated no. of birds were present, until the bait was removed or eaten. (Since the monitoring refers to all 3 corvid species at the same bait, the *n* should be equal, except that only ravens were counted for part of the study)

Count at 4 localities within 46 km of the study site over the last 5 years has yielded sightings of 118 ravens, 3895 crows and 3913 blue jays). Crows were less common than jays at my study site, and it could be that lack of crow crowds in Maine was due either to rarity, or to preference for a vegetarian diet, possibly grain.

To test for the first hypothesis, I provided 2 cut-open goats and 2 cut-open calf carcasses and other offal at 1–10 km from a roost of several thousand crows near Burlington, Vt. No more than 6 crows fed at any of these baits at the same time in 2 weeks. One bait station within 10 km of the roost(s) was maintained with offal for 4 winters and still no crowds of crows came to this bait. Therefore, lack of recruitment in crows was not likely due to scarcity of birds or to lack of roosts to recruit from.

To test for the second hypothesis I provided six 18 kg piles of meat and six equally-sized piles of cracked corn at each of 3 different sites in eastern Maine, western Maine and Vermont. None of the 18 piles of corn were utilized by either crows or ravens at any site, although most of the meat piles were visited by crows and/or ravens.

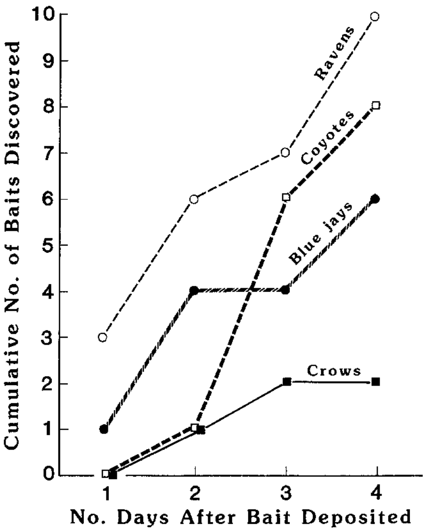

Fig. 3. Cumulative number of baits (9–11 kg meat) out of 12 available (in one experiment conducted Nov. 4 to 8) that were discovered by ravens, coyotes, blue jays and crows, as determined by tracks in the snow and visual sightings during the first 4 days after the bait was deposited

Patterns of bait discovery

As determined by direct visual observations as well as by tracks in the snow (see Methods), ravens were the first discoverers of most baits at the Maine study site (Fig. 3). Since ravens often hesitated before descending to the bait whereas blue jays and crows approached baits with relatively little hesitation, the high discovery rate by ravens as compared to the other two corvids is an under- rather than an overestimate.

In the 25 independent incidents of bait discovery by ravens that I observed, 18 were by apparently single birds (72%) and 7 were by 2 birds flying together (28%). No initial discovery was made by more than 2 birds arriving at the same time. Of 87 instances of birds seen flying at large, 60 (69%) were single, 25 (29%) were in pairs, and two were in groups of 5 and 6. Therefore, I conclude that the large numbers of birds observed at carcasses/baits are not due to chance discovery by flocks.

Species precedence

The interactions of the 3 corvids at baits were unambiguously based on a hierarchy from ravens to crows to jays. Most baits utilized by ravens were also utilized by jays, but the jays never fed until the ravens had left the bait. In several hundreds of hours of seeing baits with both ravens and jays present I saw no exception to this rule, and I never saw one of the birds visibly interact with one of the other.

During over 300 hrs of observations of baits where ravens, crows and jays were simultaneously in attendance I seldom saw ravens visibly influenced by the presence of either of the other two corvids. The presence of feeding crows did not induce the ravens to go down to feed. However, the crows always left the bait as soon as crowds of ravens came down to feed, and they then waited nearby until the ravens had left before they again flew down to resume feeding. The blue jays, in turn, waited until both the ravens and crows had fed before taking their turn.

The crows' avoidance of the ravens appeared to be tempered with experience. At one bait where 4 crows were feeding alternately with jays, the 4 crows instantly left the bait when a raven flew by for the first time. However, after about a dozen fly byes of the raven the crows stopped being interrupted in their feeding.

Although as a general rule ravens and crows fed alternately without interacting, I observed two occasions where (in the absence of raven crowds) a member of a resident raven pair pointedly chased two crows from a bait. I also observed two occasions where several crows flew to the periphery of a feeding raven crowd and then walked unmolested to feed at the bait for several hours.

I watched only two instances of simultaneous use of a carcass by a coyote and groups of ravens. The coyote fed unmolested. The ravens waited close by until the canid had fed until they themselves fed. Since no single raven was ever excluded by other corvids, and since a single coyote could feed unmolested despite a crowd of ravens, I conclude that raven crowds do not function in controlling baits from allo-specifics.

Resident vs vagrant ravens

As has been generally accepted for ravens elsewhere (reviewed by Knight and Call 1980) raven pairs with established nest sites were year-round residents near those nests in Maine and Vermont. One pair at a traditional nest near the study area was marked, and the pair came to baits in the study area during two winters, usually arriving at dawn flying directly from the nest area. A second pair (one of them radio-tagged) visited baits in the study area only when huge feeding crowds were present, and the radio tagged bird returned nightly to within 100 m of its nest throughout late January and February. A third (unmarked) pair came almost every morning at dawn for 3 out of 4 winters to a bait near my home in Vermont.

Whereas the pairs' presence was relatively regular and their habits often punctual, the crowds as well as members of these crowds were highly irregular. I assessed the presence of ravens at a food source where bait was provided on an almost daily basis throughout the year (a landfill in western Maine). During 38 cencuses at the landfill over three winters I observed 20–50 ravens on only 7 occasions. At all the other times there were either no ravens or fewer than 4 visible at any one time. In contrast, herring gulls *Larus argentatus* and greater black-backed gulls *L. marinus* were usually present in large numbers at each census.

The irregular presence of raven crowds was also apparent at baits in the forest. In the winter of 1984 a crowd of ravens consumed a cow near my home in Vermont. Afterward for a week I routinely encountered lone ravens patrolling low over the forest. Two weeks later I provided two calves, which were visited only by a pair. No crowds were seen in the vicinity for the next $3^1/_2$ winters, even though bait was continually provided. Lone ravens, however, were encountered and they approached both the pair at baits (where they were repelled) or my tame juvenile ravens (who appeared to be highly attracted to them, and vice versa).

In my Maine study area crowds were also often absent, but for months rather than years at a time. From late Nov. to early Jan. 1986, 40 or more birds routinely showed up at baits, but in late January there were quite abruptly at least twice that number of birds. In February maximum raven numbers at equally-sized baits again declined to near 20. These results give no indication where individual birds might go, but they suggest that the birds that gather at baits in flocks are not constrained by territorial boundaries.

