



Raven roosts are mobile information centres

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Abstract. Vagrant, non-breeding common ravens, *Corvus corax*, inhabiting the forested mountains of Maine are specialized to feed on rich but ephemeral carcasses of large mammals during the harsh winter months. The foraging and roosting behaviour of free-ranging ravens were studied during the winters of 1988–1990. Ravens quickly assembled at carcasses, and into communal roosts. Six lines of evidence indicate that these roosts function as information centres. (1) Roosts comprised both knowledgeable and naive foragers. (2) Departures from roosts were highly synchronized, with most members departing in one direction. (3) Direction of departure often changed from day to day. (4) Birds made naive of food sources (by being withheld from the wild and then allowed to join roosts) followed roost-mates to new feeding sites, whereas control birds held and released outside of roosts rarely found the local food bonanzas. (5) Birds made knowledgeable of food sources (by being released at new carcasses) joined roosts and led roost-mates to the food on three of 20 occasions. (6) The same individuals switched leader and follower roles depending upon their knowledge of feeding opportunities. Although ravens may form roosts at traditional areas (near stable food sources) that are used for many years, the ravens in Maine frequently shifted roost sites to be near newly discovered carcasses. Information exchange at roosts principally occurred on the night of, or the night before, the roost shift. Social soaring displays assembled birds from a wide area and were associated with mass movements to new roosts formed at nearby food.

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The hypothesis that foragers can gain information about the location of rich food patches from knowledgeable members of social groups has stimulated a great deal of research and controversy. Partial support for this 'information centre hypothesis' (Ward & Zahavi 1973) comes from laboratory and field studies of colonial animals in which the information centre is a stable group at a particular site (Galef & Wigmore 1983; Brown 1986; Greene 1987; Gori 1988; Brown et al. 1991; Galef 1991; Wilkinson 1992). Another context in which animals potentially could exchange information about the location of a resource is at a nocturnal roost away from the resource. No study has provided convincing evidence, however, that roosts serve as information centres (Weatherhead 1987; Mock et al. 1988; Richner & Marclay 1991).

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Roosts are thought to have low potential as information centres because they are visited only once per day, and have a fluid membership (Caccamise et al. 1983; Heisterberg et al. 1984; Rabenold 1987a; Morrison & Caccamise 1990). Rabenold (1983, 1987b), however, determined that naive black vultures, *Coragyps atratus*, follow knowledgeable roost-mates and are likely to find new food as a result, although the actual discovery of a new food source in this situation has not been observed. Circumstantial evidence suggests that the nocturnal roosts of common ravens, *Corvus corax*, may also function as information centres, because on some mornings many more ravens arrive at feeding sites than were previously observed at the site or could be attracted by the commotion of birds feeding at the site (Loman & Tamm 1980; Heinrich 1988, 1989; Heinrich et al. 1993).

Here we employed a series of field experiments and observations at roosting and foraging sites to test whether nocturnal roosts of ravens function as information centres despite their fluid group membership. We tested the central requirement of

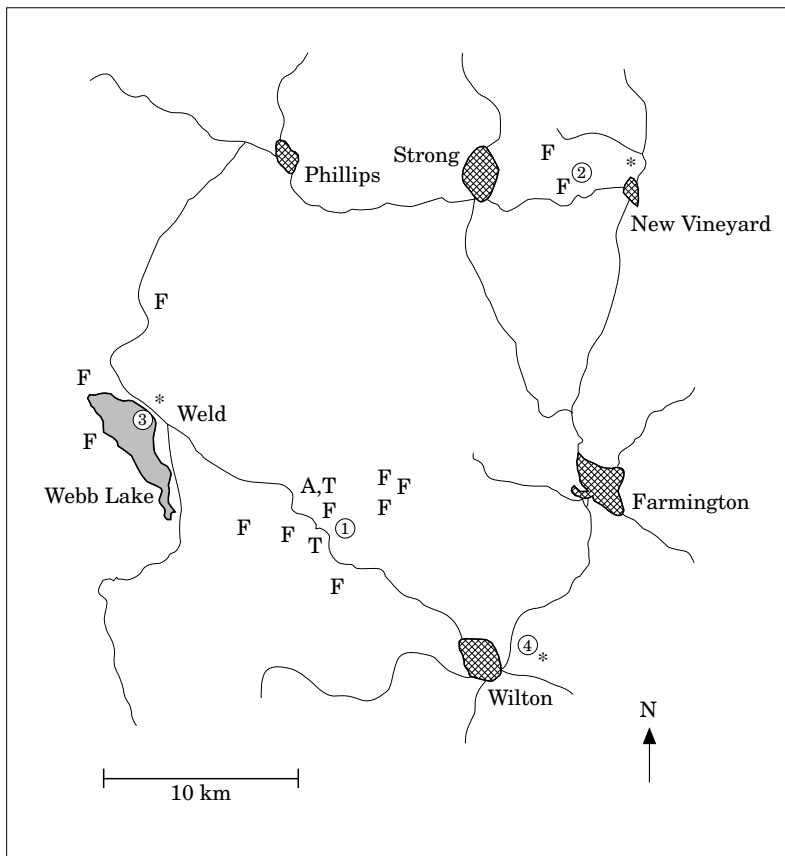


Figure 1. Map of the study area highlighting roosting areas (circled numbers), refuse dumps (*), provisioned trap sites (T), areas where carcasses were deposited (F), and the research aviary (A). Roost locations discussed in the text are numbered as follows: (1) Alder Brook, (2) New Vineyard, (3) Lake Webb, (4) Wilton. Paved roads (lines) and towns (names and hatched areas) are indicated.

the information centre hypothesis as distilled from several recent reviews (Rabenold 1987b; Weatherhead 1987; Mock et al. 1988; Richner & Marclay 1991; Wilkinson 1992): naive members of a roost follow knowledgeable members to newly discovered foods. We also described the roosting behaviour of ravens and identified possible cues used in the transfer of information.

