NOTES AND COMMENTS

DO ROOSTS SERVE AS "INFORMATION CENTERS" FOR CROWS AND RAVENS?

It has been suggested that communal roosting may be a strategy permitting the participants to increase their chances of finding food (e.g., Fisher 1963; Ward and Zahavi 1973), whether it increases the total amount found or a decreases the risk of not finding any at all (Morse 1970; Thompson et al. 1974). The same general argument should apply to communal roosting and colonial nesting in that both provide opportunities for individuals to observe where others go in search for food. Provided that birds remember the feeding situation on visited grounds, successful birds should tend to return to the same area again and again, while unsuccessful ones should tend to go to new places. In this situation a previously unsuccessful bird will probably be better off if it follows another individual rather than setting out on its own. The importance of such behavior would be enhanced in situations where food occurs in temporary local concentrations.

Krebs (1974) demonstrated that great blue herons (*Ardea herodias*) tended to follow one another from a nesting colony to feeding areas and were there attracted to other individuals. The birds used different feeding grounds on different days, suggesting that the food supply was ephemeral. He also found that the rate of food intake per bird was a function of flock size and that feeding success was less variable for flocks as compared to solitary feeders.

Our aim in this investigation was to determine the extent to which the concept of "information centers" is applicable to corvid roosting behavior. To this end we provided ephemeral food sources and recorded how birds from nearby roosts were attracted.

If the information-center mechanism is valid, one should expect the number of birds visiting such a source in the morning following the day of its first discovery to be substantially larger than the total number of visitors on the first day. The increase on the second morning should be larger than the number of birds that had found the food by chance at the corresponding time in the first day, or slightly less since a fraction of the potential newcomers had already found it during the course of the first day. Formally, this model could be expressed as follows: A = the number of birds feeding in the environs of a feeding station (These could be

Am. Nat. 1980. Vol. 115, pp. 285–305.

expected to find it, sooner or later, by chance or local enhancement); a = the number of birds that actually find the station on the first day; a' = the number of birds that find the station within a limited time after the start of activity in the first day (up to the first observation in this study); b' = the number of birds that find the station before the corresponding time in the second day.

The information-center hypothesis is supported if $b' > (a'/A)(A - a) + a$. The number a should be at least as large as the maximum number present at any one time during the first day. In this study we assume that those birds that find our food source stay there for the rest of that day. Further, the model requires that the total number of birds at the roost be greater than A.

STUDY AREA AND METHODS

In order to arrange attractive feeding stations we put out dead pigs or, in a few cases, piles of dead chickens in the field. No two feeding sites used simultaneously were less than 1.5 km apart. The response from the corvids was measured by counting all hooded crows (*Corvus cornix*) and ravens (*C. corax*) that were feeding on the carrion or were so close, either perching in a tree or feeding on the ground, that it could be taken for granted that they were aware of it. This usually meant that they were within 100 m. The counts were carried out every second hour, beginning 1 h after sunrise. Counting the birds at all stations took about 40 min each time. Every station was checked for 2 successive days, beginning on the day the carrion was first discovered by the birds.

The Revinge area in south Sweden (55°40′ N, 13°30′ E) was used for two study periods (January 31–February 5 and March 3–March 6, 1977). During these periods a total of 10 and eight stations, respectively, were visited by crows. There was no snowcover that could interfere with feeding. Most of the crows in this study area attended either of two roosts that were situated 3–6 km from the feeding stations. The landscape was open with patches of woodland. Crows frequented most of it regularly.

The other study area, situated around the Tovetorp laboratory in southeast Sweden (58°57′ N, 17°10′ E) was used for one study period (February 3–February 7, 1978). During this period a total of seven feeding stations (1–5 km from the roost) were used by crows and/or ravens. A thick snowcover prevented birds from feeding except at a few places apart from the feeding stations. One major food source was a feeding site for penned foxes and badgers close to the roost. This resource was, however, cut off from the first day of the experimental period. In addition, there are some farms in the area where the birds may have found food.

During the experimental periods about 1,000 crows attended each of the two roosts in the Revinge area. The total numbers at the Tovetorp roost were considerably lower, but in all cases well beyond the maximum numbers encountered at feeding stations on any particular day.

The crows and ravens roosted together or very close to one another at Tovetorp. The roosts concerned were attended by jackdaws (*C. monedula*) and at Revinge also by rooks (*C. frugilegus*).

RESULTS

Some feeding stations remained undiscovered for some period before they were fed upon for the first time. The mean length of this time was, for stations ultimately discovered, 0.1 days at Revinge and 1.0 at Tovetorp. During the first day a station was discovered the number of individuals present built up gradually (table 1). In the second day, the number remained roughly the same as in the evening before. There was, however, much variation in the pattern between different stations. In some cases the pattern conformed to what could be expected under the information-center hypothesis (table 2). A comparison between the increase from day 1 to the morning of day 2 and the number of birds that found the stations independently of "roost mates" on the morning of the first day at all stations suggest, however, that the observed increases may have been due to the same mechanism that revealed the station to birds in the first morning. If those stations that were visited by only one or two birds are disregarded (these could be solitary individuals or pairs not attending a communal roost), there was a stronger tendency to conform to the hypothesis for the stations studied at Tovetorp (57%, $N = 7$) compared to those studied at Revinge (28%, $N = 18$). It may be noted that three out of four cases involving ravens conformed to the hypothesis.

DISCUSSION

Lack (1968) has suggested that communal roosting is to be regarded primarily as an antipredator adaptation. Alternatively, social–food-finding hypotheses have been proposed (e.g., Ward & Zahavi 1973).