The above conclusion was substantiated with color-marked birds. My color-marked resident pair continued to be seen daily whenever bait was present for two winters. However, all others (taken from two feeding crowds) quickly drifted out of the study area. Within 6 days after marking, 36 of 61 identified birds (one radio tagged) were never seen again. During the month after marking I observed only 29 of the individually identified birds (4 could be identified by missing tail, toes, leg, and crimped leg) at a new continually replenished bait. Others showed up at other baits set out up to 50 km north from the original marking site. (The frequency of marked to unmarked birds at the distant feeding sites was 7%, close to the 5% at that time at the original marking site.) Four weeks later only 7 identified (marked) birds continued to come at the continually replenished bait.

Six weeks later only 1 of the 61 identified individuals remained, while new unmarked birds had taken their places; the ratio of marked to unmarked birds declined from 0.10 on Jan. 25 to 0.05 one month later.

Throughout the following winter the adult resident pair was seen daily whenever observations were made, but out of over 1000 other raven sightings, only 2 were of the other 54 individuals marked the previous winter. The rapid turnover of marked juveniles was repeated the next year also.

The non-resident birds (unlike the marked pair) did not come to the bait every day. For example, out of a total of 18 identified resighted individuals (from one group of 43 marked birds), 8 only showed up on a single out of 6 days when observations were made from dawn to dusk, and 5 only showed up on 2 of the 6 days. Although a similar *number* of birds attended a bait from morning until night for almost a week, many of the *individual* birds were present for little more than an hour in all that time. (However, when the meat was frozen solid at sub-zero temperatures they often hacked at the carcass for hours at a time). Some marked birds flew by without stopping. None of the 18 above individuals came on all 6 days. Only 1 bird came for 4 out of the 6 days, and this individual was also the only remaining individual a month later. These results show both that most of the crowd feeders are "vagrant" (moving through study area in a few days or weeks) and the groups of birds at baits are not necessarily coherent flocks; flock composition at the bait may change over minutes as different vagrants come and go. Nevertheless, at baits that had not been replenished and where relatively few birds were feeding, I routinely observed discrete arrival and departure of small flocks. It is therefore unlikely that the "vagrants" are totally without social ties in their feeding groups.

The following reasons make it unlikely that the above results showing apparent vagrancy can be attributed either to death or to loss of patagial tags: 1) the marked resident pair showed neither loss of tags nor death for at least one year; 2) the birds were also ringed with aluminum U.S. Fish and Wildlife bands as a check to see if the tags held; no ringed birds were seen without tags; 3) my 7 captive hand-reared birds were also ringed with the same aluminum bands and showed no adverse effects. Similarly, 20 wild-caught ravens equipped with the same patagial tags and leg bands showed no tag or ring loss during 2 weeks of captivity; 4) I at no time saw free birds near baits pecking at their patagial tags and I saw no differences in behavior of birds to each other related to whether or not they were tagged; some of the tagged birds were clearly dominant, others were submissive; 5) the individuals I could identify without having handled or marked disappeared just as rapidly as the others; 6) the birds could not have starved because in both years baits were continually provided during the experiment.

The recruitment of crowds to some baits within hours, and the absence of recruitment to other for up to 2 months (in Maine) and over 3 years (in Vermont) suggest that the crowds as well as the individuals within them are also vagrant. The evidence for crowd movements are scanty, but I offer the following anecdotes to show that the phenomenon exists. In the first instance I observed social soaring of 13 ravens in early afternoon of early February at my study site. Fifteen minutes later 10 more ravens had joined the highly vocal crowd (which I observed from about 2.5 km) before it disappeared from my view. Similarly (in Michigan in early Dec.), approximately 150 ravens gathered from several directions in about an hour one morning in a noisy aerial display, and the birds then descended to perch in a forest nearby (K. Bricker, personal communication) where they had not been seen before or since. I also observed social soaring in Maine prior to dusk where a temporary roost formed that night, and I observed it again in the morning in Vermont several days after a cow was consumed.

I only had three occasions to observe communal raven roosts in or near my study area. One roost of approximately 20 birds regrouped in the same place (a white pine grove) for 1 week each night. The second group of approximately 40 birds was discovered only after they were already settling into the trees (white pines) near a friend's home at dusk. No birds had been near that site for at least 5 years before, and none have been seen in the year since. No birds were seen before or since at the first roost site.

The third roost is a relatively "permanent" roost in Strong, Me., approximately 24 air km from my study area. It was not brought to my attention until Jan. 1988 by two observers who live from 100 m to 300 m of it and who had seen some of my marked birds there. The roost had been used winter and summer for at least one year and it usually consisted of "about two dozen" birds who, however, were not there every night. This roost was unoccupied since 29 Jan. 1988.

Frank Oatman (personal communication) reports 15–18 ravens roosting near Greensboro, Vt.

on Dec. 8, 1974. On Dec. 14 the roost held 55 birds, and on Dec. 16 it had increased to about 100. The 100 roosting ravens then disappeared on the following day and have not been seen near there since. These observations are in accord with recent studies of relatively permanent raven roosts in Idaho showing that roost composition is highly fluid, as individually identified ravens wander from one roost to another (Young et al. 1986).

Bait defense

The lack of aggregation of jays at baits was due neither to rarity nor inability to aggregate. I saw noisy aggregations of a dozen or more jays on at least 6 occasions. Up to 30 once aggregated within 1 km of a feeding station where no more than 4 ever came.

The lack of accumulation of jays at baits is likely due to strong defense. At one bait a jay (one or both of a pair) chased an intruder repeatedly up to at least 70 m from the bait. At other baits where more than two jays were present in the vicinity one pair fed while another (or two) waited within several meters for the first two to finish before taking their turn. If one of those in attendance hopped down to the bait while the other(s) were there it was immediately chased off, though not necessarily followed. I at no time saw more than 4 jays simultaneously feeding at the same carcass.

Crows did not gather in large crowds at baits even though they were weak defenders. Up to 13 crows once briefly feed simultaneously at a carcass, and during a half hour of observation I did not detect one agonistic interaction among them. Similarly, in one instance (in mid-Dec.) a pair of crows which discovered a bait where another pair was already feeding was only briefly chased in the first few minutes, and then only when they were directly on the bait itself. After about an hour all 4 fed amicably. On the next and at least 3 subsequent days the 4 always arrived, fed, and departed together as a flock.

The con-specific interactions of ravens at baits were considerably more complex.

I observed identified juveniles descend alone to baits. However, single birds or groups of 3–4 vagrants at no time descended to the bait when the resident pair was in attendance. I saw a group of 3 ravens come by (without feeding) every day for 3 days at a bait where the pair had previously fed and cached meat. (The resident adults did not descend to feed when the vagrants were near, perhaps because when they did so the vagrants sometimes tried to join them even though they were then immediately attacked, if they were few in number.) Three weeks later (the bait had been removed in the meantime) three birds again showed up every day (usually near dawn) for 5 days at a new bait in the same location. The same pair also showed up every day, perching on prominent trees above the bait. The pair now did not feed from the bait itself but probably fed on cached meat instead. Meanwhile the intruders made 6–10 daily aerial approaches to the bait vicinity before leaving in the early afternoon without feeding. The pair then also left after the intruders had departed. The intruders only fed once at this bait during those 5 days; they fed after returning during one late afternoon when there was a heavy snowstorm and the pair was apparently not nearby. The above anecdote is typical of other similar routine observations, and it is highly indicative of guarding behavior by the residents.