GENERAL METHODS

General Field Protocol

We observed the foraging and roosting behaviour of ravens in the forests of western Maine during the winters of 1988–1989, 1989–1990 and 1990–1991 (see Heinrich 1988 for a description of

the study area). Each year we observed ravens foraging on carcasses that we scattered throughout the central portion of our study area, at naturally occurring carcasses and at dumps (Fig. 1; Marzluff & Heinrich 1991). We observed the accumulation of ravens at 34 food bonanzas (ranging in size from 50 kg piles of meat to 500 kg moose, *Alces alces*, cattle and horses). All animal carcasses were natural die-offs obtained from local farmers and/or road kills donated to us by local game wardens.

Our study area included several ephemeral roosts that formed near carcasses that remained available for several days to a few weeks, and two relatively consistently used roosts near dumps (Fig. 1). Most ravens at our baits were unrelated, non-breeding vagrants that passed through, rarely

stopping for more than a few days or weeks as they congregated at food bonanzas and roosts (Heinrich 1988; Parker et al. 1994).

We captured and tagged foraging groups of ravens 5–10 times per winter (Heinrich 1988). We marked 357 birds with uniquely coloured and numbered patagial tags on one or both wings, and mounted 30-g radio transmitters on the central tail feathers of 28 birds. Typically, 10–30% of the birds under observation in the field were tagged.

Once a carcass was placed in the field, we checked it at least three times daily (just after dawn, sporadically throughout the day and in the late afternoon each day) to count the number of ravens feeding on it and to determine whether any radio-tagged birds were in the vicinity. If no ravens were present, we approached the food to check for signs of feeding (raven tracks, faeces, and/or bite marks). We observed feeding ravens for over 550 h (usually 1–4 h each day, beginning at dawn) from a blind made of spruce and fir boughs placed within 30 m of the food.

Counting the birds was difficult after more than 10 had assembled because they quickly scattered throughout the thick forest. We estimated large group sizes by counting all visible birds and those whose presence we inferred if they vocalized nearby. This approach underestimated recruitment of naive birds to food, because the comparisons of interest involved observations of small numbers (precise counts) of ravens one day and very large numbers (underestimates) the following morning.

Estimating Recruitment from a Roost to a Carcass

We estimated the importance of nocturnal roosts to the accumulation of ravens at a food source by comparing the change in the number of ravens feeding at a bonanza during a day ($NMAX_{(D)} - N2HR_{(D)}$), and the change from one day to the next ($N2HR_{(D+1)} - NMAX_{(D)}$). $NMAX$ is the maximum number of ravens counted during the day, $N2HR$ is the number of ravens arriving during the first 2 h of a day, and D denotes observation day. The change in number of ravens feeding on a given day indicates local enhancement, whereas the change in number from one day to the next indicates possible attraction of roost members.

Counts made on the day preceding expected recruitment ($D - 1$) underestimated the number of

birds knowledgeable of the food's location in three ways. (1) Some birds discovered fresh bonanzas shortly after foods were placed in the field, but did not visit them again until the morning of suspected recruitment. Observations of 25 marked birds at $N=8$ carcasses indicated that a mean (\pm SE) of $23 \pm 13\%$ of birds that previously visited a carcass did not visit that food on $D - 1$, but returned on the day of recruitment (D). (2) Some previously knowledgeable birds visited the food briefly early on $D - 1$, but were not present for the maximum count on $D - 1$. Observations of 17 marked birds at $N=14$ carcasses on $D - 1$ indicated that, on average, $18 \pm 9.9\%$ of knowledgeable birds visiting the food that morning would not be present for the maximum count later on $D - 1$. (3) Some birds discovered the food after the morning census on $D - 1$, and left before the maximum count on $D - 1$. Observations of 37 marked birds at $N=14$ carcasses indicated that, on average $63 \pm 11\%$ of birds arriving at a bonanza for the first time on $D - 1$ were present for the maximum count on $D - 1$.

Given these data, we estimated the total number of ravens knowledgeable of a food source by adjusting our maximum counts as follows. We based average adjusted counts (± 1.96 SE to allow calculation of a 95% confidence interval) on the following expression:

$$S = NMAX_{(\text{previous})} + K1 + K2 + (N2 - N1),$$

where, S is the expected number of knowledgeable ravens, $NMAX_{(\text{previous})}$ is the maximum number of ravens counted on any day previous to suspected recruitment, $K1 = (0.23 \pm 0.26) \times NMAX_{(\text{previous})}$, $K2 = (0.18 \pm 0.19) \times N2HR_{(D-1)}$, $N1 = NMAX_{(D-1)} - (N2HR_{(D-1)} - K2)$, and $N2 = N1 / (0.63 \pm 0.22)$.

For example, on 3 February 1991, 40 ravens arrived at a deer carcass placed in the field on 29 January. A maximum of 10 birds had been seen on the 4 days prior to 2 February, so we estimated that 2.3 ± 2.6 [$K1 = (0.23 \pm 0.26) \times 10$] other ravens had been at the carcass from 29 January to 1 February, but were not present on 2 February. Seven birds were counted on the morning of 2 February, and 1.3 ± 1.3 [$K2 = (0.18 \pm 0.19) \times 7$] were estimated to have been missing for the maximum count that afternoon. A maximum of 10 ravens was seen at the carcass after the morning census on 2 February. Therefore 6.8 birds must have discovered the food between the

morning and afternoon counts on 2 February, because 4.3 ± 1.3 would be present for the maximum count $\{NI = 10 - [7 - (1.3 \pm 1.3)]\}$. For these birds to still be present in the afternoon, however, 6.8 [95% CI = $5.1 - 10.5$; $N2 = 4.26$ (0.63 ± 0.22)] must have known the location of the food, and 2.5 (95% CI = $-0.5 - 7.5$) would have discovered the food and departed between censuses ($N2 - NI$). Totalling the missing birds for each estimate, $S = 16.1$ (95% CI = $9.2 - 25.0$) knowledgeable birds.