It is neither necessary nor likely that one single advantage is responsible for the evolution of communal roosting in birds (Crook 1965). Furthermore, one mechanism could be responsible for the evolution of the habit even if it is not always in operation. In such cases the adaptation could be viewed as an "insurance" against hard times (Ward & Zahavi 1973). It has also been suggested that additional advantages may come into play once the behavior has been established (Horn 1968). Therefore, it is impossible to disprove many of the various hypotheses that have been offered to explain the phenomenon. Tests like the one described in this paper could, at best, give some indication as to the hypotheses' importance or likelihood. Thus, the concept discussed in this paper cannot be considered a testable hypothesis in the strict sense. Because of these limitations, it is not possible to conclude more from our experiment than that, especially at times of presumed food shortage, it seems possible that the mechanism may work.

The pattern of increase in numbers of feeding birds during the first day is also in accordance with the concept of local enhancement (Hinde 1961), i.e. the presence of some birds at a feeding site makes it more conspicuous to others in the neighborhood. This is especially so for the stations at Tovetorp, which in most cases remained undiscovered for 1 day. When stations were found on the first day of exposure, it could, on the other hand, be possible that the increase was due to individual and independent discoveries.

TABLE 1

MEAN NUMBER OF BIRDS PRESENT IN THE VICINITY OF THE FEEDING STATIONS DURING THE OBSERVATIONS

	DAY 1					DAY 2					N
Observation	1	2	3	4	5	1	2	3	4	5	...
Crows											
Revinge Feb. 1977	3.4	13	14	16	...	16	11	14	19	...	10
Revinge Mar. 1977	4.4	11	8.1	10	13	14	19	12	12	8.6	8
Tovetorp Feb. 1978	3.9	3.6	11	6.2	...	5.7	5.7	0	0	...	7*
Ravens											
Tovetorp Feb. 1978	0	.4	1.7	3.6	...	8.0	5.8	4.5	11.0	...	4*

NOTE.—Day 1 represents the day when the station was first discovered and day 2 the following day. The observations were made every second h, beginning 1 h after sunrise. The daylength permitted no more than four observations per day in February.

*A feeding station was in one case completely consumed before the second observation of the second day and in two other cases before the third observation of that day.

TABLE 2

NUMBER OF CROWS AND RAVENS OBSERVED IN THE VICINITY OF FEEDING STATIONS

	1: 1	1: max	2: 1	1: 1	1: max	2: 1	2: 1 − 1: max
Revinge 77	0	10	0	0	2	3	1
(crows)	0	14	14	0	8	14	6
	0	16	0	0	17	20	3
	0	31	17	2	2	10	8
	(1)	(1)	(0)	7	27	49	22
	1	10	10				
	1	26	26				
	2	40	30				
	4	11	0				
	6	23	17				
	7	33	13				
	9	9	6				
	12	26	22				
	18	24	22				
Tovetorp 78	(0)	(1)	(1) I	(0)	(1)	(2)	1 II
(crows)	0	45	0	0	6	15	9 III
	(2)	(2)	(0)				
	25	27	22				
	0	5	0 IV				
Tovetorp 78	(0)	(2)	(1) I	0	0	5	5 III
(ravens)				0	7	20	13 IV
				0	18	30	12 II

NOTE.—Patterns conforming to our model for the information-center hypothesis are given in the right col. Nine stations at Tovetorp where no crows or ravens were observed have been excluded. 1: 1 = the no. of birds observed in the morning of the day when the station was first visited by birds; 1: max = the greatest no. observed in that day; 2: 1 = the no. of birds recorded at the first count in the morning of the following day. Roman numerals identify pairs of counts made at the same stations but separated according to species in the table. Cases involving no more than two birds of a species are given in parentheses.

The time lag before discovery (Tovetorp) is reassuring in that it reduces the probability that the birds found the feeding stations on a regular flight path to the roost and remembered their location the next morning. Moreover, if the birds had used the same routes when they assembled at the roost as when they dispersed in the morning, few stations would have remained undiscovered as the birds flew past on the first morning.

The lack of further increase after the first observation of the second day suggests that all birds feeding in the area of influence were usually attracted within 1 day. Or, in the language of the model, $A = a$, yielding $b' > a$ only if the information-center hypothesis applies. The high number present in the morning of the second day stresses the importance of previous experience in the food searching behaviour of the crows when selecting their feeding sites.

ACKNOWLEDGMENT

We thank Staffan Ulfstrand for comments on the manuscript.

LITERATURE CITED

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

Fisher, J. 1963. Evolution and bird sociality. Pages 87–102 *in* J. Huxley, A. C. Hardy, and E. B. Ford, eds. Evolution as a process. 2d ed. Collier, New York.

Hinde, R. A. 1961. Behaviour. Pages 373–411 *in* A. J. Marshall, ed. Biology and comparative physiology of birds. Academic Press, London.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). Ecology 49:682–694.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). Behaviour 51:99–134.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr. 40:119–168.

Thompson, W. A., I. Vertinsky, and J. R. Krebs. 1974. The survival value of flocking in birds: a simulation model. J. Anim. Ecol. 43:785–820.

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

JON LOMAN
STAFFAN TAMM*

DEPARTMENT OF ANIMAL ECOLOGY
UNIVERSITY OF LUND
S-223 62 LUND, SWEDEN
Submitted April 21, 1978; Accepted February 5, 1979

* Present address: Department of Zoology, University of Stockholm, Box 6801, S-113 86, Stockholm, Sweden.