Although I routinely saw vigorous chases in the bait vicinity (and when I could identify the individuals, the chaser was always one of the resident pair while the chased bird was a juvenile vagrant) the adults did not necessarily chase all intruders. Vagrants occasionally flew up to the guarding resident and assumed a submissive posture (pulled-in head, crouching, tail fanning, plaintive calls) to be then mildly lunged at but not pursued.

I only observed one instance of two neighboring resident pairs disputing a bait. Both pairs made loud vocalizations (specifically quorks, see later section) for hours and chased each other for many km far out of my range of vision. Only 1 pair ultimately fed at the bait.

If a feeding crowd gathered at a bait, then the dynamic interactions changed considerably. Individuals in a feeding crowd (arbitrarily defined as 15 or more birds) always had access to the bait. (However, they sometimes walked out of the way of approaching residents and/or rolled onto their side.) It appeared, therefore, that the crowds deflected or diluted the aggressive tendencies of the residents. Indeed, the vagrants always sought company in descending to the bait; they seldom went down alone, usually waiting until 9 or more were in the vicinity before descending together. It is perhaps significant that the pair which I identified that prevented the neighboring pair from feeding at its bait ignored this same pair when it fed amongst 40–50 of the vagrants, and/or this later pair only came near the bait when that many vagrants were feeding. Taken together the diversity of responses under a diversity of conditions suggests one consistent underlying conclusion: resident raven pairs attempt to inhibit other ravens from feeding at their meat piles, but the intruders are at least partially shielded when they are in a crowd.

I tested whether or not the frequent fly-byes by small groups of vagrants, coupled with their apparent unwillingness to feed for days (and possibly weeks), was due to their fear of the bait (open meat) or due to the presence of the resident pairs by simultaneously providing many baits at different locations. (I made the assumption that a resident pair could not simultaneously guard numerous scattered baits so that vagrants could find at least some undefended baits.) In the first experiment conducted in October, 6 baits (15 or more kg meat each) were put out approximately 8 air km of one another around an annually used raven nest with a year-round resident pair. Although the baits were therefore well within the boundaries of a raven territory, one of them attracted 5 ravens on the day it was put out, and by the next day this bait was attended by over 30 ravens. Two other baits were attended only by pairs, and a second bait was taken over by a crowd on the third day. The bait closest (within 100 m) of the raven nest was monopolized by the pair all winter. I repeated the experiment in early November, this time simultaneously putting out 14 baits over a linear distance of approximately 10 km spanning 2 active (starting in March) raven nests. As before, there was no apparent hesitation in bait utilization. Two of the baits attracted crowds the first day that the bait was put out and a third bait was taken by a crowd 3 days later. Five of the other baits were either visited by pairs or single ravens (as determined by tracks in the fresh snow). The latter experiment was repeated a year later with 14 more baits in the same locations, and the results were almost identical.

Yet a third version of the experiment was run in late Feb. over a much larger transect of forest (50 km) with 10 baits. Six of the baits were already discovered by ravens on the second day (as indicated by tracks) and one was taken by a crowd that second day. However, five of the baits were not consumed by crowds starting until after the 5th day. If the apparent bait shyness is due only to unfamiliarity of the bait and the birds keep checking the bait until they lose their fear of it before coming down to feed in crowds, then it would be predicted that there would be no recruitment at first and that recruitment would rise sharply after a specific waiting period following bait discovery. Instead, there is full recruitment from the beginning of the bait availability (Fig. 4). These data underestimate the extent of maximum recruitment speed when multiple baits are used, because birds being satiated at the first bait would not be expected to be recruited to a second one until the first bait is consumed.

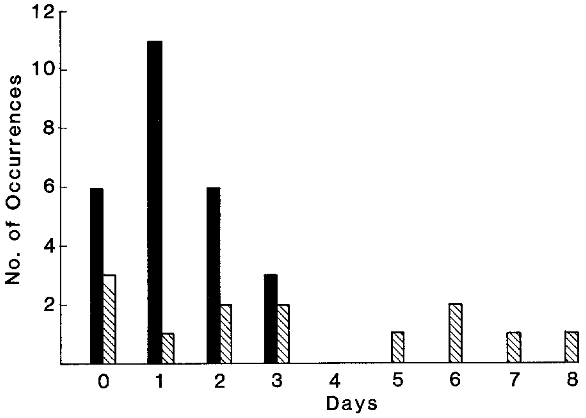

Fig. 4. Number of days after baits ($n=27$) were put out to when they were discovered (■) (1–2 birds present) and to when recruitment (▨) (defined as >15 birds present) occurred

Vocal recruitment

If birds are trying to keep a large valuable food resource such as a carcass a secret then they should remain silent. Indeed, the *pairs* of all 3 corvids were generally silent when feeding. Raven pairs, however, sometimes gave their "quorks" (see below) when guarding their baits.

The crowds of feeding raven vagrants were often vocally conspicuous. I could usually easily locate carcasses hidden in the forest after they hosted a feeding crowd of ravens. It is beyond the scope of this publication to analyze the meaning of the varied vocal repertoire that can be observed in ravens near a bait. However, one call in particular caught my attention because I heard it nowhere else besides at baits or sometimes in birds flying directly to a bait.

This call, the "yell", appears high-pitched to human ears, relative to the common gutteral raven "quork" (Fig. 5). Unlike the quorks, spectrograph analysis of these calls revealed two or three harmonics, at 1.8, 2.5 and 3.5 KHz, above the base frequency of 0.8 KHz (the predominant energy component of the quork). Yells were given singly or in irregular sequences, whereas quorks were always given in evenly spaced sequences of 3–6 per phrase (Fig. 5).