We did not add local enhancement during the 2-h census period on the morning of an influx to our estimate of knowledgeable birds because few, if any, birds other than those in roosts arrive at the food during the first 2 h after dawn (Heinrich et al. 1993).

OBSERVATIONS AT ROOSTS

Methods

To determine use of roosts by naive and knowledgeable foragers and observe signals associated with information transfer, we climbed observation trees (spruce or pine trees, 0.3–1.0 km from a roost) approximately 1.5 h before sunset and remained until it was too dark to see ravens (usually 1 h after sunset). Using 10×15 power binoculars and a small tape-recorder, one observer typically monitored roosts each evening, although occasionally two to five observers simultaneously watched several roosting areas. We focused our observations near feeding locations if they were known, or at traditional roosts if feeding locations were unknown or happened to be near traditional roosts. We made a special effort to watch roosts every night throughout complete feeding cycles at carcasses (before feeding began, throughout the build-up and decline in the number of ravens feeding, and after feeding ended).

In the evenings, we continually scanned the horizon for incoming birds, and noted the direction (using eight cardinal bearings) of their origin, the number of ravens in the group, the time they appeared in view and the time they entered the roost. We observed the time and direction of morning roost departures following evening roost watches from 1.5 h before sunrise until after the ravens left the roost.

We classified birds arriving at roosts in the evening into two categories, 'roosting' birds (those

that arrived and stayed in the roost until our observations ended) and 'departing' birds (those that arrived but then departed from the roost during our observations). We further classified the shifts made by departing birds as 'local shifts', if their new roosting spot was within our field of view (several kilometres in all directions), or 'distant shifts', if their new roosting spot was beyond our view. We assumed that some birds made distant shifts if the size of a roost under observation increased or decreased by more than 10 birds from one night to the next.

We used circular statistics to determine the mean direction of arrival and departure from roosts, the angular dispersion around the mean angle, and the randomness of dispersion (Zar 1976; Batschelet 1981). The length of the mean vector, r , varies from 0 (random) to 1 (all orientations identical) and is the statistic used in Rayleigh's test of the significance of the concentration of arrivals or departures (Batschelet 1981). We used Rao's spacing test to appraise randomness in two cases when the distribution of departure directions was bimodal and non-axial (Batschelet 1981).

We considered each day of observation at a roost an independent sample of roosting behaviour. The fact that ravens may return to the same feeding site on consecutive days does not necessarily invalidate this assumption, because we did not use the average daily arrival or departure direction as independent samples in any analyses.

Results

Description of roosts

All 15 roosts that we observed in five areas were in dense stands of white pine, *Pinus strobus*. One grove of pines in each area appeared to be the primary roost site in that it was regularly used and birds usually accumulated there first. Each area, however, had several groves within 2 km of this site that were used.

Arrival at roosts

Ravens began accumulating noisily at roosts shortly before sunset. They arrived as singles, pairs, or small groups (rarely up to 50 or more in a group) over a period of up to 1 h ($\bar{X} \pm SE$ from 15 November to 22 December 1988 at New

Vineyard roost = 33.8 ± 3.5 min; $N=25$). Arrivals were usually from a variety of directions, although half of the time dispersion around the mean arrival direction was highly non-random ($P < 0.001$; Table I).

Most birds flew directly to the roost, circled briefly and landed, but we observed exceptions to this pattern. Large groups of soaring birds occasionally formed and flew lengthy circuits around the roost site (travelling several kilometres from the roost) before returning to settle in the roost as a group or departing out of sight to a distant roost site (Table II).

The occupancy of four pine groves in the Lake Webb roost area during January 1991 illustrates the typical pattern of roost use (Fig. 2). Usually only one pine grove was occupied each evening, and shifts between neighbouring groves on consecutive days were common (e.g. between Byron Road and Far East Ridge on 10 and 11 January). Distant departures (e.g. on 21 January) and distant arrivals (e.g. on 24 January) were less common. Occasionally no birds were found in the roost area (e.g. on 16 January).

Morning departure from roosts

Ravens left roosts as highly synchronized groups at dawn, giving a few noisy 'kaws', followed by 'honking' vocalizations. On average, all birds left the roost within 7.15 ± 2.48 min of the first departure ($N=20$ departures from 16 November to 14 December 1988 at New Vineyard Roost). This time range was significantly more synchronous than arrivals the previous evenings (paired $t=7.1$, $df=18$, $P < 0.001$). Eleven of 20 departures occurred over less than a 2-min time span; the longest span was 46 min on a foggy morning. In most cases all the ravens left together in one direction (note r values of 1.0 in Table I), and in all cases the dispersion of departures was highly non-random (Table I). In two cases (6 and 9 December; Table I) the group was evenly split in two directions. The mean angle of departure varied from day to day, suggesting that the birds were tracking different resources from one roost.

Some ravens apparently moved between roosts well after dark. We saw roost departures in the evening; on seven occasions our evening counts and following morning counts disagreed by more than 10 birds, and in one case nearly 50 fewer birds left the roost than entered it (7–8 December; Table I).

Influence of foraging location on roost location

Information exchange after a new food bonanza was discovered resulted in changed roost locations. Ravens were significantly more likely to shift roost locations following a change in feeding location than following no change in feeding location ($\chi^2=74.3$, $df=2$, $P < 0.001$). We observed ravens feeding at the same food bonanza on consecutive days 86 times. Under these conditions, they usually returned to the same roost used the previous night ($N=45$, 52%), or shifted locally to a nearby grove of pines ($N=33$, 38%); distant shifts were rare ($N=8$, 9%). In 84 shifts of feeding location, they usually shifted to a distant roost ($N=62$, 74%), or occasionally to a nearby grove of pines ($N=13$, 15%), but rarely returned to their former roost site ($N=9$, 11%). Radio-tagged birds remained at a roost site an average of 3.9 ± 0.43 nights ($N=130$) before switching to a new site 1.0–12.5 km away. In 290 cases of radio-tagged birds shifting roost or feeding sites, 43 of 48 shifts in roost locations were associated with shifts in feeding locations, and 238 of 242 unchanged roost locations were associated with unchanged feeding locations ($\chi^2=228$, $df=1$, $P < 0.001$).

Ravens usually shifted roost location to be within 1 km of their new feeding site (281 of 329 observations of radio-tagged birds, 85.4%). For example, we placed a moose 25 km from the New Vineyard roost that had been occupied by at least 30 ravens on the previous day. Twenty-five ravens returned to the New Vineyard roost the second day after the moose had been placed in the field, but 20 of them left it that evening in the direction of the moose. Ravens began to feed on the moose the next morning. The birds at the moose probably came from New Vineyard, because the use of the New Vineyard roost fluctuated with the availability of the moose carcass (Fig. 3). Most birds feeding at the moose were unmarked; however, one tagged bird fed at the dump near New Vineyard prior to the discovery of the moose, then came to the moose on days 3 and 4. It returned to the dump on days 5 and 6, and then again to the moose on day 7.

Social soaring

Social soaring appeared to be the mechanism that signalled impending roost shifts and moved

Table I. Mean directions and angular dispersion around directions of arrivals in the evening and departures in the morning from one roost (New Vineyard) of common ravens in 1988

Date	Dispersion (<i>r</i>)	Mean direction (degrees)	Number of ravens	
			Arriving†	Staying‡
Arrivals				
15 November	0.82***	302	39	39
16 November	0.05	45	35	30
19 November	0.52*	301	14	12
21 November	0.80***	328	102	22
22 November	0.34	16	14	14
23 November	0.39*	12	27	27
26 November	0.34	106	13	13
27 November	0.90***	82	9	9
29 November	1.00***	315	9	9
1 December	0.04	225	32	32
2 December	0.74***	269	49	20
3 December	0.67***	319	43	43
5 December	0.81***	85	9	9
6 December	0.43***	276	27	24
7 December	0.29***	275	82	80
8 December	0.56***	286	46	46
9 December	0.03	133	50	29
12 December	0.90***	97	28	28
13 December	0.12	263	28	23
14 December	0.86***	32	13	13
15 December	0.46***	303	77	0
16 December	0.31*	4	45	5
19 December	0.42*	134	22	18
20 December	1.00***	135	21	21
Departures			Departing	
16 November	0.71***	231	29	
17 November	0.79***	95	58	
19 November	1.00***	90	100	
22 November	1.00***	315	22	
23 November	1.00***	90	20	
24 November	0.99***	43	25	
27 November	1.00***	270	13	
28 November	1.00***	135	9	
30 November	1.00***	90	9	
2 December	1.00***	315	22	
3 December	1.00***	270	25	
4 December	1.00***	315	30	
6 December	0.09‡	270	22	
7 December	0.86***	270	43	
8 December	0.97***	317	31	
9 December	0.41‡	227	71	
10 December	1.00***	270	50	
13 December	1.00***	225	25	
14 December	0.65***	225	23	
20 December	1.00***	90	18	

†Number of ravens arriving at roost and number staying in roost until too dark to see.

‡Distribution of departures was bimodal and significantly different from random, $P < 0.01$, Rao's spacing test.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table II. Numbers of ravens, frequency of social soaring, and shifts in location at three roosts during three winters

Roost	Range of dates observed	No. of evenings observed	No. of ravens*				Departing (N)	No. (%) of evenings that roost was not used	No. (%) of times roost location		
			Arriving	Roosting	Soaring (N)	Shifting locally			Shifting distantly	Did not shift	
New Vineyard	15 November–31 December 1988†	26	33.0 ± 25.1 1–105	25.4 ± 20.6 Ø-80	37.7 ± 32.0 (10) 3–103	39.6 ± 28.5 (5) 9–83	3 (11.5)	4 (20.0)	11 (55.0)	5 (25.0)	
New Vineyard	3 October–11 December 1989‡	38	20.9 ± 17.8 0–60	17.1 ± 17.8 Ø-60	30.4 ± 17.1 (13) 4–52	15.7 ± 16.0 (9) 5–50	9 (23.7)	10 (34.5)	13 (44.8)	6 (20.7)	
Alder Brook	27 December 1988–8 April 1989§	42	—	10.3 ± 13.9 0–40	—	—	24 (57.1)	—	—	—	
Alder Brook	10 October 1989–2 April 1990	81	20.7 ± 16.6 0–80	18.4 ± 17.2 0–80	22.6 ± 22.2 (22) 2–80	15.5 ± 10.7 (8) 3–30	5 (6.2)	16 (28.1)	16 (28.1)	25 (43.9)	
Alder Brook	26 December 1990–27 March 1991	41	13.7 ± 15.4 0–60	8.4 ± 11.0 0–35	10.4 ± 7.1 (5) 2–20	19.3 ± 16.2 (12) 5–55	12 (29.3)	2 (8.3)	9 (37.5)	13 (54.2)	
Lake Webb	3 November 1990–18 March 1991	100	15.3 ± 17.0 0–100	12.8 ± 15.7 0–100	29.6 ± 22.4 (22) 3–100	25.3 ± 16.1 (10) 8–40	32 (32.0)	16 (19.3)	36 (43.4)	31 (37.3)	

*Entries are $\bar{X} \pm \text{SD}$, range; N for soaring and departures are number of days each was observed; only days with soaring or departure were used to calculate $\bar{X} \pm \text{SD}$ and ranges for these variables.

†No birds present when checked again on 7 January and 20 February 1989.

‡No birds present when checked again on 18 September 1989 and 3 January 1990.

§Observations primarily intended to determine presence or absence of roosts, not arrival, soaring or departures.