To test whether or not ravens are attracted to baits by yells to the same extent that I was, I recorded yells and quorks at baits and played them

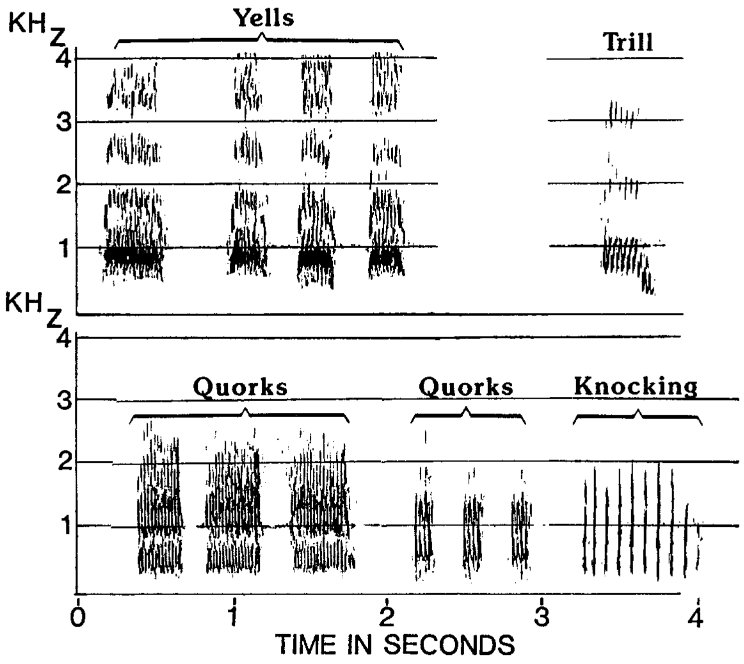

Fig. 5. Sonograms of 4 common raven vocalizations heard near baits

back at a volume of 62–66 db at 75 m (near the intensity of calls observed in the field) in the absence of bait. In 18 out of 22 trials (in areas where ravens were presumed present, such as near recently depleted baits or where ravens were recently heard or sighted), 1 to 5 ravens arrived within 1 min, flying directly toward the sound and then circling, turning their heads rapidly from side to side as if searching. No birds approach for at least 15.0 min preceding each trial. Yells recorded at my study site in western Maine were highly attractive to ravens in Passamaquoddy Bay, in northeastern Maine, and in western Vermont. Playbacks of the ravens' long deep "quorks", which were also commonly heard at baits and in many other contexts as well, did not serve as an attractant under the same conditions; only one pair flew by during 18 playbacks, and these birds did not circle. I conclude that the ravens readily distinguished between my two recordings. Furthermore, the yells are a powerful assembly call but the quorks given by the resident pairs are not.

What birds yell and when is this call normally given in the field? The yell was not given in all of my 25 instances of bait discovery by ravens. Since these 25 instances included 18 single birds and 7 pairs, I conclude that neither vagrants nor residents yell when discovering a bait. (Nevertheless, although most discoverers were silent, some were highly vociferous.) Furthermore, in several hundreds of hours of observations of baits when pairs were present and when vagrants were not present I also did not hear this call. It appears likely, therefore, that this call is not normally given by residents at baits where they feed.

The yell was heard near a bait when the first 4 to 6 birds of the vagrant feeding crowd started to arrive. It was conspicuous (always heard) when an even larger group of birds was in the vicinity of a bait, and it was often (but not always) conspicuous during feeding itself. However, it is seldom heard at baits where a large crowd has been feeding for over a week, especially when the bait is almost depleted. There are complexities here that are beyond the scope of this study (for example, generally only one or two birds yelled before they all went down for feed), but the conclusion can be drawn that it is exclusively the vagrants which yell at baits, and the call is an assembly signal at valuable food. Presumably this signal only functions over a relatively short range, since it is doubtful that it would be heard over more than several km.

Source and composition of feeding groups

The rapid recruitment I observed at baits in the relatively rare ravens (who were generally so dispersed that none were seen in the forest for days and over 100 km of driving was required to see 1 bird) could hardly be due only to random broadcasts of recruitment calls into the forest. Since *groups* of birds started coming in *after* bait discovery I speculated that there was recruitment from a distant gathering place, such as a roost.

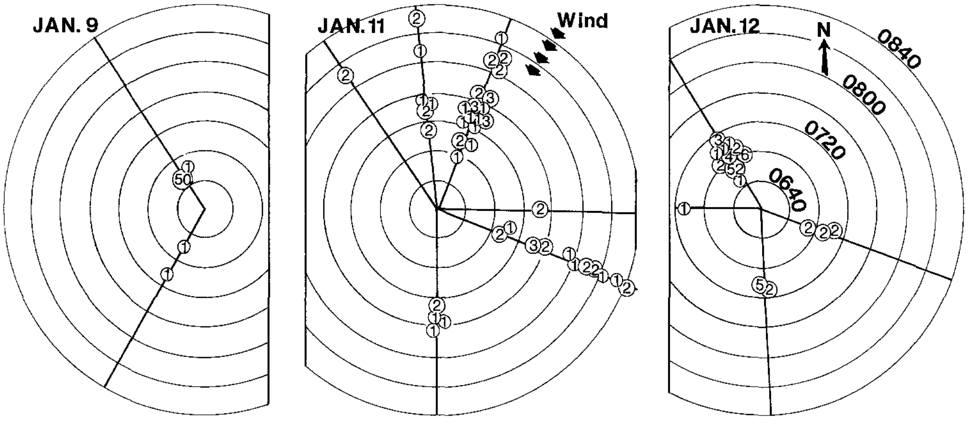

Fig. 6. Group size and direction and time of arrival on three different days at the same bait. The circled numbers denote numbers of ravens per group, the enclosing spokes denote approximate directions of arrival, and the successive concentric circles show 10 min intervals in time of arrival, from 0640 (center point) to 0750 hrs (outermost circle). Sunrise was near 0720 h. There was a strong blizzard with low visibility on Jan. 11. Note arrival of flocks of over 50 birds before sunrise on both Jan. 9 and 12

In order to find out whether feeding crowds come from roosts or from a dispersed population at large, I attempted to provide a "super" bonanza (>200 kg of fresh open meat) to compete with potential naturally-available baits and to observe directions of birds arriving at dawn. Over two winters where I observed already-discovered baits, ravens coming near dawn often came in one group from one direction, and then usually no more birds came for an hour or so consistent with the idea of a roost crowd. In one set of observations on Jan. 9 I observed at 6:53 h, 17 min before sunrise, 50 ravens arriving almost at the same time in the semi-darkness (Fig. 6). They were coming as predicted in a loose and highly vociferous flock from one direction (I later learned that a roost was located 24 km in that direction at which marked birds were sighted). Only two birds, which arrived much later, came from a different direction. None came in the next 50 min after 53 had come. (Two days later during an intense northeast blizzard the birds did not start to arrive until 12 min later and they came over the next half hour and from several directions.) On a subsequent day most of the birds again arrived at dawn primarily from the same direction as before, and most of them came in one flock of 52 birds (Fig. 6). However, on this day 35 more birds came than previously, and 14 of these were from 2 other directions. Compiling the data from 6 different dawns at this specific (replenished) bait between Dec. 11 and Jan. 12 (Fig. 7) shows that the predominant arrival direction at dawn remained the same on Dec. 11, Jan. 9, and Jan. 12. However, on Jan. 2, 3 and 8 there was a strong influx of birds from nearly the opposite directions. Since ravens are not nocturnal, the results are consistent with the idea that the feeding groups are birds predominantly from one, and apparently sometimes even from more than one communal nocturnal roost.

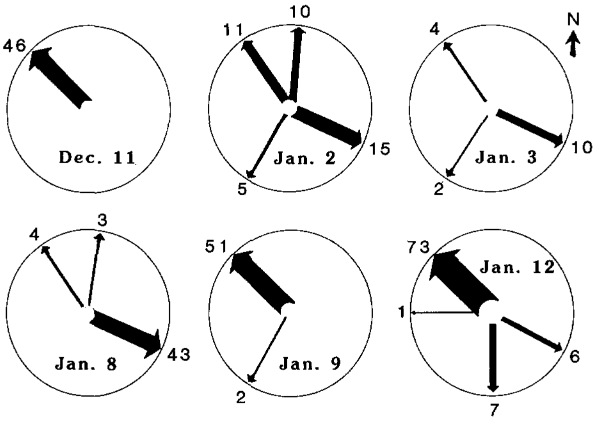

Fig. 7. Numbers of ravens and the directions of their arrival from 0620 to 0700 h at a large bait on 6 different days. Note that up to 73 birds came from the NW, while 6–43 came on 4 days from the SE

During the first two years I did not attempt to capture the wary birds for fear of complications in the data gathering. However, to help clarify why ravens were recruiting it became imperative both to be able to identify individuals as well as groups foraging at different baits, and to know the age distribution within feeding groups. After several months of preparation (see Methods) I captured 43 birds simultaneously on the first attempt at dawn on Jan. 15, 1987. This represented all of the birds at the site at that time, although more birds came by subsequently. Subsequently, other groups of 14, 25 and 10 ravens were captured, including one individual (13 Red) which had been previously captured and marked.

The sample of 91 different individuals consisted of 63 juveniles, 16 subadults and 12 adults. At least 5 of the latter were members of neighboring resident pairs (later identified after they had been marked). At least 3 more of the adults were unmated (see next section). Since the juveniles and subadults are non-breeders (Kerttu 1973) I conclude that at least 82 of my sample of 91 birds were non-breeders (ravens begin nesting in late winter near when these birds were captured). It is highly unlikely that the capture of so many non-breeders was an artifact of sampling naive vs experienced birds, because the catch included 3 members of the 2 locally nesting pairs, which is near to what could have been expected assuming that breeding adults remain resident in their territory year-round.

Body mass ranged from 1.05 to 1.52 kg, ($\bar{X}$= 1.22 kg). There was no pattern of body mass with age class. The two known males and one female (later identified by behavior in the field) weighed 1.48 and 1.38 and 1.15 kg, respectively, supporting the trend that on the average males are larger than females (Goodwin 1976).

Father posture and behavior at baits

If sharing and defense of carcasses are evolved behaviors in ravens, then they are likely mediated not only by vocal but also by other signalling, such as feather postures. As predicted feather posture of both resident adults and non-breeding vagrants varied depending on social context. In small unmixed (no resident adults) crowds *or* pairs of ravens, as in crows, the head feathers were sleek (Fig. 8). Whenever a *mixed* group of ravens were feeding, the resident adults (both members of the pair both while at the bait or while perching in the trees nearby) erected their "ear" feathers. They also lowered their "pant" feathers over their legs, and sometimes puffed out their lanceolate throat feathers. While walking near the bait they strutted in slow deliberate steps while pointing their heads high and while flashing the white nictitating membranes of their eyes. Caged submissive birds in the presence of dominant ones, as well as all of the vagrants in field (regardless of age class) tucked their heads deep into their shoulders and fluffed out their head feathers, giving them a fuzzy-headed appearance. The fuzzy-headed birds also occasionally rolled onto their sides in the presence of strutting resident pairs. No comparable obvious intraspecific feather postures were ever observed of either crows or jays at baits.

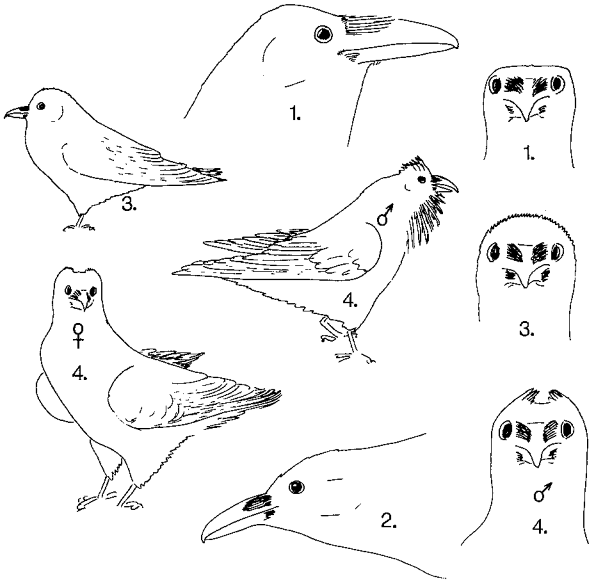

Fig. 8. Postures and feather configurations of ravens at or near baits. *1* all birds, both vagrants and residents, whether alone or in pairs at uncontested baits; *2* all birds when apprehensive in first approaching a bait; *3* all vagrants (both adults and juveniles) at baits with resident adults near or present; *4* resident adults at or near baits crowded with many other ravens

Discussion

During summer over most of its range the raven is likely to feed on insects, fruits and seeds, and on small rodents and the eggs or young birds where it can find them (Nelson 1934; Bent 1946; Harlow et al. 1975). However, in the winter most of these foods are largely unavailable, especially in regions where there are heavy snowfalls. The raven is a large bird that requires either abundant small prey or large prey, but although it may on occasion hunt and kill large prey (see Bent 1946), it is more an opportunistic generalist. Perhaps more than in other corvids a common solution of ravens in winter is to become associated with hunting carnivores and to feed from their kills, such as those of wolves (Mech 1970), polar bear (Tinbergen 1958), and gyrfalcon (Magoun 1976).

Most of the other corvids in northern regions of America (for example, magpies, crows, gray jays and blue jays) also feed on carrion left by carnivores when it becomes available, but unlike the raven none have become specialized for it. The ravens' specialization, which has previously not been examined critically, is evident morphologically as well as behaviorally. The ravens' long narrow wings help to make them strong long-distance flyers, as would be expected for finding widely-spaced carcasses. Their large bills (7.5–9.5 cm), although not strong enough to penetrate the intact hide of large mammals (Heinrich 1988b), are well suited for shearing meat from bones and for pecking into crevices among bones. Their large body mass not only increases competitive ability at the bait against other birds, it would also serve as a buffer to starvation when feeding opportunities are widely spaced in time.

In New England, the crows' solution to the winter food shortage is to migrate and/or to feed from dried berries and other fruits that remain on vegetation above the snow. Blue jays also migrate conditionally, but they may subsist from cached seeds such as acorns. Although ravens (including vagrants) sometimes vigorously cache meat at carcasses (personal observations) it is doubtful that meats stores could long sustain them because 1) they spoil during thaws, 2) they are eaten by shrews from below and by coyotes and other scavengers from above, and, 3) frequent heavy snowfalls would make retrieval not only chancy but difficult.