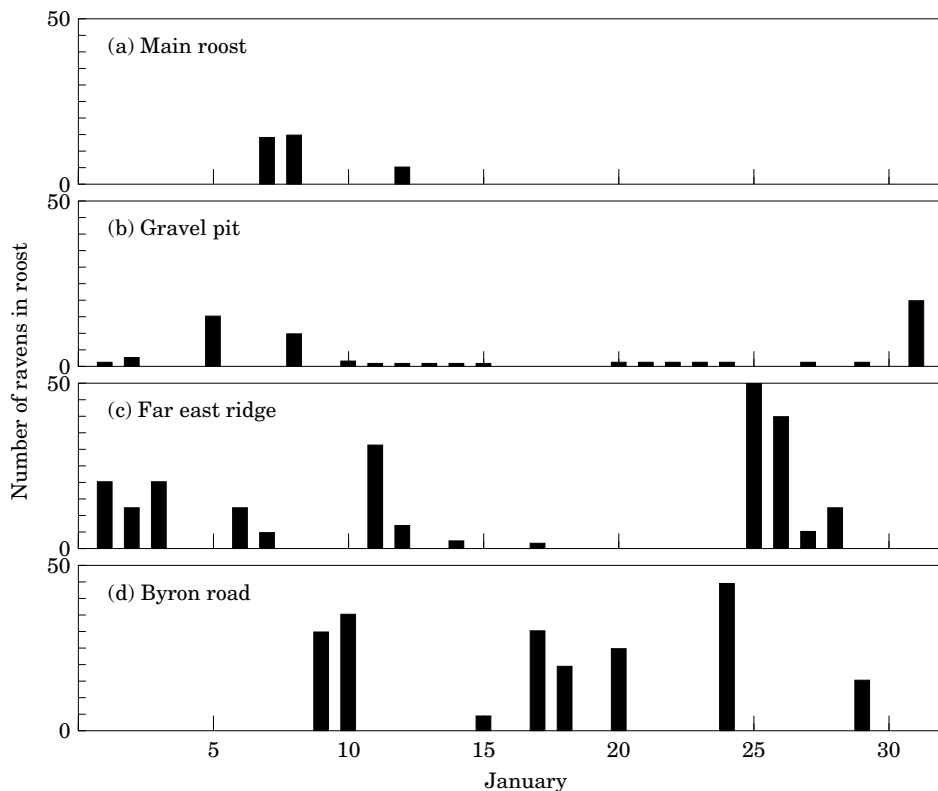


Figure 2. Roost use of four pine groves in the Lake Webb roosting area during January 1992. Groves are within 2 km of each other and were monitored from one central observation tree. Shifts in birds between groves represent 'local shifts' in roosting site.

ravens to their new roost site. Ravens united into soaring groups above their previous roost sites and flew lengthy routes around the roost that covered at least 200 km². Individual ravens were attracted from a distance of at least 10 km to those that were soaring.

During 175 days of observing roosts, we found that soaring was closely associated with changes in roost location ($\chi^2=29.8$, $df=2$, $P<0.001$). Soaring was rare ($N=4$, 8.0%) when roost location did not shift ($N=51$), frequent ($N=23$, 49%) when roost location shifted locally ($N=47$) and most common ($N=42$, 55%) when roost location shifted distantly ($N=77$). In seven instances, one of our radio-tagged ravens participated in a soaring group, and in six of these the tagged bird also changed its roost location from the previous night.

Soaring was related to the stage of feeding at a carcass ($\chi^2=26.6$, $df=2$, $P<0.001$; Fig. 4). Obser-

vations of roosting at 23 bonanzas revealed that soaring was infrequent the day before a bonanza was discovered, increased as a small group of birds began to feed and peaked the night after the primary influx. This peak in soaring was associated with birds shifting to roost close to the bonanza. Soaring declined in frequency as the large group fed at the bonanza and continued to roost next to it, but again increased as the food dwindled and birds began to switch feeding and roosting sites. Soaring was again infrequent after the bonanza was consumed, and few birds remained in the area.

EXPERIMENTAL RELEASES OF NAIVE INDIVIDUALS INTO ROOSTS

Methods

We captured and released 29 vagrant ravens to test the null hypothesis that joining a roost does

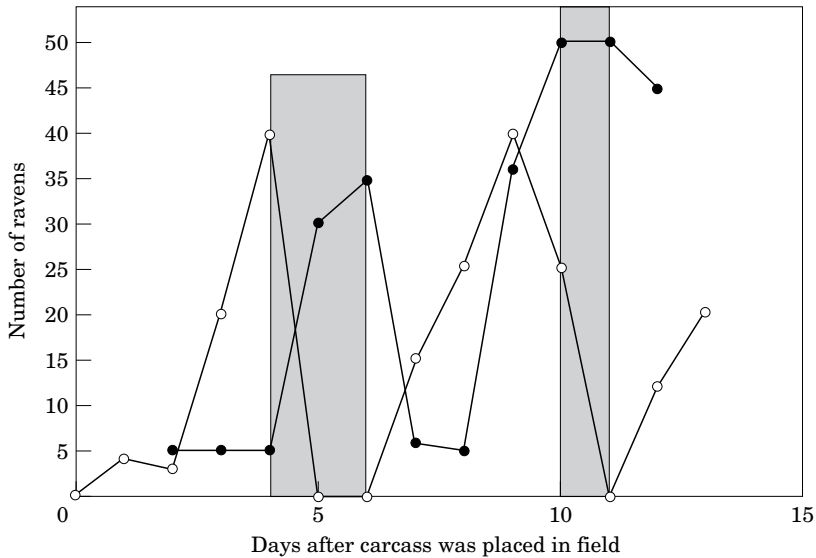


Figure 3. Concomitant changes in the numbers of ravens feeding at a moose carcass (○) and using the New Vineyard roost 25 km from the moose (●). Shaded areas show when we eliminated the moose as a feeding source by covering it with a tarp.