Ravens are well-known to be year-round residents in their territory, and those examined in the present study appeared to be no exception, even though food is likely to be scarce in the northern forests in the winter. Since most of the sightings of crows and blue jays were also of two birds simultaneously, those crows and blue jays which remained in the winter may also have been predominantly territorial pairs. Possibly the adult birds of all 3 species were able to remain without incurring the costs of migration and/or abandonment of their territories because like crows (Richardson and Verbeek 1986) magpies (Verbeek 1973) and other birds (Dunn 1972; Verbeek 1977; Ingolfson and Estrella 1978) the adults may be more proficient at procuring food than the juveniles.

The juvenile corvids of many species which leave their natal territory may join others for a variety of reasons and for varying lengths of time. At least in blue jays, widowed adults and juveniles aggregate into temporary flocks where they probably find future mates (Hardy 1961). The larger more permanent flocks in other species may serve a similar function (Verbeek 1973). For some species, however, other advantages of flocking likely include better vigilance for and protection from predators (Caraco 1981). Third, and probably more important for some species, the groupings also present an opportunity for information parasitism. If the birds roost communally, then inexperienced birds may be led to food (Rabenold 1987; Greene 1987). Potentially any bird leaving the roost to a food source may risk information parasitism from roost-mates. The voluminous recent literature since Ward and Zahavi's (1973) hypothesis of roosts serving as information centers leaves little doubt that information transfer occurs in at least some species. However, in no case has active recruitment from a roost been demonstrated, although it has been speculated for ravens (Loman and Tam 1980).

In the present study highly vocal groups of up to 50 birds were seen coming before daylight to a bait from a single direction over consecutive days. They did not likely gather as a flock during the night, because ravens are diurnal. A reasonable deduction is that they came directly from a roost, which was known to be in that direction at that time. Furthermore, as previously supposed (Hauri 1956; Mylne 1961; Stiel 1978) these crowd-feeding birds were primarily non-breeders. They were juveniles and/or non-territorial birds which were "vagrant" (usually not present in my study area for more than the few days required to consume a large carcass).

The vagrants had specific vocalizations, the "yell", that were given in the presence of other vagrants, and these vocalizations served as a powerful attractant to bring together other birds from the nearby forest for a nearly simultaneous descent to the bait. I speculate they the yell is the same as the "Standortruf" described by Gwinner (1964), the "juvenile kaah" described by R.N. Brown (1974) and the "ky" described by Dorn (1972). No studies had previously examined whether it functions as an attractant, nor does Connor's 1985) recent study mention them. Whether or not the calls which reveal the presence of food are made involves choice. And the calls were given both in flight by ravens approaching a rich bait as well as by others before and during feeding. They were rare at depleted baits or where large crowds had been feeding for many days. I conclude that the ravens are volunteering information about the presence of desirable food.

Numerous observations throughout this field study indicate that the proximate purpose of the calls is to recruit other vagrants to the immediate vicinity of the food site to form ephemeral alliances with strangers to help deflect or neutralize the defense of residents already holding the bait, or to mount a sufficient defensive shield to forestall a resident from taking possession of a bait. In view of this logic it makes sense that neither residents nor vagrants made recruitment yells when discovering a bait. The vagrants are scarce (I averaged seeing 1.8 for every 300 km of driving through raven habitat) and the likelihood of another vagrant being in the vicinity by chance is remote, yet over a half dozen vagrants are apparently required to gain access to a resident pair's food bonanza. Furthermore, recruitment yells would presumably alert the residents who would have much to gain by immediately evicting the vagrant scout. Therefore, vagrants should be silent when they discover a food source unless they have specific knowledge of other vagrants being nearby and/or of residents being absent.

The recruitment yells occurred only after several juveniles had already assembled (by some unknown mechanism) and remained in the forest near but not directly at the bait. There are many mysteries on recruitment in ravens that remain to be elucidated. Among them is potential active recruitment from the nocturnal communal roosts. If (as seems likely) recruitment by raven vagrants is intentional and adaptive, then a far more effective recruitment than by blindly broadcasting recruitment calls into the forest at large would be to bring others directly from a roost itself. My evidence strongly hints at active recruitment from the roost because the large raven crowds coming before daylight in a flock (presumably from their roost) were highly vocal when the food bonanza the day before was a large amount of fresh meat, while they were almost silent and came later and in smaller groups if the meat was less ample and/or frozen solid. Active recruitment from a roost might involve no more than the following of early-leaving vocal birds. However, this remains to be investigated.

Active recruitment is likely to lie on a continuum from information parasitism. When there is strong competition at the bait and little advantage to sharing it, then cues given by feeders should be dampened to discourage eaves-dropping. On the other hand, such cues should perhaps be accentuated if the senders gain an advantage (such as access to food as in the vagrant ravens). As the advantages for crowd-feeding increase, the recruitment message should become less ambiguous and more precise to aid both senders and receivers. Indeed, house sparrows, *Passer domesticus*, have relatively specific calls that help recruit flocks (Elgar 1986) that presumably function in mutual vigilance.

Unlike sparrows, ravens did not forage in flocks, and in an area where a raven sighting is a rare event, a carcass of a hundred kg (if cut open) was nevertheless often consumed solely by ravens in 1–2 days. On the other hand, carnivores often require many days to consume a large carcass (Magoun 1976) or they often eat only a portion of their kill before making a fresh one (Wilton 1986) thus leaving ample food for the scavengers. Observations such as these underscore the advantage for resident defenders for keeping vagrants away. (A frozen carcass could potentially supply a pair enough meat for the winter and could be their link to survival and/or reproduction.) To effectively keep their meat, resident birds must stem the recruitment in the early stages, because afer a crowd of 9 or more vagrants has assembled the resident's aggressiveness is neutralized and an avalanche of birds quickly follows; it pays residents little to expend time and energy chasing 1 vagrant while many others feed.

Because of the high stakes for survival that a carcass could provide both to the defenders and to the vagrants, one can envision an evolutionary escalation where increased vigilance and defense by the residents is countered by increased recruitment by the vagrants and vice versa.

In various species of birds (Verbeek 1973; Myers et al. 1981; Wallace and Temple 1987), fish (Foster 1985) and meliponine bees (Johnson and Hubbell 1974) groups are well-known to overwhelm territorial defenders, and it might be asked why ravens do not forage in flocks to guarantee instant access to defended carcasses and thus forego the uncertainties of effective recruitment. The perhaps obvious answer could be that carcasses are extremely rare and ephemeral, and there is likely to be a large premium to locating them quickly. Some ravens fly at least 90 km/day to feed (Stiehl 1978) even to known food sources, and daily search flights are likely to be even greater. It may be necessary to cover large distances to find a carcass, but there is little to be gained by having many overlapping fields of vision while searching for a conspicuous target. For example, if 20 birds fly as a flock they should encounter nearly 20 times fewer carcasses than 20 birds flying independently.

I observed marked ravens from one site spread out in a linear distance of 50 km finding 9 out of 10 baits set out into within one week. By information sharing the birds thus potentially have access to most of the meat piles (carcasses) spread out over $\pi r^2 = 3.14$ (50 km^2) = 7850 km^2. The one known roost from which vagrants commuted was 24 km distant, indicating a minimum foraging area of 1810 km^2. It remains to be elucidated, however, how vagrant (and presumably unrelated) ravens can evolve a system of deliberate information sharing without being swamped by cheaters.

Baits were routinely visited by birds who flew on without feeding. Furthermore, my data of marked birds feeding at a bait show that individuals, even when having a large food bonanza available, spent most of their time away. Therefore, the birds simultaneously "track" and/or search for other baits besides the ones they feed from. Presumably they could save considerable energy by staying at one bait until it is all eaten. However, from a flock perspective it would be best if a bird which has fed continues to look for other baits to share. The individually marked ravens who stayed away from a bait for many days at a time presumably had located and fed from baits elsewhere. Do the birds search for baits also for some other reason than for immediate satiation, thus providing selective pressure against cheaters and thus making these birds' extraordinary sharing system possible?

At the present time no mechanism has been presented to account for what might induce juvenile or vagrant ravens (who have already gained access to a bait through a crowd) to continue searching individually when the benefits they thereby accure are communal. I can only offer a question for future research: Do individuals who recruit gain social status relevant to mate selection? (I observed caged juveniles who contacted feared large food items to be routinely followed by submissive birds.) The ability of juveniles to offer (show) a carcass to potential mates might be a direct extension or an exaggeration of the courtship feeding which is so ubiquitous in birds.

The social system as here described whereby ravens remain fed in the winter provides another striking example of several diverse ones that have evolved in the Corvidae from common traits. All seem to involve similar responses or combinations of social responses that relate to energy balance in the context of potential competition from offspring. In the pinyon jays communal breeding and communal foraging flocks (Van der Wall and Balda 1977; Marzluff and Balda 1988) are possible because the birds' geographically varying resources, the pinyon nuts, are not likely to be depleted in a forest by any one bird. The resource base is thus amenable to the protective advantages that communal living affords (Wilson 1975). Mexican jays (J.L. Brown 1963) and scrub jays (Woolfenden and Fitzpatrick 1984) in contrast, face relatively little seasonal and geographic food patchiness and an environment with few vacant territories. As a consequence, the juveniles have little to gain by moving out of their home territory and they may then have more to gain by staying and helping their parents. In this case, the possession of the territory, per se, is the mechanism that provides both food resources and a mate, and therefore the youngs' strategies should be geared to gaining it. In ravens, in contrast, access to rare carcasses (and mates?) may be not so much related to a territory per se but to individual qualities that affect search and access to food. Furthermore, it might be risky for inexperienced offspring to stay in any one territory where a carcass may only rarely be found, because even if one is found it would likely be easily monopolized by the dominant birds, its parents.

If ravens have specialized their biology around winter feeding on carcasses in the way I have here speculated, then it might be expected that their foraging strategy has converged on that of vultures, the paragon carcass specialists. Indeed, many parallels exist. First, vultures are large, and both in the Old World vultures (Accipitridae) and New World vultures (Cathartidae) large body size confers dominance during aggressive encounters at the bait (Wallace and Temple 1987) and it presumably also enhances surviving long fasts while subsisting on an ephemeral and unpredictable food supply.

In the guild of corvids at baits in New England, the largest birds, the ravens, were clearly dominant over the crows, who were dominant over the still smaller blue jays. Dominance hierarchies based on size (as well as age) also exist among the vultures on the African plains (Petrides 1959; Houston 1975; Kruuk 1967; Anderson and Horwitz 1979; König 1983) and in northern Peru (Wallace and Temple 1987).

The guilds of vultures differ from the guilds of corvids in their greater specialization for carcass foraging. Thus, although the ravens rely on mammalian carnivores to open the carcasses of large animals, within the vulture guilds there are species large and powerful enough to open carcasses themselves. In Peru, the smaller species, such as black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) wait at a carcass until the much larger king vultures (*Sarcoramphus papa*) and Andean condors (*Vultur gryphus*) arrive. The first became "noticeably excited" as the latter arrived, and they swarmed onto the carcass in a "feeding frenzy". These normally subordinate birds may then swamp out the larger birds who then find the resource temporarily impossible to defend (Wallace and Temple 1987).

Rabenold (1983, 1987) provides evidence indicated that naive (primarily juvenile) turkey vultures follow experienced birds to baits from their communal roosts. Over 200 black vultures may arrive at a bait in less than 1 h (Wallace and Temple 1987), possibly through information parasitism where unsuccessful birds follow previously successful ones. Information parasitism apparently accounts for the vulture crowds at carcasses in the African plains, in that soaring birds watch each other and follow those who descend to a carcass they or some other individual has discovered (König 1983). However, in either case, whether by "active" recruitment as in ravens through one immediately selfish mechanism, or by information parasitism by vultures, the end result in either case is that the resource unpredictability becomes reduced through the mutual reliance. The reliance on conspecifics may ultimately make the specialization on caracasses possible, and it suggests that there is a potential optimum between the minimum possible population density to *find* carcasses, and the maximum competition that determines duration to *feed* at them. The larger the prey, the greater the expected information sharing.

Inuit caribou hunters listen to the sounds flying ravens make when the herds come near, believing that the birds deliberately guide them to their prey (Bruemmer 1984). Perhaps, instead, the hunters are hearing raven vagrants recruiting other ravens to the kills of the wolves who follow the herd.

Acknowledgements. I thank D. Capen and D. Hirth, D. Person, M. Ingle and M. Kramer for loaning recording and telemetry equipment and for giving instructions for its use. The sonagrams were made possible with the help of L. Fairchild, P. Marler and P. Duell. L. Young generously provided advice and invaluable help, especially with regard to telemetry and marking techniques. The project would not have been possible without the generous help by O. Jennersten, G. Lisi, J. Marden, J. Marzluff, B. Mooney, A. Rosenquist, C. Sewall, S. Smith, B. Y. Garrondo and W. Wagman who gave critical help marking the ravens during the raven roundups, and P. Cross, R. Wattles and A. Moody who provided invaluable information during the follow-up. Logistic help was given by V. Adams, D. Eames, C. Lehmann, and L. Lipsitz. P. Sherman gave greatly appreciated advice and criticism. Last but not least I thank B. Gaudette, D. Hirth and M. Pratt for alerting me to animal carchasses which were essential for the study. The manuscript was greatly improved by the comments of Jos. Schall, K. Engel and an anonymous reviewer. Supported in part by NSF grant BNS-8611933.