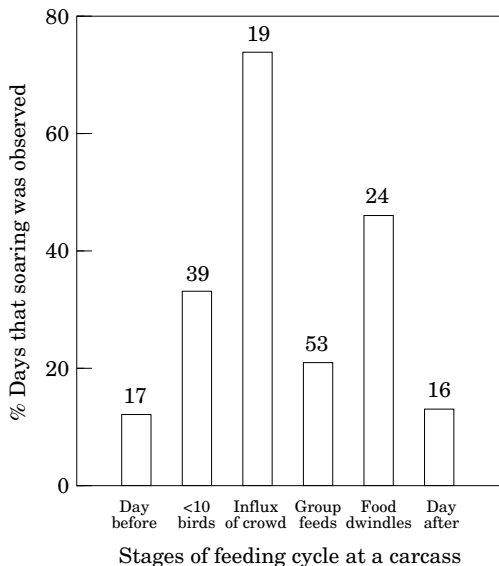


Figure 4. Occurrence of soaring throughout the various stages of feeding at 23 carcasses (see text). The number of days that roosts were observed for each stage of feeding is given above each bar. 'Day before' and 'day after' refer to days when no birds fed at the carcass just before it was discovered and just after it was consumed or removed.

not help naive birds determine the location of new feeding sites. We made birds naive of the location of new food bonanzas by isolating them from roosts (holding them in aviaries for 2–30 days) and then providing new baits in the field. Birds were randomly assigned to experimental ($N=14$) or control ($N=15$) groups, marked with a uniquely coloured and numbered patagial tag, and deprived of food for 1 day prior to release. One bird released outside of a roost was fitted with a radio transmitter.

We released control and experimental birds from small pet carrier cages 2–10 km from a feeding site. Experimental birds were released near where a roost was forming. We conducted the release of control birds so that they were isolated from birds in the roost either in space ($N=13$) or in time ($N=2$). Spatially isolated controls were released 5–10 km from the roost on the night that an experimental bird was released into a roost. Temporally isolated controls were released at the roost site the morning after the roosting ravens had departed. Regardless of the type of release experiment, both birds were held together prior to release, usually had been captured together and had not fed at the food currently being used by members of the roost under investigation. All

release experiments were conducted on separate days, but the same roost site was used more than once. We used five roost sites (two for one release, one for two releases, one for five releases, and one for six releases). Feeding sites were either carcasses ($N=9$ releases) or dumps ($N=5$ releases).

Following each release, we observed the sites known to be visited by the roost members on mornings to determine the success at which our marked released birds found feeding sites. Morning observations lasted from at least 0.5 h before sunrise to 3 h after sunrise.

Results

Changes in numbers of ravens at carcasses during day versus overnight

The relative importance of local enhancement and information exchange at roosts varied during the stages of a feeding cycle. The initial stage began with the discovery of the food ($\bar{X} \pm SE = 1.4 \pm 0.4$ days after being placed in the field, $N=19$ bonanzas) and lasted while the food was visited by less than five birds (territorial adults and vagrants). Group size rarely changed by more than five birds during this phase, and changes in numbers typically occurred during the day (Fig. 5a; see also Heinrich et al. 1993). The second stage (6–10 birds feeding) began 4.8 ± 1.2 days after the food was discovered ($N=18$) and was characterized by dramatic increases in group size overnight (Fig. 5b). The third stage (>10 birds feeding) began 5.6 ± 1.4 days after discovery ($N=18$) and lasted until the food began to dwindle. Group size during this time often greatly increased overnight (Fig. 5c). During the fourth stage, group sizes decreased rapidly as many birds left the food in the afternoon and did not return the following morning (Fig. 5d).

During the first and second stages, some individuals roosted near food and others returned to distant roosts. Once large groups arrived, however, most roosted within 1 km of the food. Departures to distant roosts were less common after feeding group size increased by 10 or more birds overnight than before such an increase (11 of 16 observations before, nine of 46 after, χ^2 with Yate's correction = 10.98, $df=1$, $P < 0.001$).

Large changes in group size occasionally occurred during the day and were thus not dependent upon recruitment from roosts (Fig. 5). An initially small group (<11 birds) swelled by

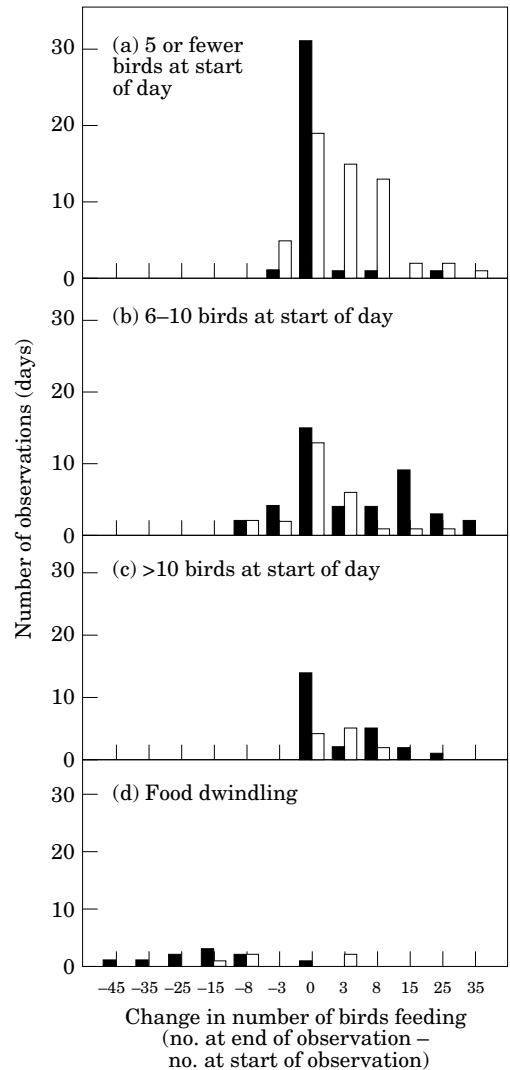


Figure 5. Changes in the numbers of ravens observed feeding at food sources placed in the field within a day (\square) and from one evening to the next morning (\blacksquare). A positive change indicates an increase in foragers during the period of interest and a negative change indicates a decrease. Changes are plotted separately for four major stages of the typical feeding cycle: (a) shortly after a carcass is discovered, (b) as the first group begins to assemble, (c) just after the first influx, and (d) as the group begins to break up and food is consumed.