References

Anderson DJ, Horwitz RT (1979) Competitive interactions among vultures and other avian competitors. Ibis 121:505–509

Bent AC (1946) Life histories of north american yays, crows and titmice. US National Museum Bulletin 191

Brown JL (1963) Social organization and behavior of the Mexican jay. Condor 65:126–153

Brown RN (1974) Aspects of vocal behavior of the raven (*Corvus corax*) in interior Alaska. MSc thesis, University of Alaska, Fairbanks, p 139

Bruemmer F (1984) Ravens. Int Wildl 14:33–35

Cade TJ (1960) Ecology of the peregrine and gyrfalcon populations in Alaska. Univ Calif Publ Zool 63:151–290

Caraco T (1981) Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). Behav Ecol Sociobiol 8:213–217

Connor RN (1985) Vocalizations of common ravens in Virginia. Condor 87:379–388

Dorn JL (1972) The common raven in Jackson Hole, Wyoming. MS thesis, Univ Wyoming, Laramie

Dunn EK (1972) Effect of age on the fishing ability of Sandwich Terns *Sterna sandvicencis*. Ibis 114:360–366

Elgar MA (1986) House sparrows establish foraging flocks by giving chirrup calls if the resource is divisible. Anim Behav 34:169–174

Foster SA (1985) Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. Anim Behav 33:782–793

Greene E (1987) Individuals in an osprey colony discriminate between high and low quality information. Nature (London) 329:239–241

Gwinner E (1964) Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkraben (*Corvus corax corax* L.). Z Tierpsychol 21:657–748

Hardy JW (1961) Studies in behavior and phylogeny of certain New World jays (Garrulidae). Univ Kansas Sci Bull 42:13–149

Harlow RC, Hooper RG, Chamberlain RD, Crawford HS (1975) Some winter and nesting season food of the Common Raven in Virginia. Auk 92:298–306

Hauri R (1956) Beiträge zur Biologie des Kolkraben (*Corvux corax*). Ornith Beob 53:28–53

Heinrich B (1988a) Why do ravens fear their food? Condor (in press)

Heinrich B (1988b) Foodsharing in the Raven, *Corvus corax*. In: Slobodchikoff CN (ed) The ecology of social behavior. Academic Press, New York, pp 285–311

Houston D (1975) Ecological isolation of African scavenging birds. Ardea 63:55–64

Hutson HPW (1945) Roosting procedure of *Corvus corax laurenci* Hume. Ibis 87:455–459

Ingolfson A, Estrella JT (1978) The development of behavior in Herring Gulls. Auk 95:577–579

Johnson LK, Hubbell SP (1974) Aggression and competition among stingless bees: field studies. Ecology 55:120–127

Kenward RE (1978) Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. J Anim Ecol 47:449–460

Kerttu ME (1973) Aging techniques for the common raven *Corvus corax principalis* Ridgeway. MS thesis, Michigan Tech Univ, Houghton, pp 55

Knight RL, Call MW (1980) The Common raven. Techn note # 344 (60 p) US Dept Interior

König C (1983) Interspecific and intraspecific competition for food among old world vultures. In: Wilbur SR, Jackson JA (eds) Vulture biology and management. Uni Calif Press, Berkeley, pp 153–171

Kruuk H (1967) Competition for food between vultures in East Africa. Ardea 55:171–193

Loman J, Tamm S (1980) Do roosts serve as "information centers" for crows and ravens? Am Nat 80:285–289

Magoun AJ (1976) Summer scavenging in northeastern Alaska MS thesis, University of Alaska, Fairbanks

Marzluff JM, Balda RP (1988) Resource and climatic variability: influence on sociality of two southwestern corvids. In: Slobodchikoff CN (ed) The ecology of social behavior. Academic Press, New York, pp 255–283

Mech LD (1970) The wolf: The ecology and behavior of an endangered species. The Natural History Press, Garden City, New York, pp 279–287

Myers JP, Connors PG, Pitelka FB (1981) Optimal territory size and sanderlings: compromises in a variable environment. In: Kamil AC, Sargent TD (eds) Foraging behavior, Garland Press, New York, pp 135–158

Mylne CK (1961) Large flocks of ravens at food. Br Birds 54:206–207

Nelson AL (1934) Some early summer food preferences of the American raven in Southeastern Oregon. Condor 36:10–15

Petrides GA (1959) Competition for food between five species of East African vultures. Auk 76:104–106

Pulliam HR (1973) On the advantages of flocking. J Theor Biol 38:419–422

Rabenold PP (1983) The communal roost in black and turkey vultures – an information center? In: Wilbur SR, Jackson JA (eds) Vulture biology and management. Univ Calif Press, Berkeley, pp 303–321

Rabenold PP (1987) Recruitment to food in Black Vultures: evidence for following from communal roosts. Anim Behav 35:1775–1785

Richardson H, Verbeek AM (1986) Diet selection and energy optimization by Northwestern crows feeding on littleneck clams. Ecology 67:1219–1226

Schwan MW, Williams DD (1978) Temperature regulation in the common raven of interior of Alaska. Comp Biochem Physiol A 60:31–36

Stiehl RB (1978) Aspects of the ecology of the common raven in Harney Basin Oregon. PhD Thesis, Portland State Univ, Portland

Tinbergen N (1958) Curious naturalists. Doubleday, New York, p 38

Van der Wall SB, Balda RP (1977) Coadaptations of the Clark's Nutcracker and the pinyon pine for efficient seed harvest and transport. Ecol Monogr 47:89–111

Verbeek NAM (1973) The exploitation system of the Yellow-billed Magpie. Univ California Publ Zool No 99

Verbeek NAM (1977) Age differences in the digging frequency of Herring Gulls on a dump. Condor 79:123–125

Wallace MP, Temple SA (1987) Competitive interactions within and between a build of avian scavengers. Auk 104:290–295

Ward P, Zahavi A (1973) The importance of certain assemblages of birds as "information centres" for food finding. Ibis 115:517–534

Williamson FSL, Rausch R (1956) Interspecific relations between Goshawks and Ravens. Condor 58:165

Wilson EO (1975) Sociobiology. Haravard University Press, Cambridge

Wilton ML (1986) Scavenging and its possible effects upon predation – a selective review of literature. Alces 22:155–180

Woolfenden GE, Fitzpatrick JW (1984) The Florida scrub jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton

Young LS, Engel KA, Brody AJ (1986) Implications of communal roosting by common ravens to operation and maintenance of the Malin to Midpoint 500 kV transmission line. Snake River Birds of Prey Ann, Report pp 36–60. US Dept Interior, BLM, Boise District, Idaho

Note added in proof

The juveniles may be even more vagrant than here supposed. Of those banded January 19, 1987, one was recovered (captured by a captive wolf) April 10, 1988, near Edmundston, New Brunswick, Canada, an air distance of 352 km from the marking site. The bird's patagial disc was still intact.