10–40 more birds within a day on seven occasions (Fig. 5a, b). In all cases, we knew of another dwindling food source within 2 km and saw birds from this food source switch to the new source. In

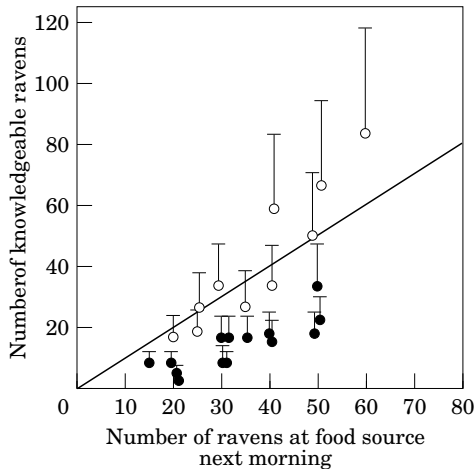


Figure 6. Recruitment of ravens to feeding locations from roosts. The line indicates the numbers of birds arriving at a feeding location equalling the number previously knowledgeable of the location. Points below line indicate recruitment from roosts, because more birds arrived at the food after roosting than previously knew of its location. Error bars indicate upper 95% confidence intervals, determined by variation in the probability of counting all knowledgeable birds. ●: Cases of significant recruitment (upper 95% CI is below diagonal line).

six cases we suspected that birds discovered the new food by hearing ‘begging’ vocalizations given by birds under attack at the new food. In one case, however, we saw a bird leave one food source and discover a new one 2 km away (it flew low, within 1 m of the ground and gave ‘kaw’ vocalizations), and then fly out of sight in the direction of the old food. Within 1 h, 30 birds arrived at the new food flying directly from the old food.

Recruitment of naive birds

In 18 out of 24 increases of 10 or more birds at a food bonanza, more birds came in the morning than the average number expected to be knowledgeable (Fig. 6). The 14 significant increases resulted in more than a doubling of foraging group size overnight from an average of 14.2 ± 2.16 knowledgeable birds to 32.9 ± 3.18 . Increases were nearly always (85.7%) significant if fewer than 20 birds were knowledgeable (i.e. if it was shortly after the food was discovered). Few (20.0%) significant increases occurred if more than 20 birds knew of the food’s location, because

there was too much uncertainty in the estimation of knowledgeable birds (many were expected to be missing during the evening census; see Methods).

Releases of naive birds into roosts versus at control locations outside of roosts demonstrated that naive birds found new feeding locations by following their roost-mates. All birds released into roosts ($N=14$) followed their roost-mates to food the next morning, but only four of 15 control birds found the food in that time (χ^2 with Yate’s correction = 13.5, $df=1$, $P<0.001$). Two other control birds found the food the following morning.

The control birds that did find the food were released less than 2 km from the food, but birds released into roosts found food from up to 6.7 km away. Neither bird released at a roost site in the morning after the group had departed found the feeding site. The nine control birds that did not find the food were rarely seen again, although two remained in the release area an hour after dawn following their release the previous evening. The radio-tagged control bird left the release area shortly after dawn the next day and was out of radio contact (≥ 30 km from the release site) for 19 days before returning to feed at a different bonanza 2 km from the one used in its release experiment.

Observations of free-ranging, radio-tagged birds also indicated that naive birds found feeding locations by following knowledgeable roost members. On nine occasions we followed a radio-tagged bird to a communal roost of ravens that was feeding at a known location. The radio-tagged bird had not previously fed at the location, but in every case it followed its roost-mates to the food the next morning.

EXPERIMENTAL RELEASES OF INDIVIDUALS AT NEW FEEDING SITES

Methods

In the converse experiment to the above, we created knowledgeable foragers by capturing non-breeding vagrants in the study area and then releasing them at new food sources that we placed in the field. These birds were housed in a large outdoor aviary 1–3 weeks before release, a sufficiently long period of time to deplete carcasses that they had previously used in the field.

Birds were held without food for 2 days prior to their release, transported to the release site in a cage measuring $0.6 \times 0.6 \times 1$ m and released 1–2 h before sunset. We placed the cage in the forest within 5 m of the new food. We allowed the bird 30 min to acclimate, then gently pulled a string to open the door from a spruce-bough blind 20 m from the cage. The cage was covered with spruce boughs to reduce the hesitancy of wild and released birds to approach the new food. We remained in the blind after the release until dark and then removed the cage. Most of the released birds behaved calmly immediately after their release; five of 40 approached and immediately ate from the new food after walking out of the release cage, and only seven appeared to avoid the release site.

Of our 20 releases, 15 were releases of single birds and five were of groups of five ($N=40$ birds). All birds released singly were radio- and patagial-tagged. For the releases of five, only two birds per group were radio-tagged, although all were patagial-tagged.

Results

The experimental releases of radio-tagged birds at new food sources enabled us to monitor the movements of the first birds that 'discovered' foods. Of the 26 released birds that were radio-tagged, five left the area the morning after release, two joined a nearby group of foraging birds, 10 joined a nearby communal roost, and nine remained near their discovery and fed on and off until a group formed at the food.

Of the 10 knowledgeable birds that joined communal roosts, four returned to their discovery; three of these were accompanied by their roost-mates with latencies of 1, 3 and 17 days after discovery. In two cases the eventual leaders initially followed roost-mates to other feeding sites. The most dramatic case was the bird that returned with roost-mates on the day after discovery. We had released the radio-tagged bird at a pile of meat 2 h before sunset. It remained near the food, but did not feed. It 'kawed' briefly as another bird flew over the food near dusk, then joined a roost that had formed 2 km away. Before dawn the following morning 30 ravens arrived at the food, flying directly from the nearby roost and the radio-tagged bird was one of the first five to arrive.

DISCUSSION

Our experiments and observations of tagged ravens suggest that the assembly of a group is a critical feature of successful foraging for non-breeding vagrants (Marzluff & Heinrich 1991), that this is facilitated by communal roosting and that roosts function as information centres. Releasing naive ravens into roosts and at new foods and following their movements has confirmed a key prediction of the information centre hypothesis: when knowledgeable foragers that join communal roosts return to their feeding sites the next day, naive members of the roost may sometimes follow them and thereby exploit previously unknown foods.

Our observations also confirm less critical requirements of the information centre hypothesis. When few birds were at a feeding site, their numbers quickly doubled over 1 night. Most of these birds simultaneously arrived at dawn, suggesting that they came from one or a few roosts. Therefore, not all members of a roost know the locations of all carcasses currently being exploited by their roost-mates. For example, in one release of a radio-tagged bird at a new carcass, only one (or possibly two) birds knew where our experimental food source was located; the remaining 30–40 birds in the roost were naive. The same individuals are not always knowledgeable or naive, which is more conducive to information sharing than information parasitism (Galef 1991; Wilkinson 1992). Two of the released discoverers that led naive roost members to food also followed their roost-mates to other foods.

Information centres may be especially important to ravens inhabiting northern forests for three reasons. (1) The dead animals they feed upon are patchily distributed and ephemeral (Coombes 1948; Bruggers 1988; Heinrich 1988), an important prerequisite for the evolution of information sharing (Waltz 1982). (2) Their communal roosts are composed of vagrant non-breeders that may need information on current food dispersion because they are often in new and unfamiliar environments (Coombes 1948; Davis & Davis 1986; Bruggers 1988; Heinrich 1988; Skarphedinsson et al. 1990). (3) Vagrants are subordinate to local territory holders and have difficulty foraging at defended foods until a group is assembled (Davis & Davis 1986; Heinrich 1988; Marzluff & Heinrich 1991). In contrast, the costs

of information sharing are minor. Attraction of competitors to a limited resource shortens the life span of the resource, but heavy snowfall and mammalian scavengers often remove a resource before a small group can eat all of it.

We know of no obvious signals that individual ravens use to advertise their knowledge of a newly discovered food source. We can, however, rule out any signals associated with direct feeding, such as soiled feathers, distended crops or the smell of carrion: in many cases, including all three where a radio-tagged discoverer led other naive birds to a feeding location, the knowledgeable birds had not yet fed at the site prior to recruitment from the roost. Vocal signals may play a role. For example, prior to a morning departure from a roost, a few ravens initiate a conspicuous 'honking' vocalization which builds to a crescendo prior to the group's synchronous departure. Whether knowledgeable ravens start the honking, however, is unknown. Possibly, of course, knowledgeable ravens use no special advertisement. Rather, birds that know the location of a good feeding area could simply leave the roost first and be followed by naive birds (Ward & Zahavi 1973).

Recruitment from roosts is not the only foraging tactic used by ravens; local enhancement also occurs as ravens are attracted to vocalizations at the actual feeding site (Heinrich 1988; Heinrich *et al.* 1993). Our release experiments suggest that local enhancement attracts fewer than five naive birds from within 2 km of the feeding site.

Instability in the membership of feeding and roosting groups may counter the effectiveness of an information centre for two reasons (Mock *et al.* 1988): (1) knowledgeable foragers may remain at a feeding site, so naive foragers cannot benefit from their knowledge; (2) the potential of kin selection and reciprocity to favour cooperative information transfer is reduced. Instability in the feeding group also reduces the ability to detect information exchange, because many knowledgeable individuals are not at a food source on the day before suspected recruitment (Richner & Marclay 1991). Our results dispute the importance of stable group membership to the operation of an information centre. Raven roosts and foraging groups are fluid assemblies of unrelated individuals (Parker *et al.* 1994), but information exchange occurs. The key factor in the evolution of information exchange is that both leaders and followers benefit by forming a group

at newly discovered foods (Marzluff & Heinrich 1991).

Changing location of roosts and roosting near feeding locations have also been viewed as inconsistent with the information centre hypothesis, because many species shift roosts to reduce commuting costs from regularly used feeding locations to recently discovered foods (Caccamise *et al.* 1983; Caccamise & Morrison 1986; Stouffer & Caccamise 1991). Ravens regularly shift roost sites, however, and reduce commuting costs by roosting near food. Travel distances to multiple feeding sites are minimized by such a strategy (Chapman *et al.* 1989). These habits are not inconsistent with the information centre hypothesis because, in contrast to the species studied by Caccamise and his associates, many ravens initially learned of the new feeding site through information exchanged at the original roost site. The shifting of roosts to feeding sites does indicate that roosts do not function as information centres every night. Once a crowd is assembled at a feeding site and the roost shifts to that site, little if any information about feeding site location is shared among roost-mates; any naive birds joining the roost immediately know about the food by direct observation or local enhancement.

Conspicuous social soaring displays were often accompanied by roost shifts. Soaring has been postulated to signal the movement of a roost site that may alert naive birds to the discovery of a new feeding site in several species, including ravens (Zahavi 1971; Ward & Zahavi 1973; Servheen & English 1979; McClelland *et al.* 1982; White & Tanner-White 1985). These displays attract naive and knowledgeable ravens from a wide area to a new roosting location that is in proximity to a new carcass that the group feeds from next.

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